Developing a standardized definition of ecosystem collapse for risk assessment

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Developing a standardized definition of ecosystem collapse for risk assessment

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The International Union for Conservation of Nature (IUCN) Red List of Ecosystems is a powerful tool for classifying threatened ecosystems, informing ecosystem management, and assessing the risk of ecosystem collapse (that is, the endpoint of ecosystem degradation). These risk assessments require explicit definitions of ecosystem collapse, which are currently challenging to implement. To bridge the gap between theory and practice, we systematically review evidence for ecosystem collapses reported in two contrasting biomes – marine pelagic ecosystems and terrestrial forests. Most studies define states of ecosystem collapse quantitatively, but few studies adequately describe initial ecosystem states or ecological transitions leading to collapse. On the basis of our review, we offer four recommendations for defining ecosystem collapse in risk assessments: (1) qualitatively defining initial and collapsed states, (2) describing collapse and recovery transitions, (3) identifying and selecting indicators of collapse, and (4) setting quantitative collapse thresholds.


Ecosystems are dynamic by nature, but concern arises when they undergo substantial loss of biodiversity and re-organization of ecological processes (Scheffer et al. 2001). Such large detrimental changes, collectively termed “ecosystem collapse” (see Panel 1 for a glossary of terms), have important implications for conserving biodiversity and maintaining ecosystem services, and are fundamental to assessing risks to ecosystems (Keith et al. 2013).

Understanding the risks of ecosystem collapse is critical to ecosystem management, and requires consideration of an ecosystem’s exposure and vulnerability to various hazards (Burgman 2005). With respect to biodiversity conservation, two tools are commonly used to assess risks to ecosystems and species: Red Lists (decision-rule-based protocols) and probabilistic models. Red Lists assign ecosystems to ranked categories of risk (e.g. Vulnerable, Endangered, or Critically Endangered) based on decision rules that incorporate multiple symptoms of threat exposure and vulnerability, such as rates of decline in spatial and functional indicators (Nicholson et al. 2009). Red Lists for both ecosystems and species have strong theoretical foundations (Burgman 2005; Mace et al. 2008; Keith et al. 2013), and ecosystem Red Lists have been implemented in many countries, including Finland, South Africa, and Australia (Nicholson et al. 2009). In contrast, probabilistic models quantitatively estimate the risk of ecosystem collapse based on a mathematical representation of ecosystem dynamics, threats, and social–ecological relationships (Bland et al. 2017). The International Union for Conservation of Nature (IUCN) Red List of Ecosystems was endorsed by IUCN in 2014 and is the only global protocol for assessing risks to ecosystems. The protocol is based on five rule-based criteria, one of which pertains to estimating the probability of collapse through models (Keith et al. 2013).

Risk is defined as the probability of an adverse outcome within a specified time frame (Burgman 2005). Whether using decision rules or probabilistic models, defining the characteristics of a collapsed ecosystem is essential to estimating risk. In the absence of a clear theoretical framework and practical recommendations, defining collapse is often perceived as judgement-laden and impractical (Boitani et al. 2015; Cumming and Peterson 2017). Early
ecosystem assessment protocols defined collapsed ecosystem states poorly (Nicholson et al. 2015), severely limiting the consistency and robustness of risk assessments. Defining collapsed states can be difficult because ecosystem collapse is expressed through symptoms that may vary across ecosystems and scales of investigation, and may be characterized by subtle rather than clear-cut changes. For instance, collapse of mountain ash (Eucalyptus regnans) forests in southeast Australia is characterized by the loss of large cavity-bearing trees, and not just through reductions in the forests’ distributional extent (Burns et al. 2015). Decisions on whether to classify an ecosystem as collapsed depend on the objectives of the risk assessment and on the needs of the decision makers. Accordingly, lists of threatened ecosystems are focused on averting the loss of characteristic biota and ecological function (e.g. Keith et al. 2013).

