Summary Report

LTER Synthesis Working Group: State Changes and Threshold Dynamics

Organizers: Aaron M. Ellison* (HFR) and Brandon Bestelmeyer (JRN)
*Contact: Harvard Forest, 324 North Main Street, Petersham, MA 01366; aellison@fas.harvard.edu

A three-day workshop on state changes and threshold dynamics was held at the Harvard Forest LTER May 2-4, 2011 (May 1 and May 5 were travel days). Participants included (*graduate student; **post-doc): Brandon Bestelmeyer (JRN), Aaron Ellison (HFR), Bill Fraser (PAL), Kristen Gorman (PAL)*, Sally Holbrook (SBC), Christine Laney (JRN)*, Mark Ohman (CCE), Finn Pillsbury (JRN)**, Andrew Rassweiler (SBC)**, and Sapna Sharma (NTL)**. This workshop built on a 2009 Ecotrends workshop at JRN (May 1-2, 2009: http://intranet2.lternet.edu/content/workshop-promote-synthesis-products-ecotrends-project) and a follow-up workshop at the 2009 ASM (http://asm.lternet.edu/2009/workgroups/understanding-state-change-long-term-datasets).

The workshop had two goals: (1) complete the analysis and synthesis of time-series data from JRN, PAL, CCE, and SBC that were assembled for the 2009 state-change workshops; and (2) complete a manuscript on state changes and thresholds that links concepts and models with empirical data. The workshop met these two goals. Datasets from CCE, PAL, JRN, and SBC were compiled, analyzed, and used to test a conceptual model of state changes (Fig. 1). Data and accompanying metadata have been accessed into the Harvard Forest Data Archive (http://harvardforest.fas.harvard.edu/data/archive.html), dataset HF-170. A manuscript was completed and was submitted to *PNAS* on 8 June 2011. A copy is included with this report.

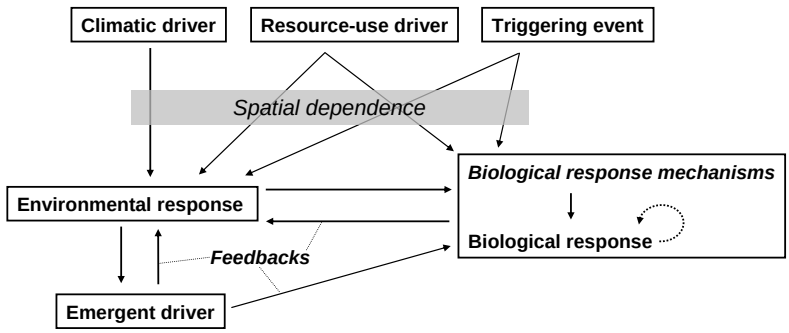


Figure 1 – *Conceptual model of interaction of drivers, responses, and feedbacks leading to state changes.*

Classification: Biological Sciences: Ecology

Detecting and managing abrupt transitions in ecological systems

Brandon T. Bestelmeyer[a, 1], Aaron M. Ellison[b], William R. Fraser[c], Kristen B. Gorman[c, d], Sally J. Holbrook[e, h], Christine M. Laney[f], Mark D. Ohman[g], Debra P.C. Peters[a], Finn C. Pillsbury[a], Andrew Rassweiler[h], Russell J. Schmitt[e, h], Sapna Sharma[i]

[a]USDA-ARS Jornada Experimental Range, New Mexico State University, MSC 3JER Box 30003, Las Cruces, NM, 88003, USA

[b]Harvard Forest, Harvard University, Petersham, Massachusetts, 01366, USA.

[c]Polar Oceans Research Group, Sheridan, MT 59749, USA

[d]Simon Fraser University, Department of Biological Sciences, 8888 University Drive, Burnaby, BC V5A 1S6, Canada

[e]Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, California, 93106, USA

[f]Environmental Science and Engineering Program, University of Texas at El Paso, El Paso, Texas, 79968, USA.

