Review

Threshold models in restoration and conservation: a developing framework

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The recognition that a system can appear resilient to changes in the environment, only to reach a critical threshold of rapid and unexpected change, is spurring work to apply threshold models in conservation and restoration. Here we address the relevance of threshold models to habitat management. Work to date indicates these concepts are highly applicable: human impacts can widen the range of habitats where threshold dynamics occur and shift communities into new states that are difficult to reverse. However, in many applied settings, threshold concepts are being adopted without evaluation of evidence and uncertainty. We suggest a framework for incorporating threshold models that reflects an emphasis on applicability to decision making and management on relatively short timescales and in human-impacted systems.

Introduction

Over the past several years, conservation and restoration biologists have increasingly recognized that ecosystem dynamics can be complex, nonlinear, and often unpredictable [1]. The potential for sudden shifts or flips in state is alarming to habitat managers, because it indicates that a system can be more vulnerable than it appears. Previous application of threshold models was limited to semi-arid rangelands and lake ecosystems (e.g. [2–4]), whereas habitat management in other systems traditionally assumed largely linear successional-like trajectories. Recently, there has been growing recognition that threshold dynamics can apply to a broad range of systems [5–10]. This recognition is resulting in a collective shift in the conceptual underpinnings of habitat management.

The recent utilization of threshold models in habitat management is largely heuristic, usually lacking rigorous testing of underlying assumptions [11]. Practitioners applying the concepts seem to be using constructs that appear to work, rather than striving to prove or follow particular elements. Does this disconnect between theory and application matter, and what happens if we get the translation wrong? Drawing upon recent research on ecosystem dynamics and their underlying mechanisms, we suggest a framework for incorporating threshold models that reflects an emphasis on applicability to decision making and management on relatively short timescales and in human-impacted systems. In particular, we focus on new evidence indicating that threshold models are highly

Glossary

Alternative stable states: multiple (alternative) basins of attraction within a system. In such a system, a given habitat or environment would be able to support two or more different assemblages of species, and these assemblages would be stable (self-replacing).

Cross-scale interactions: processes at one spatial or temporal scale interact with processes at another spatial or temporal scale. For example, fine-scale processes such as competition for resources can interact with broader-scale processes such as dust transport or dispersal.

Dynamic regime: a set of states that a system can occur in and still behave the same way (same basic structure and function). Dynamic regimes could be alternative stable states or more simply systems that exhibit threshold dynamics.

Ecological resilience: the amount of change a system can undergo and retain the same structure, function and feedbacks (i.e. stay in the same regime or state, not cross a threshold).

Feedbacks, positive and negative: positive feedbacks occur when the response of the system is to change a variable even more in the same direction. The end results of positive feedbacks are often amplifying; that is, small perturbations result in big changes. These feedbacks will drive the system away from its original state. Negative feedbacks have a dampening effect because the response of the system is to counteract the original change.

Hysteresis: describes the situation in alternative stable states where the pathway of degradation (or change in one direction) differs from recovery (or change in the opposite direction). Hysteresis can occur when two alternative states persist in one environment, necessitating that external conditions change beyond the area of alternative states for an assemblage to revert back to its original state.

Intransitive networks: situations of complex species interactions where it is not possible to establish a consistent ranking of interaction performance or success. For instance, species A > species B, species B > species C, but species C > species A. These rankings can refer to a range of different types of species interactions (i.e. competition, predation). They can also be broken down to different size or life-history classes (e.g. species A > juveniles of species B, but adults of species B > species A). Sometimes termed trophic triangles or demographic triangles to reflect specific intransitivity.

Priority effects: initial conditions influence the outcome of an interaction, where species or functional groups influence other species that arrive at a later time.

Response diversity: the diversity of groups (of species, populations or functional types) that can perform similar ecosystem functions (and might be considered redundant by traditional ecosystem management focused on optimizing function) but have different capacities to respond to disturbance, imparting greater resilience to the system as a whole.

Self-organized structure: situations where strong species effects or strong interaction networks are main determinants of community structure, as opposed to cases where abiotic constraints more strongly control species abundances and diversity.

State: indicates values of community or ecosystem attributes that primarily constitute the system of interest. For example, if a rangeland system is defined by the amounts of grass, shrub and livestock, then the state space is the three-dimensional space of all possible combinations of the amounts of these three variables. The dynamics of the system are reflected as movement through this space.

State and transition models: flowchart diagrams in which boxes represent vegetation states and arrows indicate transitions among states. Often these models are developed through a combination of expert knowledge, analysis of vegetation data and feedback from stakeholders. These models are a general and flexible management tool not exclusive to threshold dynamics.

