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Ecosystem collapse has become the focus of international attention in recent years, reflecting growing concern about the impact of human activities on the biosphere. Global environmental assessments such as the Global Biodiversity Outlook (Secretariat of the Convention on Biological Diversity, 2014) and the Global Environmental Outlook (UNEP, 2012) refer repeatedly to the collapse of specific ecosystems, focusing primarily on coral reefs and marine fisheries. Global trends in biodiversity loss documented by WWF's Living Planet Report have similarly been interpreted as increasing the risk of ecosystem collapse (WWF, 2006, 2016). It has been suggested that the entire global ecosystem might soon transition irreversibly to another state as a result of human influence (Barnosky *et al.*, 2014), although this has been contested (Brook *et al.*, 2013). Human civilisation itself may be at risk of collapse at the global scale owing to environmental degradation (Ehrlich and Ehrlich, 2013), although it has to be admitted that the researchers making this contention have a somewhat uneven record in predicting the future (Sabin, 2013). At the same time, as a response to widespread environmental degradation, international policy commitments are increasingly focusing on supporting ecological recovery, as illustrated by the target of restoring at least 15% of degraded ecosystems adopted by parties to the Convention on Biological Diversity (Aichi Target 15; CBD, 2012).

What is meant, though, by terms such as 'ecosystem collapse' and 'recovery'? How do these terms relate to associated concepts such as thresholds, tipping points, stability and resilience? Are these operational scientific concepts that can be applied in a practical context to support environmental management and conservation, or are they simply metaphors? Unfortunately, ecologists seem to delight in defining concepts in multiple alternative ways, which can generate confusion and hinder the development of scientific understanding (Peters, 1991). One need only think of the 163 definitions of 70 different stability concepts discovered by Grimm and Wissel (1997) in the ecological literature to appreciate the

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magnitude of the problem (and there have been many further definitions proposed in the two decades since that paper was published). I therefore consider here how ecosystem collapse and recovery are defined in the literature, along with associated concepts. I then examine the key features of both collapse and recovery, including their potential causes. Finally I describe how the rest of this book is structured. First, though, I provide an overview of how ecosystem collapse is being addressed by a new initiative attempting to develop an IUCN Red List of Ecosystems. The debate generated by this initiative provides a valuable entry point for considering what ecosystem collapse entails.

1.1 The IUCN Red List of Ecosystems

The IUCN (International Union for Conservation of Nature) Red List of Threatened Species™ (www.redlist.org) is widely recognised to be the most authoritative global assessment of the extinction risk of species (Mace *et al.*, 2008; Rodrigues *et al.*, 2006). Although principally designed to evaluate the extinction risk of individual species throughout their geographic ranges, the IUCN criteria are also used to develop regional, national and local lists of threatened species. Red List assessments have been widely used to inform the development of conservation strategies and plans and to develop indicators of biodiversity loss, including at the global scale (Butchart *et al.*, 2010; Mace *et al.*, 2008). During Red List assessments, species are assigned to one of a series of categories by applying five quantitative criteria (IUCN, 2001). The criteria are principally based on a declining or small population size, or the declining geographic range of a species. Taxa that meet the appropriate threshold for at least one of the five criteria may be categorised either as Extinct (EX) or as Critically Endangered (CR), Endangered (EN) or Vulnerable (VU); those failing to meet the thresholds may be categorised as Near Threatened (NT), Least Concern (LC), or Data Deficient (DD) (IUCN, 2001).