[g]Scripps Institution of Oceanography, University of California at San Diego, La Jolla, CA 92093, USA

[h]Marine Science Institute, University of California, Santa Barbara, California, 93106, USA

[i]Center for Limnology, University of Wisconsin-Madison, Madison, Wisconsin, 53706, USA

[1]To whom correspondence should be addressed. E-mail: bbestelm@nmsu.edu

Manuscript in review
Do not cite or distribute

Abstract

The occurrence and causes of abrupt transitions, thresholds, or regime shifts between ecosystem states are of great concern and the likelihood of such transitions is increasing for many ecological systems. General understanding of abrupt transitions has been advanced by theory, but hindered by the lack of a common, accessible, and data-driven approach to characterizing them. We apply such an approach to 30 – 60 years of data on environmental drivers, biological responses, and associated evidence from pelagic ocean, coastal benthic, polar marine, and semi-arid grassland ecosystems. Our analyses revealed one case in which the response (krill abundance) linearly tracked abrupt changes in the driver (Pacific Decadal Oscillation), but abrupt transitions detected in the three other cases (sea cucumber abundance, penguin abundance, and perennial grass production) exhibited hysteretic relationships with drivers (wave intensity, sea-ice duration, and amounts of monsoonal rainfall, respectively) through a variety of response mechanisms. The use of a common approach across these case studies illustrates that: the utility of leading indicators is often limited and can depend on the abruptness of a transition relative to the lifespan of responsive organisms and observation intervals; information on spatiotemporal context is useful for comparing transitions; and ancillary information from associated experiments and observations informs interpretations of response-driver relationships. The understanding of abrupt transitions offered by this approach provides information that can be used to manage state changes and underscores the utility of long-term observations in multiple sentinel sites across a variety of ecosystems.

Manuscript in review
Do not cite or distribute

/body

Many ecological systems can exist in two or more states that differ in abundance or composition of species, rates of ecological process, and ecosystem services provided by them (1, 2). Smooth, gradual transitions between ecosystem states are unremarkable, occurring during succession or as ecosystems track gradually changing environmental conditions. In contrast, abrupt transitions between ecosystem states usually are unexpected and can have wide-ranging, negative impacts. Abrupt transitions happen either when the gradually changing environment passes a critical point or when discrete perturbations cause sudden changes in underlying environmental drivers. Abrupt and irreversible transitions are forecast to increase as climatic changes and depletion of natural resources both accelerate (3, 4), but such forecasting is difficult because there are many different causes of state changes (5) and because existing approaches demand far more data than are normally available (6).

Managing state changes is as difficult as forecasting them. When environmental changes are not severe, or when organisms with short lifespans and generation times rapidly track environmental drivers, some state changes can be reversed in relatively short periods of time (≤50 years) if drivers are returned to pre-change conditions or perturbations are eliminated (7). When environmental change initiates feedbacks between ecosystems and the environment, or when organisms have long lifespans and generation times, state changes can persist long after environmental drivers have returned to earlier conditions. The persistence of these so-called "ecological thresholds", "regime shifts", "phase shifts", or "catastrophes" (8-10) is caused by time-lags in the responses of biological systems to environmental change (hysteresis), differences in the relationships between state variables and environmental drivers before and

Manuscript in review
Do not cite or distribute

after the state change, or the appearance of novel feedbacks among state variables and drivers that reinforce the new state (9, 11-13).

Forecasting abrupt transitions and managing new states requires strong linkages among theory, data, and case studies, but there is little guidance available for using historical or contemporary, ongoing studies to detect or respond to abrupt transitions. There is confusion and disagreement about what changes constitute transitions (14, 15) and a limited understanding of ecological mechanisms causing them (16, 17). Empiricists disagree about how to best gather and interpret relevant data (15, 18, 19), while theoreticians develop leading indicators of abrupt transitions and state changes that demand far more data than realistically can be collected (20-22). There is little clarity regarding the use of existing data and the design of future studies to detect and mitigate state changes (10, 23).