Thresholds: points where even small changes in environmental conditions (underlying controlling variable) will lead to large changes in system state variables.

Trigger: a temporary perturbation that can have long-term repercussions. Often, the trigger is a perturbation that changes priority in the system, causing disturbance effects to persist even after the disturbance factor is moderated.

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relevant but do not apply to all systems uniformly, that human impacts might widen the range of habitats where threshold dynamics occur and that there are both benefits and risks to conservation and restoration decisions that presuppose threshold dynamics [10–14]. Finally, we emphasize several future research directions to guide the application of threshold models in conservation and restoration, including methods to correctly diagnose ecosystem dynamics, identify thresholds related to collapse and recovery, and anticipate—or in the case of degraded systems, overcome—such thresholds.

The gap between threshold models in theory and application

Theory

Although ecosystem dynamics can be multifaceted, one common distinction is between linear continuum responses and discontinuous threshold responses (Figure 1). Continuous change models predict that a change in the environment leads to a proportional change in species composition. Increasing or decreasing the environmental conditions over time will lead to responses down or up the same trajectory. Discontinuous threshold models describe the situation where changes in environmental conditions lead to very little change in species composition or function until a threshold is reached, when a sudden change in composition or function occurs. Ecological theory predicts that thresholds (see Glossary) occur when a trigger switches the pull of negative feedbacks from one attractor to another attractor (Figure 1b,c). These triggers are often either long-term abiotic perturbations that modify site characteristics or shorter-term modifications to biotic structure within communities [8,15]. Complex interactions, often in the form of positive feedbacks, can magnify these small changes, causing the system to rapidly change and cross a threshold to an alternative state characterized by different structure and function. Just before crossing a threshold, key ecosystem variables are predicted to show increased variability (i.e. rising standard deviations) and slower return rates after perturbation [16–18].

There are several types of theoretical models that predict threshold dynamics. Particularly applicable are discontinuous threshold models without hysteresis (Figure 1b), where the same response pathway occurs regardless of the direction of the environment change (i.e. no hysteresis). In this case, a sudden change in one direction, although discontinuous, could be reversible and result in a sudden recovery in the opposite direction. Hysteresis threshold models (Figure 1c), by contrast, describe a situation in which there are two or more stable point attractors (basins of attraction) for one given external environmental condition. In this case, because multiple states occur at one given environmental condition, the pathway to a restored system can be very different from the one that led to the degraded state [5].

Ecological theory yields a rigorous and detailed set of constructs needed to determine whether a system exhibits threshold behavior [19,20]. However, many tests of these constructs are hard if not impossible to apply in a practical setting. For instance, theory indicates that it is important to demonstrate long-term stability for a period that exceeds the lifespan of any one individual, which would