Recently this assessment approach has been extended to ecosystems. The IUCN Red List of Ecosystems protocol has been developed to provide a tool for assessing the conservation status of ecosystems, which can be applied at a variety of scales (Bland *et al.*, 2017a). The approach closely parallels that developed for Red List assessments of species, with five rule-based criteria (A–E) used to assign ecosystems to a risk category. These categories relate to the risk of ecosystem collapse (Figure 1.1), mirroring how categories in Red List assessments of species relate to the

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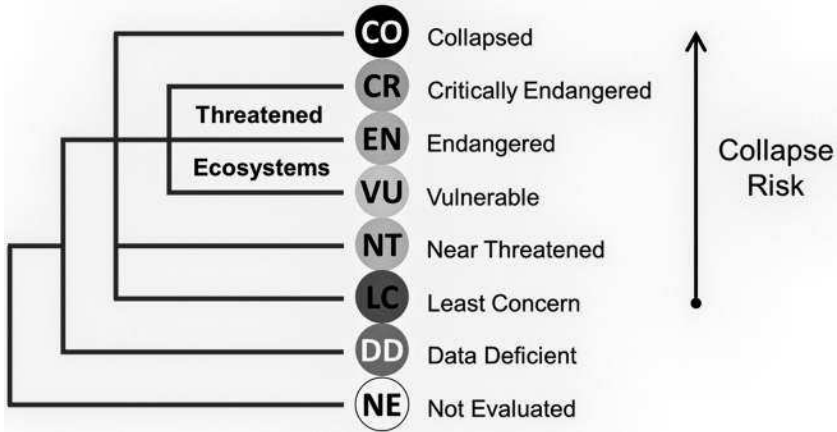


Figure 1.1 Structure of the IUCN Red List of Ecosystems categories (from Bland *et al.*, 2017a). Note how ‘Collapse’ of an ecosystem is considered as a category, equivalent to ‘Extinct’ in the Red List assessment of species.

risk of extinction. 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) (Figure 1.2). The final category (E) is based on producing quantitative estimates of the risk of collapse using an appropriate modeling approach (Bland *et al.*, 2017a).

While describing the Red List protocol, Bland *et al.* (2017a) make a number of valuable points about ecosystem collapse and its relationship to recovery:

- Ecosystem collapse is not directly analogous to species extinction, as, after undergoing collapse, ecosystems do not typically disappear but transition into some other type of ecosystem. This ecosystem may retain some of the species characteristic of the original ecosystem, but the abundance, interaction and ecological functions of these species may change after collapse.
- Many characteristic features may disappear from an ecosystem undergoing collapse, long before the last characteristic species disappears from the ecosystem.
- Ecosystem collapse is therefore a transformation of identity, a loss of defining features and/or replacement by a different ecosystem.
- An ecosystem is considered as collapsed when, after it loses its defining biotic or abiotic features, it can no longer sustain its characteristic native

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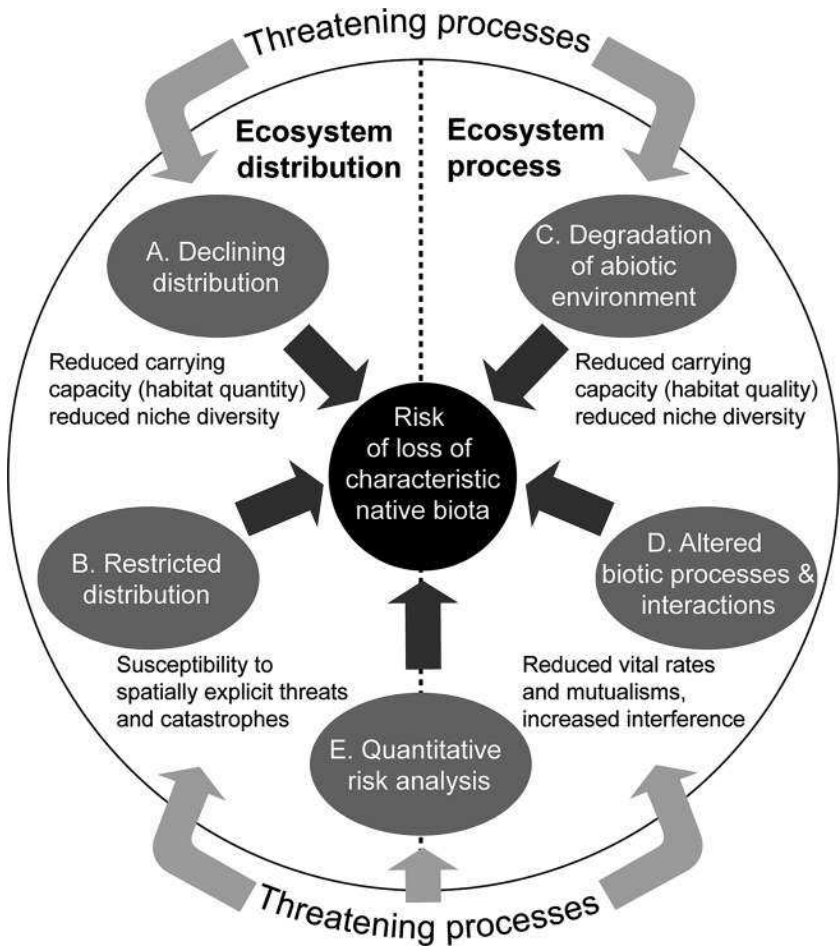