The first step in ecosystem risk assessment is to describe initial or baseline states that reflect the natural range of spatial and temporal variability in ecosystems (Panel 1). In the IUCN Red List of Ecosystems, these baselines are defined for three different time frames (“current”, “future”, and “historic”; Keith et al. 2013) and provide important contextual information for understanding how the defining features of an ecosystem change during a transition to collapse (Sato and Lindenmayer 2017). The second step is to identify potential pathways of collapse and symptoms of degradation (Scheffer et al. 2001). This step can be informed by ecological models (textual, diagrammatic, or mathematical), and is key to selecting indicators (Panel 1) that reflect changes in ecosystem states (Rumpff et al. 2011) and that can be used as proxies for risk in Red Lists or probabilistic models. In the third step, collapsed states should be defined with quantitative decision thresholds (Panel 1) in key indicators, which can be informed by observation, experimentation, modeling, or expert elicitation. Uncertainty in the resulting thresholds may be substantial and is quantifiable with upper and lower bounds (Keith et al. 2013).

Despite challenges in defining ecosystem collapse, a large amount of evidence exists for collapses in a variety of ecosystems (Washington 2013), but much of this evidence – which could help inform ecosystem risk assessment – has yet to be synthesized. For example, over-harvesting and burning of forest ecosystems on Easter Island in the 16th century CE led to the extinction of the foundation (i.e. habitat-forming) species of palm and to the transformation of forests to grasslands, with extreme consequences for the human population (Diamond 2007). Similarly, water extraction from the Aral Sea caused a 92% reduction in water volume between 1960 and 2010, leading to the extirpation of most fish and invertebrate species, the disappearance of reed beds and associated waterbirds, and a transformation to saline lakes and desert plains (Micklin 2010). Such extreme transformations, and losses of defining biological and environmental features, are characteristic of ecosystem collapse as it is conceptualized in ecosystem risk assessments.

### Panel 1. Glossary

**Bounded threshold**: Represents uncertainty in the occurrence of the collapsed state based on two or more values of an ecosystem indicator (Bland et al. 2016).

**Decision threshold**: Value of an indicator above or below which a decision differs (Martin et al. 2009), such as a decision to list an ecosystem as collapsed.

**Ecological model**: Written, pictorial, or mathematical representation of key ecosystem components and processes, which effectively summarizes ecosystem dynamics to a broad audience (Suter 1999).

**Ecological threshold**: Value of an indicator above or below which non-linear or specific changes in ecosystem dynamics occur.

**Ecosystem**: Although definitions vary, the IUCN Red List of Ecosystems defines ecosystems as: a biotic complex or assemblage of species, an associated abiotic environment or complex, the interactions within and between those complexes, and a physical space in which they operate (Bland et al. 2016). These four elements assist in identifying and classifying ecosystems and understanding their susceptibility to threats.

**Ecosystem collapse**: Indicates a transition beyond a bounded threshold in one or more indicators that define the identity and natural variability of the ecosystem (Bland et al. 2016). Collapse involves a transformation of identity, loss of defining features, and/or replacement by a novel ecosystem. It occurs when all ecosystem occurrences (i.e. patches) lose defining biotic or abiotic features, and characteristic native biota are no longer sustained.

**Indicator**: Metrics that quantify complex changes in ecosystem structure, composition, and function (Niemeyer and de Groot 2008). In different risk assessment protocols, spatial, biotic, or abiotic indicators may quantify threats to ecosystems and/or ecosystem responses to threats. Thresholds in indicators indicate ecosystem collapse.

**Natural variability**: The ecological conditions, and the spatial and temporal variation in these conditions, within a period of time and geographical area appropriate for the study objectives (Keane et al. 2009).

**State**: A numerical description of multiple biotic components of an ecosystem, typically including values of species abundances or biomasses and of ecosystem processes, such as primary production and respiration (Bestelmeyer et al. 2003).

**Transition**: Can describe both a change in ecosystem state, and the value of a driver at which the change in ecosystem state occurs (Bestelmeyer et al. 2003).
Here, we bridge the gap between theory and practice by critically examining how ecologists have defined ecosystem collapse in two globally important biomes – marine pelagic ecosystems and temperate forests – in part by exploring the ecosystem features that were studied and the methods used. We then present a standardized framework for defining ecosystem collapse, based on the outcomes from the review and the needs of ecosystem risk assessments such as the IUCN Red List of Ecosystems (Bland et al. 2016). Importantly, our review neither defines ecosystem collapse (but see Panel 1 and Bland et al. 2016 for a definition) nor directly addresses the decision rules or models used in ecosystem risk assessments; rather, it focuses explicitly on developing a systematic method for defining collapse so that ecosystem risk assessments may be applied more effectively.