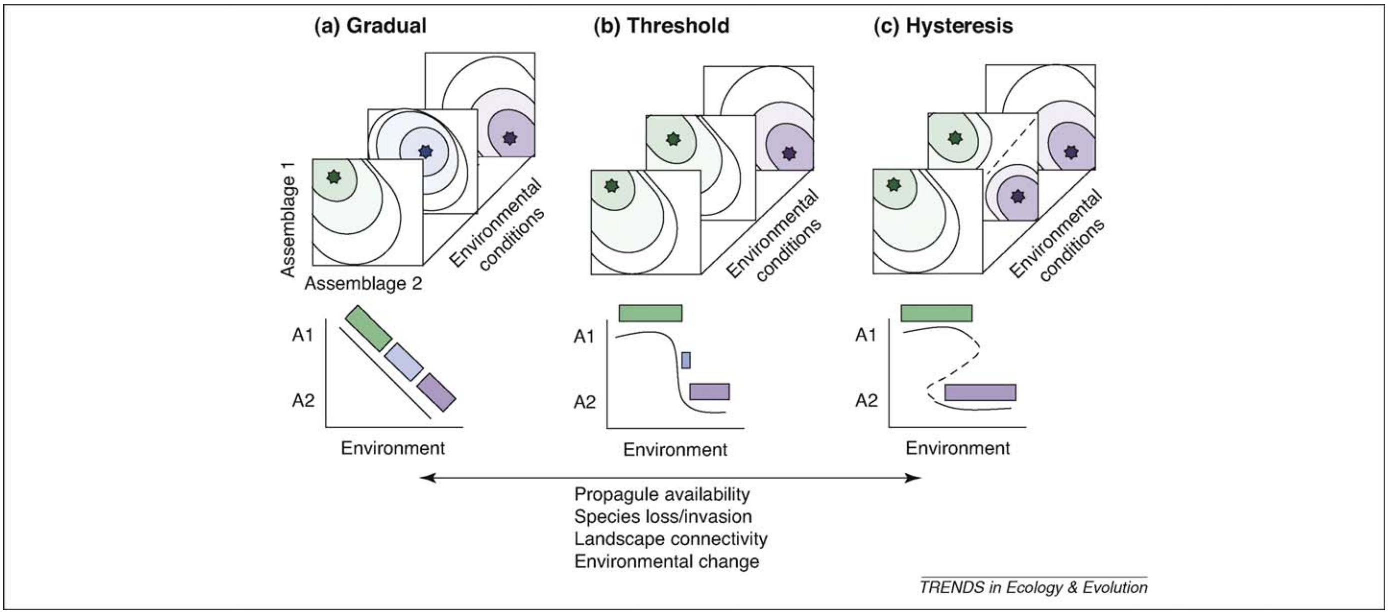

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Figure 1. Alternative models of ecosystem dynamics. Gradual change **(a)**, and two threshold models, non-hysteresis **(b)** and hysteresis **(c)**. Each square defines possible relative abundances of two state characters (different species, functional groups or ecosystem processes), which we have labeled assemblage 1 and assemblage 2. Ovals represent isoclines of standard units of perturbation strength (resilience) and the stars represent attractors. The dotted line in (c) indicates boundaries of basins of attraction. Each of these isocline graphs is arrayed along an environmental axis. Changes in the isoclines across the environmental gradient represent changes in composition and stability landscape. Below the isoclines, two-dimensional relationships between the biotic community composition (vertical axis) and environment (horizontal axis) are shown. Gradual change (a) occurs when there is a linear succession of species or groups along an environmental gradient. Non-hysteresis threshold change (b) occurs where species composition rapidly changes at a given point on the environmental gradient. Changes in the environmental gradient (or other external drivers) can push a system from one state to the other. Hysteresis thresholds (c) can occur if there are multiple basins of attraction (states) within the same habitat so that the threshold where assemblage 1 will decline (collapse) differs from where assemblage 1 will increase (recovery). Human activities can change the frequency and nature of threshold events by influencing resilience, which can affect the arrangement of isoclines as well as shift the system from one to another type of dynamics (i.e. from [a] to [b] to [c], as indicated by the colored rectangles).

require management decision making to last decades or longer in systems with long-lived organisms. Spatial scales needed for monitoring and experimental tests need to be large as well, beyond the resources of most managers. Theory also specifies low disturbance frequencies relative to the timescale of population dynamics, even though most degraded lands are prone to multiple complex disturbances. Lastly, human-caused species losses or introductions are not well developed in these models, even though they are often one of the largest priorities in conservation and restoration.

Application

Given the urgency with which management problems need to be tackled, managers often do not have the luxury to wait for rigorous testing of threshold theory to determine whether the system they endeavor to manage exhibits threshold or hysteresis dynamics. This urgency is particularly true in our current situation, where rapid environmental change threatens to swamp all other considerations. Perhaps due to the need to assume ecosystem dynamics with incomplete knowledge, threshold models applied to conservation and restoration have been largely heuristic [10,11,15]. Although these conceptual models still adopt ideas about abrupt shifts among states, they encompass systems larger and more complex than can be properly analyzed using the available theoretical constructs. In addition, they do not specify the need for stability, enabling managers to apply these ideas to systems that exhibit more stochastic and transient dynamics.

One important group of applied models, state and transition [2,21], are flowchart diagrams representing vegetation change along several axes, including fire regimes, weather variability and management prescriptions. They often have more than ten different specified states and even more transitions. States and transitions are often defined in a workshop of experts in a given system. Whereas these models have roots in rangeland science, recently their utilization has spread to a broad range of management settings [e.g. 22,23].

Another type of applied conceptual model that has resonated widely is a two-threshold model [24]. In the first threshold, disturbances are assumed to switch feedbacks by modifying biotic structure and interactions within communities. In the second, further down the degradation trajectory, harder-to-reverse thresholds between states can be crossed in response to abiotic changes that modify site characteristics (e.g. climate change, severe soil erosion, soil salinization, eutrophication). Recently, many variations of this conceptual model [25–27] have been developed, as they are proving to be consistent with land managers' perceptions of the management process [1].