Figure 1.2 The mechanisms of ecosystem collapse and symptoms of collapse risk (from Keith *et al.*, 2013). Note that the five ellipses labelled A–E represent the five criteria used in the IUCN Red List of Ecosystems protocol, based on different thresholds of decline (Bland *et al.*, 2017a; Keith *et al.*, 2013).

species, and it has moved outside its natural range of spatial and temporal variability in composition, structure and/or function.

- Ecosystem collapse may result from a variety of different threatening processes (Table 1.1) and occurs through a variety of different pathways. Such pathways include trophic cascades, loss of foundation or keystone species, environmental degradation and climatic forcing. The

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Table 1.1 *Selected definitions of some key terms*

Term	Definition	Reference
Degradation	The incremental and progressive impairment of an ecosystem on account of continuing stress events or punctuated minor disturbances that occur with such frequency that natural recovery does not have time to occur.	Clewell and Aronson (2013)
	Direct damage to an ecosystem's biotic and/or abiotic biological condition.	Salafsky <i>et al.</i> (2008)
	A state or process in which ecosystem resources or attributes are reduced relative to some reference state or goals owing to human disturbance.	Ghazoul and Chazdon (2017)
Disturbance	Any relatively discrete event in time (or space) that disrupts ecosystem, community or population structure and changes resources, substrate availability or the physical environment.	White and Pickett (1985)
	Anything that causes disruption to a system.	Resilience Alliance (2010)
Driver or pressure	The ultimate factors – usually social, economic, political, institutional or cultural – that enable or otherwise add to the occurrence or persistence of proximate direct threats. There is typically a chain of drivers behind any given direct threat.	Bland <i>et al.</i> (2017a)
Ecosystem	The whole system (in the sense of physics), including not only the organism-complex but also the whole complex of physical factors forming what we call the environment of the biome – the habitat factors in the widest sense.	Tansley (1935)
	A biotic community or assemblage and its associated physical environment in a specific place. The main components of the ecosystem are its abiotic and biotic features and the interactions between them.	Pickett and Cadenasso (2002)
	Complexes of organisms and their associated physical environment within	Bland <i>et al.</i> (2017a)

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Table 1.1 (*cont.*)

Term	Definition	Reference
	a specified area. They have four essential elements: a biotic complex, an abiotic environment, the interactions within and between them and a physical space in which these operate.	
	All the organisms and the abiotic pools with which they interact. Ecosystem processes are the transfers of energy and materials from one pool to another.	Chapin <i>et al.</i> (2002)
	A unit comprising a community (or communities) of organisms and their physical and chemical environment, at any scale, desirably specified, in which there are continuous fluxes of matter and energy in an interactive open system.	Willis (1997)
Ecosystem collapse	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 <i>et al.</i> (2017a)
	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	Keith <i>et al.</i> (2013)

