Author/s:
Bland, LM;Rowland, JA;Regan, TJ;Keith, DA;Murray, NJ;Lester, RE;Linn, M;Rodríguez, JP;Nicholson, E

Title:
Developing a standardized definition of ecosystem collapse for risk assessment

Date:
2018-02-01

Citation:
Bland, L. M., Rowland, J. A., Regan, T. J., Keith, D. A., Murray, N. J., Lester, R. E., Linn, M., Rodríguez, J. P. & Nicholson, E. (2018). Developing a standardized definition of ecosystem collapse for risk assessment. Frontiers in Ecology and the Environment, 16 (1), pp.29-36. https://doi.org/10.1002/fee.1747.

Persistent Link:
https://hdl.handle.net/11343/283474

Article Type: Reviews

Reviews

Developing a standardized definition of ecosystem collapse for risk assessment

Lucie M Bland[1*,2], Jessica A Rowland[1], Tracey J Regan[2,3], David A Keith[4,5,6], Nicholas J Murray[4], Rebecca E Lester[7], Matt Linn[1], Jon Paul Rodríguez[8,9,10], and Emily Nicholson[1]

[1]*School of Life and Environmental Sciences, Deakin University, Burwood, Australia* [*]*(l.bland@deakin.edu.au);* [2]*School of BioSciences, The University of Melbourne, Parkville, Australia;* [3]*The Arthur Rylah Institute for Environmental Research, Department of Environment, Land, Water and Planning, Heidelberg, Australia;* [4]*Centre for Ecosystem Science, School of Biological, Earth and Environmental Science, University of New South Wales, Kensington, Australia;* [5]*New South Wales Office of Environment and Heritage, Hurstville, Australia;* [6]*Long Term Ecological Research Network, Terrestrial Ecosystem Research Network, Australian National University, Canberra, Australia;* [7]*Centre for Rural and Regional Futures, Deakin University, Waurn Ponds, Australia;* [8]*Centro de Ecología, Instituto Venezolano de Investigaciones Científicas, Caracas, Venezuela;* [9]*Provita, Caracas, Venezuela;* [10]*IUCN Commission on Ecosystem Management and IUCN Species Survival Commission, Gland, Switzerland*

Running heads:

LM Bland *et al.*

How to define ecosystem collapse

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.
Front Ecol Environ 2018;

In a nutshell:

- The difficulty of defining ecosystem collapse has challenged the classification of threatened ecosystems
- We reviewed 85 studies of collapse in two biomes to inform the design of a robust framework to better define ecosystem collapse
- Most studies defined collapsed ecosystem states quantitatively, but many lacked a description of ecosystem processes leading to collapse
- Our recommended framework can be applied to define ecosystem collapse in IUCN Red List of Ecosystems assessments and national ecosystem risk assessments

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 (eg 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 (eg 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, overharvesting and burning of forest ecosystems on Easter Island in the 16th century CE led to the extinction of the foundation (ie 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 conceptualized in ecosystem risk assessments.

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 forests 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 (eg 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. Identifying intermediate or transition states toward collapse can be informative in some ecosystems (eg woodlands; Rumpff *et al*. 2011), but no studies identified intermediate states in our review.

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 (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 (Scheffer *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 pre-collapse 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 (Niemeijer 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 (hereafter "symptom") 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 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.

Acknowledgements

This work was supported by Australian Research Council Linkage Project (LP130100435). EN and LMB acknowledge the support of Veski and the Victorian Government through an Inspiring Women Fellowship. JAR was supported by a Deakin University Postgraduate Research Scholarship. We thank R Ferrari for coral reef photos.

References

Bestelmeyer BT, Brown JR, Havstad KM, *et al*. 2003. Development and use of state-and-transition models for rangelands. *J Range Manage* **56**: 114–26.

Bland LM, Keith DA, Miller RM, *et al*. 2016. Guidelines for the application of IUCN Red List of Ecosystems categories and criteria, Version 1.0. Gland, Switzerland: IUCN.

Bland LM, Regan TJ, Dinh MN, *et al*. 2017. Using multiple lines of evidence to assess the risk of ecosystem collapse. *P Roy Soc B Biol Sci* **284**: 20170660.