Expansion of threshold theory to human-impacted systems

Whereas the theoretical development of threshold (particularly hysteresis) models in ecology historically excluded human impacts [28], in the last decade most empirical examples of threshold dynamics have a strong human component [29,30]. Consequently, ideas about stability, timescale and disturbance are shifting to reflect the inclusion of humans in the framework. There are several important areas where threshold theory is expanding to encompass these advances.

Habitat managers are often dealing with systems experiencing unprecedented change in multiple directions. Thus, threshold models that include multiple interacting axes and incorporate realistic disturbance frequencies are likely to be most applicable to management. Human activities can introduce new threshold triggers by transforming transient events into persistent disturbances, introducing chronic stress in the form of new disturbances, or suppressing important disturbance events [31]. For instance, catastrophic mortality events might be extremely rare under natural conditions but not unexpected in the context of severe overexploitation, land-use change or environmental contamination [32,33]. In addition, there is abundant evidence that humans are altering disturbance regimes (e.g. suppression of fires in grasslands and forests, damming of rivers) and changing climatic extremes (e.g. increased bleaching of coral reefs due to warming); the combined and often synergistic effects of these pressures can make ecosystems more vulnerable to changes that previously could have been absorbed [34].

Increasing evidence indicates that humans influence the ecological resilience of a system by altering the biotic capacity of the system to cope with disturbance triggers. Thus, managers are often faced with situations where functional groups have been either lost (e.g. overexploitation of top predators by overfishing) or gained (e.g. introduction of exotic N-fixing plants) in many systems. Work indicates that these changes in diversity can affect the capacity of an ecosystem to rebuild after change through a combination of top-down and bottom-up impacts, as many groups have critical roles in community reassembly following a disturbance. For instance, Hughes *et al.* [35] found that the trajectory of coral reassembly after a warming-induced bleaching event depended on whether herbivorous fishes were present (similar to conditions in reserves) or absent (similar to overfished areas). Comparable ideas about the role of specific functional groups in reorganization after a disturbance have developed in restoration ecology, such as assisted succession [36] and assembly theory [37], and have great applicability to threshold models. For instance, the idea that absence of particular functional groups can delay or prevent recovery is well documented in restoration, but threshold models are often not expanded to include propagule limitation as a driving force maintaining different states. Without a native propagule source, fragmentation can permanently reduce the ability of degraded habitat to recover, creating a new human-caused alternative state [38,39]. Similarly, the addition of new functional groups via invasion can create new basins of attraction that also change recovery dynamics.

In addition to functional group diversity, ensuring high functional response diversity [34] might be critical to habitat management that aims to ensure ecological resilience. For example, Steiner *et al.* [40] found that diversity increased community resilience in experimental aquatic food webs because more diverse communities had a greater likelihood of containing a particularly resilient species, a finding mirrored in annual grassland plant communities [41]. Response diversity might be particularly important for conservation and restoration considerations in light of uncertain future disturbance regimes and environmental change. To increase response diversity and ecological resilience, management will often need to create restoration mixes with many seemingly 'redundant' species from a wider range of environments, increase emphasis on population-level diversity in addition to local adaptation and consider assisted species migration and reintroduction.

Human impacts on biological legacies and connectivity can also diminish ecological resilience. Maintaining and, when necessary, reintroducing biological legacies—woody debris, larvae, fungi, microorganisms and seeds—are important in restoration [38,42] and also a key component of resilience. For instance, seed banks are a critical means by which the biodiversity of a system is able to rebuild following a disturbance, and can be destroyed by extreme disturbance events or altered owing to high propagule pressures from exotic species. When local legacies are depleted, biodiversity at larger spatial scales ensures that appropriate key species for ecosystem functioning are recruited to local systems after disturbance or when environmental conditions change. Thus, landscape links among communities through dispersal and pollinators need to be further connected to resilience; breaks in this 'rebuilding capital' might cause reduced resilience and increased probability of crossing a critical threshold into another basin of attraction [43].

Threshold models need to incorporate transient dynamics and a degree of stochasticity to be applicable to conservation and restoration. Due to high frequencies of disturbance and rapid rates of environmental change, many managed systems might never meet stability criteria. Despite not meeting theoretical assumptions, we suspect that threshold dynamics might be more prevalent in areas experiencing substantial environmental change in one or a combination of drivers [44,45]. It will be important to understand how these changes influence the resilience of a system [44], whether temporal climate variability can cause threshold shifts [46,47] and how novel combinations of external drivers (e.g. changed precipitation and nitrogen deposition) [31] can influence the probability of these shifts. These advances are beginning to modify experimental and observational methods to incorporate transient states, particularly those that persist in the time frame of human decision making, into the framework of threshold models.