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Table 1.1 (*cont.*)

Term	Definition	Reference
	abundances may differ and they may be organised and interact in different ways with a new set of operating rules.	
	An abrupt and undesirable change in ecosystem state.	Lindenmayer <i>et al.</i> (2016)
	Major changes in ecosystem conditions are widespread and are either irreversible or very time- and energy-consuming to reverse.	Lindenmayer and Sato (2018)
Ecosystem recovery	The process by which an ecosystem returns to a previous condition after being in a degraded or disrupted condition.	Based on Elliott <i>et al.</i> (2007)
	An ecosystem has recovered when it contains sufficient biotic and abiotic resources to continue its development without further assistance or subsidy. It will sustain itself structurally and functionally.	Society for Ecological Restoration (2004)
	A pathway of ecosystem redevelopment towards a less compromised state, or the attainment of a fully functioning system comparable to ‘target’ reference sites.	Simenstad <i>et al.</i> (2006)
Threatening process, or threat	A tractable agent, mechanism or process that causes either a continuing decline in distribution, continuing environmental degradation or continuing disruption of biotic interactions or a future decline in those factors that is likely to occur in the near future (i.e. within 20 years).	Keith <i>et al.</i> (2013)
	Direct threats are the proximate activities or processes that have impacted, are impacting, or may impact the status of the ecosystem being assessed. Threats can be past (historical), ongoing and/or likely to occur in the future. Natural phenomena are also regarded as direct threats in some situations.	Bland <i>et al.</i> (2017a)

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process of collapse may be gradual or sudden, linear or non-linear and deterministic or stochastic.

- The process of ecosystem collapse may be influenced by abiotic or external factors (e.g. weather patterns or human disturbance), internal biotic processes (e.g. competition or predation), historical legacies (e.g. climatic history, extinction debts or history of exploitation) and spatial context (e.g. the location, size and connectivity of ecosystem remnants).
- Symptoms of collapse may differ between ecosystems depending on their particular ecological characteristics, the nature of threatening processes and the pathways of collapse.
- Ecosystem collapse can be evidenced by time series data for relevant variables, or it could be inferred by comparing occurrences of the ecosystem where defining features have been lost with other areas where such losses have not occurred. Major changes in functionally similar ecosystems can also provide insights into the process of collapse in ecosystems of interest.
- Ecosystem collapse may be reversible. After sufficient time has passed, or characteristic species and/or ecological function have been reintroduced, an ecosystem could potentially recover. However, in many cases recovery will not be possible.

According to the IUCN Red List protocol, collapse therefore refers to a process of transformation of an ecosystem, leading to its conversion to a different ecosystem type (Table 1.1). This raises the question of how much change in the ecosystem is required to have occurred before collapse is considered to have taken place. This is defined in the thresholds associated with the Red List criteria, which are used to define a category of risk. For example, thresholds for the application of criteria A and B are typically defined as 100% loss of spatial distribution of the ecosystem type, for an ecosystem to be classified as collapsed (Bland *et al.*, 2017a).

The Red List of Ecosystems represents the first time that ecosystem collapse has formally been incorporated into an environmental assessment process, and it is being used as a basis for classifying the conservation status of ecosystems. Development of the process has been supported by a growing body of scientific literature, aiming to ensure that the protocol is objective, transparent and rigorous. The idea of adapting the Red List approach to systematically assessing the conservation status of ecosystems has been under discussion for some years. For example, Rodríguez *et al.*

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(2007) provided some initial suggestions regarding how a Red List assessment of ecosystems might be conducted, which were further developed by Rodríguez *et al.* (2011), although neither publication explicitly considered the phenomenon of ecosystem collapse. In relation to the Red List, collapse is first mentioned by Rodríguez *et al.* (2012), who refer to it as analogous to the extinction of a species. Use of ecosystem collapse in this context is further elaborated by Keith *et al.* (2013), in their review of the science underpinning the Red List initiative.