### Literature review

We systematically reviewed the scientific literature on ecosystem collapse using a standard method (Pickering and Byrne 2014) that complies with the guidelines of the Preferred Reporting Items for Systematic reviews and Meta-Analyses (PRISMA) statement (Moher et al. 2009). We reviewed publications on marine pelagic and temperate forest ecosystems that reported ecosystem collapses, regime shifts, or trophic cascades with a strong focus on loss of biodiversity and ecosystem function (rather than economic or societal losses; Cumming and Peterson 2017), to conform to the objectives of most ecosystem risk assessment protocols (Nicholson et al. 2009).

We searched Web of Science and Science Direct on 9 Sep 2016 with standardized search terms (WebPanel 1). We screened papers based on abstracts and then full text according to set criteria (WebPanel 1), recording the number of papers retained at each screening stage according to the PRISMA statement (WebTable 1). Our final selection included 35 publications reporting collapses in 37 marine pelagic ecosystems (hereafter referred to as “studies”) and 48 publications reporting collapses in 48 temperate forest ecosystems (Figures 1 and 2). In those publications, we reviewed: (1) what research methods were employed to identify collapse; (2) whether initial and collapsed states were described, and what ecosystem features were examined; (3) whether studies used ecological models to describe pathways to collapse; (4) what mechanisms were involved in the transition to collapse; (5) what variables were identified as useful indicators of collapse; (6) whether studies defined quantitative thresholds of collapse; and (7) whether studies accounted for uncertainty in their definitions of collapse.

We found significant differences between biomes in research methods used to define ecosystem collapse (WebTable 2). Spatial comparisons between initial and collapsed states were applied more often in temperate forest studies (21%) than in marine pelagic studies (0%), where temporal comparisons were always used. In addition, 21% and 49% of temperate forest and marine pelagic studies, respectively, described all four features of initial ecosystem states required in IUCN Red List of Ecosystems assessments (biota, abiotic environment, processes, and spatial distribution; Bland et al. 2016). Conversely, collapsed states were quantitatively described more often in temperate forests (79%) than in marine pelagic ecosystems (65%). Approximately one-half and three-quarters of temperate forest studies (54%) and marine pelagic studies (78%), respectively, relied on ecological models of transitions to collapse. In both biomes, text descriptions of ecological processes were more often used than conceptual diagrams (WebTable 2). Trophic restructuring (43%) and climatic shifts (40%) were the most common transitions to collapse in marine pelagic ecosystems, whereas distribution shifts (52%) and climatic shifts (23%) were more common transitions to collapse in temperate forests.

The application of indicators and quantitative thresholds to measure transitions to collapse differed significantly between temperate forests and pelagic ecosystems. Spatial indicators (eg distribution size, distribution limits) were used in 60% of temperate forest studies, whereas biotic or abiotic indicators were used in 100% of marine pelagic studies (WebTable 2). Spatial thresholds of collapse were frequently quantified in temperate forests (90%), but not in marine pelagic ecosystems. Collapse thresholds in biotic and abiotic indicators were quantified in most studies, except for biotic indicators in temperate forest studies (31%). All marine pelagic studies (100%) and almost all temperate forest studies (94%) accounted for uncertainty by measuring collapse with multiple indicators. One study accounted for uncertainty in ecological models and none...
accounted for uncertainty in quantitative collapse thresholds.

Discussion

Consistent methods for defining ecosystem collapse are needed to meet increasing demand for tools to monitor the status of biodiversity from local to global scales (Keith et al. 2013; CBD 2014; Nicholson et al. 2015). Of the marine pelagic and temperate forest studies reviewed here, most defined quantitative collapse thresholds with empirical data or predictive models, but often failed to adequately define features of the initial ecosystem state and ecological processes leading to collapse, especially for temperate forests. The use of conceptual models was more common in marine pelagic ecosystems, illustrating a stronger focus on ecosystem functioning compared to forests. Indicator selection protocols were also applied more often in marine ecosystems, where clear guidelines have been developed to inform ecosystem-based management of fisheries (Rice and Rochet 2005). Marine pelagic studies quantified collapse with biotic and abiotic indicators, while temperate forest studies typically quantified collapse with spatial and biotic indicators, reflecting a focus on multiple trophic levels in marine pelagic ecosystems (e.g., plankton, planktivorous fish, and piscivorous fish) and on the distribution of foundation tree species in temperate forests.