A common, systematic approach to analyzing state changes could allow ecologists to marshal a large body of useful data and detailed knowledge to help society better understand and manage abrupt transitions. Here, we illustrate such a general, data-based, and mechanism-centered analysis of abrupt transitions using four datasets from the US Long-Term Ecological Research (LTER) program on pelagic ocean, coastal benthic, polar marine, and semi-arid terrestrial ecosystems. These LTER data include some of the longest time-series available for both causal environmental drivers and biological response variables, and interpretations of associations between the drivers and the response variables are enhanced by experimental and mechanistic studies conducted on the same systems at the same sites.

We first lay out a common framework for describing abrupt transitions and state changes that can be used to compare and contrast among case studies. We then propose a standardized analytical approach that provides strong tests for detecting abrupt transitions between states. This

Manuscript in review
Do not cite or distribute

approach revealed unexpected results for the pelagic ocean system for which a "regime shift" had been described previously, provided stronger evidence for hypothesized state changes in the coastal benthic ecosystem, and yielded new evidence for state changes in the polar marine and semi-arid terrestrial ecosystems. Our analyses illustrate how to identify and understand causes of abrupt transitions, and also illustrate limitations common to many datasets used to study abrupt transitions and state changes. We conclude with recommendations for improving ongoing and nascent long-term research programs aimed at detecting and forecasting state changes.

A common framework for describing state transitions

Studies across a wide range of ecosystems reveal five common data elements used in the recognition and analyses of transitions: *environmental drivers; triggers; biological responses; response mechanisms;* and *contextual information* (Fig. 1) (9, 13, 24).

State changes in biological responses are caused directly or indirectly by changes in *environmental drivers*. Drivers are usually abiotic and include changes in climate (*e.g.*, temperature, precipitation), or land-use (*e.g.*, resource extraction, nutrient input rates). Environmental drivers usually are considered "slow variables" (*e.g.*, 20, 25) because they typically change much more slowly than biological response variables (Fig. 2A). The textbook example of a slow environmental driver leading to a state change is long-term phosphorus input leading to an abrupt shift from oligotropic (clear blue) to eutrophic (muddy green) lakes (20).

Drivers can also change abruptly, however, with dramatic effects. *Triggers* (a.k.a. pulse disturbances) are either abrupt shifts in drivers or singular events, such as droughts, hurricanes, disease outbreaks, invasive species introductions, or fire, that directly affect biological responses (13). State changes often are caused by interactions among multiple drivers and triggers (26)

Manuscript in review
Do not cite or distribute

(27). Whereas drivers are typically presented as time series concurrent with biological responses (Fig. 2A), triggers are discrete events in time or relatively short, discrete sections of a time series (*e.g.*, an El Niño period) (28).

Biological responses (a.k.a. response variables or state variables) are used to recognize alternative states (15, 24, 29). Response variables are especially important because they usually can be measured or monitored easily, and persistent changes in their mean or increases in their variance are used as key indicators of state changes. Like environmental drivers, biological response variables typically are represented as time series of the abundance or biomass of individual species or suites of trophically-similar species (30) (Fig. 2A).

Response mechanisms describe how drivers and triggers interact and affect responses (Fig. 1). Of particular importance are changes in relationships between drivers and responses caused by positive feedbacks between them that amplify changes in both drivers and responses and reinforce alternative states (31). Positive feedbacks often involve complex chains of interactions involving biological and physical processes, including Allee effects (32), trophic cascades (6, 33), habitat fragmentation and extinction cascades (34, 35), land surface-climate feedbacks (36, 37), or spreading desertification (38). Data on response mechanisms are derived most frequently from manipulative experiments, natural history observations, and expert knowledge (39).