Interactions as a tool to bridge theory and practice

One reason for the gap between theory and practice concerning the application of threshold models is that managers have limited tools available to evaluate evidence and the uncertainty of threshold behavior in a given management situation. Because a characteristic feature of threshold dynamics is a change in system feedbacks and interactions, evaluation of the mechanisms that control recovery or resilience in managed habitats could be a relevant and applicable focus to bridge this gap. Recent evidence indicates that several mechanisms might be important to focus on in management settings (Box 1). Understanding these mechanisms can inform appropriate management actions to build resilience or—in the case of degraded systems—guide recovery.

There are several emerging generalities about feedbacks and interactions that might indicate types of systems more likely to exhibit threshold dynamics. According to some theories, managers could expect threshold dynamics to be more prevalent in systems that have a self-organized structure among biotic components (i.e. strong species effects, priority effects, strong interactive networks) owing to the increased likelihood of biotic feedbacks. Additionally, the more species that can potentially colonize communities (the greater the species pool), the greater chance of threshold effects through priority effects [48,49]. One important exception to these general predictions is the occurrence of threshold dynamics associated with shifts between vegetated and non-vegetated states due to strong plant–geomorphic (abiotic) interactions [6,50].

In cases with strong self-organization, thresholds can be particularly likely where intransitive networks occur among interacting species or functional groups. Because these are situations without a simple interaction hierarchy (e.g. $A > B > C$ but $C > A$), priority effects can invert or otherwise rearrange interactions. Intransitive networks can occur due to (i) size-selective predation [47], where temporary reduction in predation can allow prey to grow to a big enough size to escape predation, (ii) intraguild predation [51], where the competitively inferior species can prey upon juveniles of the competitive dominant or (iii) competitive asymmetries [52,53], where rankings of recruitment ability differ from adult competitive rankings. Interaction networks that have the potential to change from top-down (controlled by predation or herbivory) to bottom-up (controlled by resource competition) control can also cause similar feedback switches [54].

A trigger common to all these mechanisms is a temporary change in abundance of one species that permanently changes the nature of species interactions—a common occurrence in habitats subject to changed management objectives or decision making. Likewise, habitats that have experienced a persistent loss of a species [14,55], either from direct exploitation (hunting) or indirect drivers such as land-use change (e.g. loss of a propagule source combined with a disturbance event), can have substantially changed species interaction networks and a higher probability of threshold dynamics, particularly if the species lost is a keystone or foundation species. Even small changes in abundance of species that have strong abiotic effects, such as ecosystem engineers, can change the abiotic environment (e.g. nutrient cycling, fire regimes) and create feedbacks that cause further divergence in abundance and ecosystem effects [9].

Thresholds should also be expected to be more frequent in situations where processes at one spatial or temporal scale interact with processes at another spatial or temporal scale [56], termed cross-scale interactions. For instance,

Box 1. Implications of recent findings for restoration and management

Four recent studies in very different systems (Figure I) indicate how threshold concepts can be applied to restoration decision making. We break down each example by observational patterns, threshold triggers, feedback mechanisms, restoration measures and examples of similar dynamics.

Eelgrass seabeds, Wadden Sea, The Netherlands [70] (Figure Ia)

Pattern	In the 1930s, large seagrass meadows of *Zostera marina* (eelgrass) disappeared over several years and have not recovered.
Trigger	Combination of wasting disease and turbidity from dam construction.
Feedback mechanism	Eelgrass shoot density reduces suspended sediment turbidity, which creates optimal growth conditions. Wasting disease reduced shoot density to a point where it no longer reduced turbidity, thus diminishing its ability to recover.
Restoration	Along with transplanting eelgrass, actively reduce turbidity to allow eelgrass to establish. Transplant at a large scale (several hectares) to initiate turbidity effects.
Similar dynamics	Plant species affect environmental characteristics to their own competitive advantage [71].

Willows, Yellowstone National Park, USA [14,72] (Figure Ib)

Pattern	Willows (*Salix* spp.) were a large component of the riparian systems of the northern winter range but have declined 50–60% since the early 1900s.
Trigger	Elk overbrowse willow following the elimination of gray wolves circa 1920.
Feedback mechanism	Overbrowsing of willows excludes beaver. Beaver loss results in changed hydrology that is not optimal for willows. Willows are not able to recover even when wolfs are reintroduced, and elk populations decrease owing to hydrological changes.
Restoration	Along with decreasing browsing pressure, actively change hydrology (dam and/or reintroduce beaver) to allow willow re-establishment.
Similar dynamics	Species loss due to bleaching in coral reefs, allowing for algae dominance and lack of recovery due to subsequent loss of herbivores [35,55].