On the basis of our literature review, we propose a common, systematic framework for defining ecosystem collapse in four key steps: (1) qualitatively defining initial and collapsed states, (2) describing collapse and recovery transitions, (3) identifying and selecting indicators of collapse, and (4) setting quantitative collapse thresholds. Such a framework can be applied to representative marine pelagic and temperate forest ecosystems (WebPanel 2) as well as to other types of ecosystems not reviewed here (Figure 3). Our recommendations are particularly relevant to the IUCN Red List of Ecosystems (Keith et al. 2013), but can inform other risk assessment protocols and management tools for ecosystems.

(1) Qualitatively defining initial and collapsed states

We found that few studies described initial ecosystem states. This fundamental omission makes it harder to identify characteristic ecosystem features, infer patterns of natural variability as being distinct from directional change, and select adequate indicators of ecosystem change. Most ecosystem assessment protocols specify baselines to quantify initial ecosystem states (Nicholson et al. 2009). Indeed, the IUCN protocol specifies three temporal baselines: historic (since 1750 CE), current (within the past 50 years), and future (50 years from the present day or “any 50-year period including the present and future”) (Keith et al. 2013). An ecosystem’s initial state may be characterized by a large degree of uncertainty (especially with respect to historical baselines), which may affect the definition of key ecological features and processes lost during a transition to collapse (Figure 2 in Keith et al. 2015). It is therefore important to examine the sensitivity of assessment outcomes to the plausible range of initial states. The majority of studies defined ecosystem collapse quantitatively, suggesting that there may be greater consensus on collapsed states than on initial ecosystem states. For example, “limit reference points” are often defined in marine ecosystem management (Cury et al. 2005), while “thresholds of probable concern” are defined in river management (Rogers and Biggs 1999). These quantitative definitions reflect the large amounts of empirical data on collapsed ecosystems in specific biomes (as opposed to a perceived lack of data in more general reviews; Sato and Lindenmayer 2017), which can inform the implementation of ecosystem risk assessment worldwide.

Direct evidence of historical and geographic variation can help to establish bounds of natural variability in ecosystem features (Keane et al. 2009). Most studies relied on temporal rather than spatial comparisons to define ecosystem states, suggesting that time-series analysis is a preferred method to detect deviations from natural variability.
How to define ecosystem collapse

(eg with sequential t-test algorithms; Litzow and Mueter 2014). Only two temperate forest studies used information on locally collapsed patches, although these comparisons can inform clear definitions of collapsed states. For instance, invasion by arctic foxes (Alopex lagopus) reduced populations of seabirds and nutrient transport on some Aleutian Islands and led to major vegetation transformations from grasslands to tundra (Croll et al. 2005), providing a comparative framework between fox-free and fox-infested islands to define ecosystem collapse. Analogous but collapsed ecosystems can provide a basis for delineating collapsed states in a focal ecosystem. For instance, collapse thresholds for the extant southern Benguela upwelling ecosystem can be inferred from the collapsed northern Benguela, which underwent a regime shift in the 1970s due to overfishing and environmental pressures (Roux et al. 2013). For ecosystems dominated by foundation species, environmental tolerances of those species can be used as proxies to define the abiotic components of initial states (eg bioclimatic correlates of the distribution of temperate forests; WebPanel 2; Peñuelas and Boada 2003). Few studies relied on experiments to define collapsed states, most likely due to the difficulty of manipulating large interconnected ecosystems as compared to relatively smaller or isolated estuaries and lakes (Schaefer et al. 2001; Mac Nally et al. 2014). No studies involved expert elicitation to define ecosystem states, although expert-derived data can help identify transitions to collapse (Rumpff et al. 2011).