Boitani L, Mace GM, and Rondinini C. 2015. Challenging the scientific foundations for an IUCN Red List of Ecosystems. *Conserv Lett* **8**: 125–31.

Burgman MA. 2005. Risks and decisions for conservation and environmental management. Cambridge, UK: Cambridge University Press.

Burgman MA. 2015. Trusting judgements: how to get the best out of experts. Cambridge, UK: Cambridge University Press.

Burns EL, Lindenmayer DB, Stein J, *et al*. 2015. Ecosystem assessment of mountain ash forest in the Central Highlands of Victoria, south-eastern Australia. *Austral Ecol* **40**: 386–99.

Coetzee JC, Van der Lingen CD, Hutchings L, and Fairweather TP. 2008. Has the fishery contributed to a major shift in the distribution of South African sardine? *ICES J Mar Sci* **65**: 1676–88.

CBD (Convention on Biological Diversity). 2014. Aichi Biodiversity Targets. https://www.cbd.int/sp/targets/default.shtml. Viewed 7 Nov 2017.

Croll DA, Maron JL, Estes JA, *et al*. 2005. Introduced predators transform subarctic islands from grassland to tundra. *Science* **307**: 1959–61.

Cumming GS and Peterson GD. 2017. Unifying research on social–ecological resilience and collapse. *Trends Ecol Evol* **32**: 695–713.

Cury P, Mullon C, Garcia S, and Shannon L. 2005. Viability theory for an ecosystem approach to fisheries. *ICES J Mar Sci* **62**: 577–84.

Diamond J. 2007. Easter Island revisited. *Science* **317**: 1692–94.

Feng Q, Liang T, Huang X, *et al*. 2013. Characteristics of global potential natural vegetation distribution from 1911 to 2000 based on comprehensive sequential classification system approach. *Grassland Sci* **59**: 87–99.

Frank KT, Petrie B, Fisher JA, and Leggett WC. 2011. Transient dynamics of an altered large marine ecosystem. *Nature* **477**: 86–89.

Hare SR and Mantua NJ. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Prog Oceanogr* **47**: 103–45.

Keane RE, Hessburg PF, Landres PB, and Swanson FJ. 2009. The use of historical range and variability (HRV) in landscape management. *Forest Ecol Manag* **258**: 1025–37.

Keith DA, Rodríguez JP, Brooks TM, *et al*. 2015. The IUCN Red List of Ecosystems: motivations, challenges and applications. *Conserv Lett* **8**: 214–26.

Keith DA, Rodríguez JP, Rodríguez-Clark KM, *et al*. 2013. Scientific foundations for an IUCN Red List of Ecosystems. *PLoS ONE* **8**: e62111.

Litzow MA and Mueter FJ. 2014. Assessing the ecological importance of climate regime shifts: an approach from the North Pacific Ocean. *Prog Oceanogr* **120**: 110–19.

Mac Nally R, Albano C, and Fleishman E. 2014. A scrutiny of the evidence for pressure-induced state shifts in estuarine and nearshore ecosystems. *Austral Ecol* **39**: 898–906.

Mace GM, Collar NJ, Gaston KJ, *et al*. 2008. Quantification of extinction risk: IUCN's system for classifying threatened species. *Conserv Biol* **22**: 1424–42.

Martin J, Runge MC, Nichols JD, *et al.* 2009. Structured decision making as a conceptual framework to identify thresholds for conservation and management. *Ecol Appl* **19**: 1079–90.

Micklin P. 2010. The past, present, and future Aral Sea. *Lakes Reservoirs Res Manage* **15**: 193–213.

Moher D, Liberati A, Tetzlaff J, and Altman DG. 2009. Preferred Reporting Items for Systematic reviews and Meta-Analyses: the PRISMA statement. *PLoS Med* **6**: e1000097.

Möllmann C, Müller-Karulis B, Kornilovs G, and St John MA. 2008. Effects of climate and overfishing on zooplankton dynamics and ecosystem structure: regime shifts, trophic cascade, and feedback loops in a simple ecosystem. *ICES J Mar Sci* **65**: 302–10.

Nicholson E, Keith DA, and Wilcove DS. 2009. Assessing the threat status of ecological communities. *Conserv Biol* **23**: 259–74.