Desert wetlands, Sycamore Creek, Arizona, USA [50] (Figure Ic)

Pattern	Replacement of cienegas (desert riverine wetlands) in the early 1900s by arroyo gravelbeds without vegetation.
Trigger	Flooding events.
Feedback mechanism	Plant density reduces surface flow velocity and creates sediment conditions that facilitate the increased vegetation growth. Flooding removes sparse vegetation but does not affect denser vegetation.
Restoration	Along with elimination of cattle grazing, actively protect recovering wetland vegetation from monsoon floods. Conduct activities in years with sustained baseline flow and low flooding probability.
Similar dynamics	Desertification due to the reduction of plant cover by grazing, and the subsequent changes in resource distribution [58].

Brown trout, Lake Takvatn, Norway [51] (Figure Id)

Pattern	Replacement of brown trout (*Salmo trutta*) with introduced arctic charr (*Salvelinus alpines*).
Trigger	Overfishing.
Feedback mechanism	Size-selective predation where small-sized charr are prey for trout but larger charr compete with small trout for invertebrates. Overfishing (drop in predator density) allows prey to grow larger, resulting in less small-sized prey. These changes inhibit predator recovery even when fishing pressures decline.
Restoration	Along with reducing fishing, reduce prey density to stimulate prey reproduction and shift prey-size distribution toward smaller individuals. Smaller prey will allow for sustainable predator recovery.
Similar dynamics	Demographic triangles where plant species recruit in situations where the competitive dominant populations have decreased or in size-symmetric conditions [52].

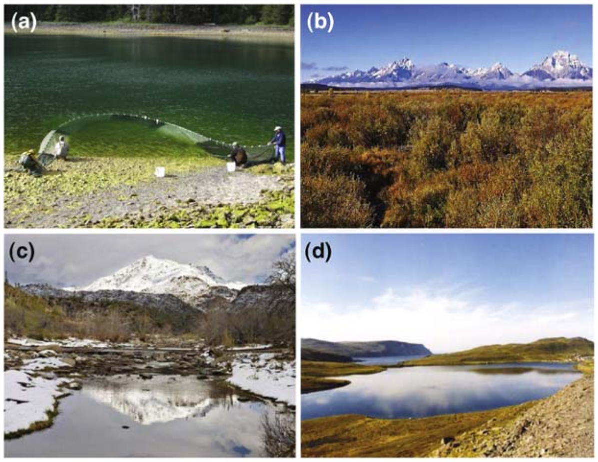

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Figure I. Systems in which threshold concepts have been applied to restoration decision making. Eelgrass seabeds **(a)**, willow riparian areas **(b)**, desert wetlands **(c)** and arctic lakes **(d)**. Photos reproduced with permission from (a) NOAA, (b) M. Menefee, (c) D. Garman and (d) E. Manchon.

recruitment dynamics interact with topography, propagule dispersal interacts with animal movement and sediment transport, and individual growth interacts with disturbance regimes [57,58]. When broad-scale processes overwhelm fine-scale processes, a system can pass a critical point, producing threshold dynamics.

There are many challenging issues in conservation and restoration that likely are characterized by these feedback mechanisms. Desertification, for example, has been shown to be a result of strong biogeomorphic feedbacks that operate across several spatial scales [58]. Many invasive species, including salt cedar (*Tamarix* sp.) and cheatgrass (*Bromus tectorum*), have been shown to have large effects on the abiotic environment, including resource cycling and disturbance regimes [59]. Trophic interactions have been well documented in the context of threshold effects in the restoration of rangeland and lake systems [4,10]. Thus, assessing predominant interaction and feedback mechanisms might serve as one line of inference to guide habitat managers about whether threshold models are appropriate and to suggest approaches for intervention.