(2) Describing collapse and recovery transitions

A qualitative understanding of ecosystem processes is essential for defining transitions to collapse and selecting indicators of ecosystem change (Bland et al. 2016), yet many studies did not employ ecological models to describe transitions. For example, most vegetation distribution models predict the presence or absence of suitable environmental conditions (eg temperature, precipitation), but do not explicitly describe ecosystem processes leading to collapse (Feng et al. 2013). Understanding the pathways to collapse helps to identify intermediate ecosystem states, indicators of risk, and corresponding collapse thresholds, especially for ecosystems threatened by declines in ecological function such as changes in fire or hydrological regimes, or species invasions (Nicholson et al. 2015).

Representations of ecosystem dynamics such as conceptual diagrams are particularly useful for risk assessment, given that these can effectively summarize initial and collapsed states, clearly depict assumptions and uncertainties about ecosystem processes, and are less prone to semantic uncertainties than written descriptions (Suter 1999). Two types of conceptual diagrams are commonly used in risk assessment: state-and-transition models (which explicitly depict transitions between ecosystem states based on various drivers) and cause–effect models (which depict interactions and dependencies among ecosystem components and processes; Bland et al. 2016). Uncertainty in ecological models potentially affects all subsequent components of risk assessment but was addressed in only one study (forests of southwest Tasmania; Wood and Bowman 2012). If plausible alternative models of ecosystem dynamics exist, multiple
ecological models should be applied in replicated risk assessments (Burgman 2015).

Ecological models help to organize evidence on ecosystem degradation and recovery, thereby providing management-related insights. Four studies—two from marine pelagic and two from forest ecosystems—demonstrated potential recovery from a collapsed state, so recovery may be possible for some collapsed ecosystems following effective restoration actions (Keith et al. 2013). Clearly, ecosystems that have experienced global extinctions of key species are unlikely to recover (eg foundation palm species on Easter Island; Diamond 2007). Reversal of collapse may be possible in other ecosystems if all ecological components are available and re-assembled through active management (as was the case in both marine examples), or if granted sufficient time for recovery (in both temperate forest examples). The interpretation of novel ecosystems as collapsed states of antecedent ecosystems may be relevant for ecosystems subject to a variety of threats, including climate change. Antecedent ecosystem states may or may not be recoverable (Keith et al. 2015). For example, the current dominance of haddock (Melanogrammus aeglefinus) over cod (Gadus morhua) in the eastern Scotian Shelf suggests that the species composition of the ecosystem “recovering” from overfishing may be different from that of the precollapse ecosystem (Frank et al. 2011). The likelihood of ecosystem recovery can be estimated based on the characteristics of initial and collapsed states, transitions to collapse, and possible hysteretic (ie path-dependent) mechanisms maintaining collapsed states (Frank et al. 2011). Yet in the absence of an ecological model, determining the likelihood of ecosystem recovery is difficult.

(3) Identifying and selecting indicators of collapse

Informative and sensitive indicators of ecosystem collapse act as proxies for niche diversity, habitat availability, and stabilizing biotic interactions that are key to the persistence of ecosystem biodiversity. To accommodate different mechanisms of collapse, the IUCN Red List of Ecosystems requires assessors to define ecosystem-specific biotic and abiotic indicators (Bland et al. 2016). Effective comparison and selection of indicators relies on rigorous protocols (Niemeyer and de Groot 2008), but few studies applied explicit protocols to select indicators of ecosystem collapse. No studies used quantitative criteria to score and compare indicators, limiting the exploration of trade-offs among indicators, which can be important in ecosystem risk assessment (Bland et al. 2017).

Because ecosystems can collapse through multiple pathways and exhibit different symptoms of degradation, definitions of collapse based solely on one type of indicator may underestimate risks to ecosystems (Bland et al. 2017). Although the majority of studies accounted for uncertainty in indicator selection by applying multiple indicators within each type (spatial, biotic, or abiotic), few studies included different types of indicators (eg spatial indicators and biotic indicators). We found important differences in indicator use between biomes, with biotic and abiotic indicators commonly used in marine pelagic ecosystems, and spatial and biotic indicators commonly used in temperate forests. Although this may reflect genuine differences in mechanisms of collapse, definitions of collapse in marine pelagic ecosystems may ignore spatially explicit transitions to collapse (such as species distribution shifts; Coetzee et al. 2008), while definitions of collapse in temperate forests may ignore changes in the physical environment. Ecological models can help diagnose multiple symptoms of collapse (Figure 3), inform indicator selection according to explicit criteria, and identify trade-offs among indicators.