Keith *et al.* (2013) highlight a number of issues and challenges in developing a risk assessment of ecosystems. These include the definition of units of assessment, which they refer to as ecosystem types; developing an operational definition of ecosystem collapse as the endpoint of environmental degradation; identifying the relationships between threatening processes, mechanisms and symptoms of ecosystem collapse; and identifying thresholds of collapse, on which the assessment criteria might be based (Figure 1.2). The suggestions made by these authors were challenged by Boitani *et al.* (2015), who pointed out that there is no consistent approach to ecosystem classification that might be used for assessing their conservation status and that there is limited scientific support for the criteria and thresholds that were proposed. They also question the use of ecosystem collapse in this context. This debate usefully highlights a number of issues that are relevant to the theme of this book and are consequently considered a little later in detail.

1.2 What Is an Ecosystem?

I once spent an entertaining international flight discussing ecology with a fellow researcher I'd met at a meeting that we'd both been attending. She admitted that she had never really liked the term 'ecosystem', nor fully understood what an ecosystem actually was. This was all the more remarkable, given that the event we had just attended was part of the Millennium Ecosystem Assessment (MEA). With hindsight, publication of the MEA (2005a) turned out to be a landmark event, which firmly established the concept of ecosystem services – the benefits provided by ecosystems to people – in the international policy arena. It also stimulated renewed interest in ecosystems as a focus of research. At the preparatory workshops, a large international community of researchers and policy-makers convened to design the assessment, which provided the first global appraisal of the condition and trends in the world's ecosystems

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and the services that they provide. For me, as a participant in some of the meetings, the sight of this community discussing how best to conduct the assessment was enormously entertaining and instructive. I vividly remember calls for the MEA to produce a comprehensive map of global ecosystems being roundly rejected despite this being seen as a logical first step by a number of participants. I ended up sympathising with my colleague on the plane, as I shared her confusion. (Interestingly, her semantic uncertainty didn't prevent her from going on to play a leading role in the development of ecosystem service science.)

It may seem surprising that a concept so fundamental to the science of ecology might still be under discussion, but my colleague was not alone in wondering what an ecosystem actually is. For example, in the 1990s, the *Bulletin of the Ecological Society of America* published a series of commentary articles debating the definition of an ecosystem (Blew, 1996; Fauth, 1997; Marín, 1997; Rowe, 1997; Rowe and Barnes, 1994). These authors agreed that there is a lack of consensus on how the 'troublesome' term 'ecosystem' should be defined and that this confusion is hindering both the development of ecological theory and its practical application. Semantic uncertainty and conceptual fuzziness are nothing new in ecology, and although they do indeed impede progress (Peters, 1991), they also illustrate how the world can appear differently depending on how you look at it. Rowe and Barnes (1994), for example, highlighted the different perspectives from those approaching ecology from the point of view of organisms ('bio-ecologists') *versus* those coming from an Earth science background ('geo-ecologists'). For bio-ecologists, with their organism-centred view, ecosystems are biotic communities of plants and animals, plus the features of the abiotic environment that are used by organisms as resources. From this perspective, an ecosystem is flexible in time and space, depending on the location of the organisms of interest. The challenges of rigidly applying the ecosystem concept when the focus is an individual, highly mobile species are beautifully illustrated by a quote from Drury in 1969: 'I have struggled unsuccessfully with the problem of defining ecosystems into which a seagull can be fitted' (Rowe and Barnes, 1994).

This relates to the issue of whether ecosystems can be meaningfully mapped, the same problem that I encountered at the MEA workshop. For geo-ecologists, an ecosystem is a defined area of the earth's surface, defined by abiotic factors such as landforms, topography and climate (Rowe and Barnes, 1994). For bio-ecologists, whose organisms of interest may not respect the boundaries between such areas as they disperse