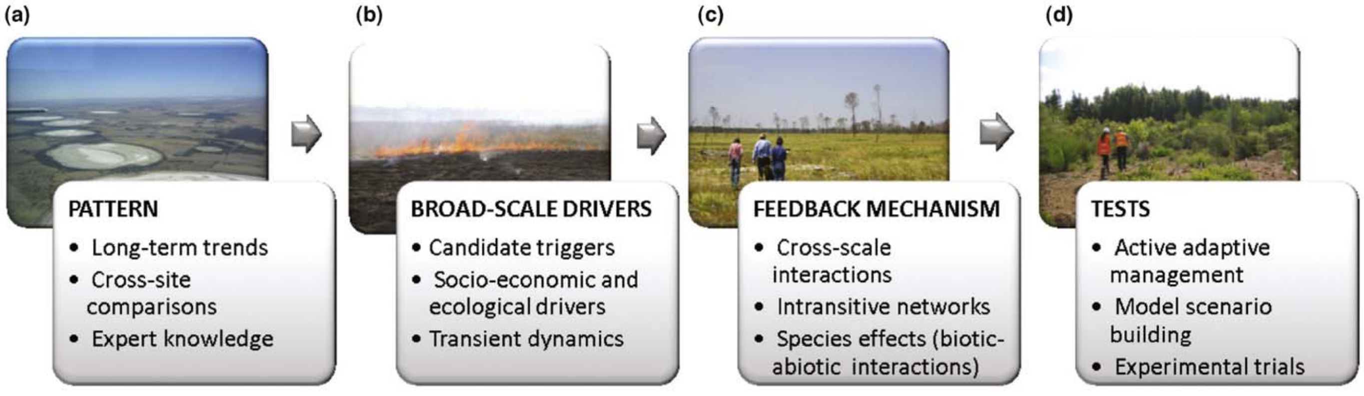

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Figure 2. A framework for the application of threshold models to conservation and restoration. A framework focused on the processes that determine nonlinear dynamics, and the dimensions of these processes across management-realistic spatial and temporal scales, can be developed in habitat management by emphasizing four steps: **(a)** understanding the temporal and spatial patterns of change, **(b)** identifying broad-scale processes that can affect resilience and act as triggers for thresholds, **(c)** determining feedback mechanisms in a system that have the potential to cause rapid change and **(d)** developing tests of the framework using adaptive management, focused experiments and scenario model building. Photos reproduced with permission from R.J.H. (a,c,d) and K.N.S. (b).

Making the link: a framework for management

An increasing number of studies are attempting to use conceptual models adopting threshold approaches to understand system dynamics and provide management guidance [11]. However, relatively few studies use statistical or analytical tools to consider whether the system being studied might conform to a threshold model, and virtually all rely partially or entirely on observation or expert opinion to infer the types of dynamics involved. Assuming ecosystem dynamics with incomplete knowledge could result in undesirable scenarios. For example, there could be a hands-off approach where there are, in fact, unidentified thresholds. Alternatively, active intervention could be carried out when, in fact, the ecosystem or species could have recovered adequately anyway. Because both scenarios result in adverse habitat management and conservation outcomes [7,10,60], it is important to weigh the relative danger (or relative efficacy) in assuming a threshold dynamic model. A few evidence-based points of inference can be invaluable in these situations.

An essential part of the decision-making process is evaluating the evidence for, and the uncertainty of, threshold behavior in a given management situation. Here we frame solutions to bridging this gap as a combination of improving knowledge transfer (theory in a form that can be readily transferred to the field) and two-sided knowledge creation (utilizing practical knowledge to advance theoretical progress) [61]. To increase utility and progress on this front, we suggest several ways in which threshold dynamics can be incorporated into a conservation and restoration framework (Figure 2).

First, although it might be impossible to rigorously test many of the assumptions of threshold models, we suggest the need for an increased emphasis on pattern-based knowledge, incorporating indicators, long-term monitoring and expert knowledge to better understand temporal and spatial patterns of change. Surveys to explicitly test whether threshold patterns are occurring in a managed landscape are relatively feasible and a very informative step for management decisions. Threshold patterns can be discerned in time series analyses, indicated by abrupt transitions over time, or spatial analyses, indicated by sharp spatial boundaries in the absence of associated sharp discontinuities in environmental parameters [62]. Several recent studies have shown nonlinear patterns, either along environmental gradients [12,63,64], in space [65] or in time [41,66]. For example, Sasaki and others [64] surveyed vegetation along grazing gradients at ten sites in Mongolia. They found strong evidence of threshold changes in floristic composition, where changes in composition were relatively constant below a critical grazing level, above which the vegetation changed sharply. This observational 'on the ground' knowledge is a forte of managers, and should be formalized into data sets and shared resources for decision making. Given results to date, it is important not to assume threshold dynamics but rather make evidence-based inferences utilizing a range of tools and information sources (Box 2).