Nicholson E, Regan TJ, Auld TD, *et al*. 2015. Towards consistency, rigour and compatibility of risk assessments for ecosystems and ecological communities. *Austral Ecol* **40**: 347–63.

Niemeijer D and de Groot RS. 2008. A conceptual framework for selecting environmental indicator sets. *Ecol Indic* **8**: 14–25.

Payet K, Rouget M, Esler KJ, *et al*. 2013. Effect of land cover and ecosystem mapping on ecosystem-risk assessment in the Little Karoo, South Africa. *Conserv Biol* **27**: 531–41.

Peñuelas J and Boada M. 2003. A global change-induced biome shift in the Montseny Mountains (NE Spain). *Glob Change Biol* **9**: 131–40.

Pickering C and Byrne J. 2014. The benefits of publishing systematic quantitative literature reviews for PhD candidates and other early-career researchers. *High Educ Res Dev* **33**: 534–48.

Regan T, Taylor B, Thompson G, *et al*. 2009. Developing a structure for quantitative listing criteria for the US Endangered Species Act using performance testing, phase 1 report. NOAA technical memorandum. Rockville, MD: NOAA. NOAA-TM-NMFS-SWFSC-437.

Rice JC and Rochet MJ. 2005. A framework for selecting a suite of indicators for fisheries management. *ICES J Mar Sci* **62**: 516–27.

Rogers K and Biggs H. 1999. Integrating indicators, endpoints and value systems in strategic management of the rivers of the Kruger National Park. *Freshwater Biol* **41**: 439–51.

Roux JP, van der Lingen CD, Gibbons MJ, *et al*. 2013. Jellyfication of marine ecosystems as a likely consequence of overfishing small pelagic fishes: lessons from the Benguela. *B Mar Sci* **89**: 249–84.

Rumpff L, Duncan DH, Vesk PA, *et al*. 2011. State-and-transition modelling for adaptive management of native woodlands. *Biol Conserv* **144**: 1224–36.

Sato CF and Lindenmayer DB. 2017. Meeting the global ecosystem collapse challenge. *Conserv Lett*; doi.org/10.1111/conl.12348.

Scheffer M, Carpenter S, Foley JA, *et al*. 2001. Catastrophic shifts in ecosystems. *Nature* **413**: 591–96.

Suter GW. 1999. Developing conceptual models for complex ecological risk assessments. *Hum Ecol Risk Assess* **5**: 375–96.

Washington H. 2013. Human dependence on nature: how to help solve the environmental crisis. New York, NY: Routledge.

Wood SW and Bowman DM. 2012. Alternative stable states and the role of fire–vegetation–soil feedbacks in the temperate wilderness of southwest Tasmania. *Landscape Ecol* **27**: 13–28.

Supporting Information

Additional, web-only material may be found in the online version of this article at

Figure 1. *Cumulative publication numbers through time, for marine pelagic (*n *= 35; blue line) and temperate forest (*n *= 48; green line) publications selected for the systematic literature review. No papers published prior to 1995 met the selection criteria.*

Figure 2. *Spatial distribution of marine pelagic studies (*n *= 37; blue circles) and temperate forest studies (*n *= 41; green circles), with circle size indicating the number of studies. One marine pelagic publication included studies of three different ecosystems. Seven temperate forest studies of global extent were not mapped. Studies focusing on all ecosystems from a certain biome within a country were mapped as the centroid of the country.*

Figure 3. *Recommendations for defining ecosystem collapse in practice, using coral reefs as an example. (a) Collapse of the reef is qualitatively defined as an algae-dominated state, with very low coral cover. The initial state is defined as a coral-dominated state. (b) Drivers of ecosystem transitions to collapse include warming, exploitation, and acidification (shown as red boxes) in a cause–effect conceptual model. (c) Indicators of ecosystem collapse are identified based on the ecological model. (d) Bounded collapse thresholds are defined based on ecological evidence: here, a coral cover <1% indicates an algae-dominated state. (e) Uncertainty affects each step in the framework. This framework was used to support the application of the IUCN Red List of Ecosystems criteria to the Meso-American Reef (Bland* et al. *2017).*

Image credits: R Ferrari

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. For example, small changes in an environmental indicator can produce disproportionately large responses in biotic indicators (Mac Nally *et al*. 2014).

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 (ie 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 (Niemeijer 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).