(4) Setting quantitative collapse thresholds

The outcomes of ecosystem risk assessment hinge on the definition of discrete endpoints to ecosystem degradation (ie transitions beyond quantitative collapse thresholds in one or more indicators). Despite applying quantitative indicators of ecosystem change, many studies did not use quantitative thresholds to define collapsed states (eg 38% of marine pelagic studies applying abiotic indicators), falling one step short of requirements for ecosystem risk assessment.

A distinction exists between decision thresholds, which specify the conditions required to invoke a decision (eg classification as collapsed), and ecological thresholds, which describe non-linear changes in ecosystem dynamics (Panel 1). Collapse thresholds qualify as decision thresholds because they inform the assessment decision to assign an ecosystem to a particular category of risk. Most studies we reviewed did not provide clear ecological rationales for setting collapse thresholds. An implicit collapse threshold of $0 \text{km}^2$ when measuring percent declines in spatial distribution, for example, may be inappropriate if ecosystems lose the ability to sustain their native biota below a certain distribution size (eg fish reproductive volume; Möllmann et al. 2008). Many marine pelagic studies relied on regime shift-detection algorithms to pinpoint the timing of ecosystem collapse and thresholds in indicators, with little consideration for the ecological importance (if any) of these thresholds (eg regime shifts in the North Pacific; Hare and Mantua 2000). Unless derived explicitly and based on ecological evidence (Cumming and Peterson 2017), collapse thresholds may provide misleading estimates of risk and little insight into possible management actions to revert ecosystem degradation. When applied collectively, spatial, biotic, and abiotic indicators can provide a comprehensive description of collapsed states, but very few studies assigned quantitative collapse thresholds to multiple indicator types (WebTable 2). Careful comparisons are needed to derive consistent collapse thresholds among multiple indicators, given that inconsistent thresholds can severely affect estimates of degradation and outcomes of risk assessments (Payet et al. 2013).
Collapse thresholds should be bounded to represent inevitable uncertainty in collapsed states (Panel 1; Bland et al. 2016), but no studies characterized uncertainty in collapse thresholds. In both species and ecosystem risk assessment, bounded thresholds accommodate a suite of uncertainties related to the timing, likelihood, and effects of management actions on extinction or collapse (Regan et al. 2009). Explicit consideration of these uncertainties can help risk assessors identify appropriate collapse thresholds for each indicator, and sensitivity analyses can help identify which collapse thresholds trigger changes in risk assessment outcomes. For example, in simulations of the mountain ash forest in southeast Australia (Burns et al. 2015), the collapse threshold would need to decrease by 30% from an average of 1.0 to 0.7 cavity-bearing trees per hectare to modify the risk assessment outcome from Critically Endangered to Endangered.

Conclusions

Previous studies have highlighted the difficulty of defining ecosystem collapse (Boitani et al. 2015) and the perceived scarcity of descriptions of collapsed ecosystems (Sato and Lindenmayer 2017). Here, we revealed a wide array of studies of ecosystem collapse that could support ecosystem risk assessments and found that these studies often overlooked the ecological processes leading to collapse, despite the importance of such processes for inclusion within risk assessments. A consistent framework to define ecosystem collapse (Figure 3 and WebPanel 2) promotes practical comparisons between ecosystems, which can be applied to ecosystem risk assessment protocols from local to global scales. To improve definitions of ecosystem collapse for biodiversity risk assessment, we recommend: (1) qualitative description of initial and collapsed states (based on defining biotic and abiotic components, ecological processes and distributions) to provide a robust assessment of characteristic features; (2) use of ecological models (in particular conceptual diagrams) to diagnose mechanisms and pathways of ecosystem change and thus inform indicator selection; (3) application of spatial, biotic, and abiotic indicators to capture multiple symptoms of collapse, with careful consideration of indicator selection and consistency among collapse thresholds; and (4) explicit definition of quantitative collapse thresholds based on ecological evidence, quantifying uncertainty with bounded thresholds and sensitivity analyses. Our recommendations are particularly relevant to scientists and managers applying IUCN Red List of Ecosystems assessments (Keith et al. 2013) and other ecosystem assessment tools.

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References


**Supporting Information**

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