Second, due to high frequencies of disturbance and rapid rates of environmental change, transient dynamics and a degree of stochasticity need to be incorporated into threshold models to be applicable to conservation and restoration. It is important to continue to identify broad-scale disturbance and climate drivers that affect resilience and act as triggers for thresholds. Due to the importance of cross-scale interactions, larger-scale processes such as historic legacies, landscape heterogeneity, dispersal limitation and climate change can be important, and need to be included in both theoretical considerations and management decisions. These drivers make it crucial to continue to modify research and applied approaches to incorporate the occurrence and importance of transient states, particularly those that persist in the time frame of human decision making.

Third, we recommend expanding the focus on interactions that might contribute to regime shifts and resilience. Although the question of whether a system exhibits hysteresis is very important to expand the underpinnings of threshold models, it is extremely difficult to test [19]. A more immediately relevant question for conservation and

Box 2. Toolbox for managing complex dynamics in changing environments

Faced with significant uncertainty when predicting ecosystem dynamics, six tools will be essential to add to (or keep in) the restoration and conservation toolbox.

Defined measurable objectives

A step in understanding ecological dynamics relevant to management is to define basic objectives that can be quantified, cover multiple scales and are adaptable. Likewise, because there is every reason to believe that human impacts and decisions will drive increased threshold dynamics, ecologists need to consider cases with multiple management objectives or when stakeholder groups value different objectives.

Model and scenario development

Models are a crucial component allowing for integration of monitoring data, testing assumptions of system behavior and building alternative scenarios. Conceptual models, such as state-transition models, are heuristically useful for initiating investigations with high uncertainty. Ultimately, quantitative models are a desirable and powerful extension of a conceptual framework (e.g. [67]).

Adaptive management

Complex dynamics require a flexible approach to management that considers management actions as a set of experimental treatments. These management experiments must be done at appropriately large landscape or watershed spatial scales, which at times might make extensive replication infeasible. Although it is important to consider the risk of undesirable outcomes in the learning process, risk will often be outweighed by the benefits of simultaneously exploring several management options.

Mechanistic trials

Select mechanisms can be identified using trials at relatively small (plot-level) scales. Small-scale replicated experimental trials can be used to direct larger-scale adaptive management experiments, particularly if the results of the small-scale trials are considered in the context of cross-scale interactions.

Key leading indicators

Monitoring is an integral key to decision making for complex systems. Although still an emerging area, determination of leading indicator variables could be a particularly important tool to identify thresholds before they occur [16,17]. Monitoring data can also be used to assess temporal dynamics, nonlinearities in space and feedback relationships among variables [64].

Learning from elsewhere

Habitat management projects are ubiquitous in most regions of the world. Although some of these efforts are being catalogued, few are evaluated for ecological success and even fewer are shared outside an organization [68] (but see Ref. [69]). Project-specific data can be combined into larger assessments of when, and under what conditions, certain management projects meet their objectives. More incentives and organizational support should be given for these initiatives, as a small investment in synthesis and sharing will lead to large returns on management efficacy.

restoration research is whether interactions and feedbacks control recovery or resilience in managed habitats and, if so, then what these interactions and feedbacks are. Inferring important feedback mechanisms (e.g. Box 1) might be a sufficient first step in the evidence needed for adaptive management, and deserves increased emphasis in scientific research and management efforts.

Fourth, because evidence indicates that we can expect complex dynamics, particularly with increasing human impacts, it is important to develop tests using active adaptive management, focused experiments and scenario model building (Box 2). Many of these techniques can be incorporated into planned management actions, but they require that management be seen as a learning process where alternatives are frequently evaluated and assessed.

In closing, work to date indicates that threshold models are a highly applicable framework in managed systems and that human-impacted habitats can be particularly susceptible to threshold shifts. However, it is likely that not all systems exhibit threshold dynamics and that there are both costs and benefits to their incorporation in management frameworks. Despite the difficulty of rigorous testing of theoretical assumptions of threshold models in applied settings, theory is beginning to provide tools for the evaluation of evidence and the uncertainty of threshold behavior in a given management situation. Assumptions are being modified to be more realistic in management settings by including such factors as high disturbance frequencies, species loss and invasion, and transient dynamics. Practical knowledge about the importance of such factors as legacy effects, feedbacks and species interaction networks, and rapid environmental change is being utilized to advance theoretical progress. Collaborative involvement among scientists, managers and stakeholders—within projects and across projects—will be a key step in future progress in the science and application of these models to habitat management on relatively short timescales and in human-impacted systems.

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