Finally, *contextual information* documents characteristics of the environmental setting that can influence driver-response relationships and that can vary among case studies. For example, lake morphometry (40), stream channel geometry (41), soil texture (42), and distance to source populations (43) result in spatial variation in biological responses to drivers and triggers. Similarly, the timing of disturbance events with respect to seasonal period can

Manuscript in review
Do not cite or distribute

determine their effects on biological responses (26). Understanding spatiotemporal context can help to reconcile differences among case studies illustrating general types of transitions and state changes (e.g., ref. 44). Contextual information also can help translate scientific analyses into meaningful policy recommendations and management interventions (6).

An approach for identifying abrupt transitions and state changes in ecological systems

Three general classes of mechanisms are postulated to cause abrupt transitions and, therefore, alter the relationships among environmental drivers, triggers, and response variables (following refs. 9, 13, 24): *linear tracking*, *threshold response*, and *hysteresis* (Fig. 2). An integration of exploratory data analysis, time-series analysis, and linear or non-linear modeling (see Materials and Methods) provide evidence for assigning each case to a class.

The distinction between linear tracking and threshold responses is whether: the distribution of the biological response variable is unimodal or weakly bimodal (Fig. 2B); the variance in the biological response is constant or only increases slightly as the environment changes or a trigger occurs (Fig. 2C); and the relationship between the environmental driver and the biological response is linear or nonlinear (Fig. 2D). Both linear tracking and threshold responses can be reversed; as the driver returns to its initial (pre-change) value, environmental conditions and biological response variables often track them with at most short time-lags.

In contrast, hysteretic responses result from persistent environmental changes, changes in feedbacks between drivers and response variables, or long time lags in biological responses to drivers. In such systems, even if the environmental driver returns to earlier values, the biological response may not return to its earlier state, or does so only slowly, at a markedly different magnitude of the driver, or along a different path from the one it took to reach its new state (Fig.

Manuscript in review
Do not cite or distribute

2D). The functional form of the relationship between environmental driver(s) and biological response(s) typically differs before and after a state change.

Results from case studies

A Pelagic Ocean Ecosystem: The California Current System

Data collected within the California Current System (CCS) provide an example of abrupt transitions with a linear tracking mechanism. The CCS includes a major coastal upwelling biome that extends from British Columbia to Baja California. A variety of directional changes in the ocean environment (including rising sea level, oceanic warming, increased density stratification, decreased transparency, acidification, and changes in hypoxia) may be affecting planktonic populations and the pelagic food web. There are also important sources of interannual (*e.g.*, El Niño-Southern Oscillation [ENSO]) and decadal (*e.g.*, Pacific Decadal Oscillation [PDO]) (45) variability in this ecosystem. Long-term variations in abundance of the euphausiid (krill), *Nyctiphanes simplex*, are correlated with the PDO (46) and time series of *N. simplex* abundance display abrupt shifts from one persistent state to another, which may imply hysteresis (Fig. 2) and/or a positive feedback mechanism (47). We assessed the evidence for alternative states in the krill population in the southern sector where temperate-subarctic, cool-water zooplankton fauna enter from the north, and subtropical, warm-water fauna, including *N. simplex* (48), enter from the south. This geographic location is therefore likely to be sensitive to changes in large-scale ocean circulation patterns incorporated into the PDO.

The six-decade CalCOFI record revealed that *N. simplex* generally was rare when the PDO was in the negative phase (anomalously cool waters in the NE Pacific). Abrupt changes of the PDO from negative to positive were tracked by increases in *N. simplex* abundance and *vice-*

Manuscript in review
Do not cite or distribute

versa (Figs. 3A, 3B). Strong El Niño (1958-60, 1997-98) and La Niña (1998-99) events had positive and negative influences, respectively, on *N. simplex* abundance that interacted with changes in the PDO to accentuate abrupt changes or interrupt relationships with PDO (SI Text S2).

Although the warm phase between 1977-1998 was a period of consistently high abundance of *N. simplex* relative to the time period before and after, our data indicate that contrary to previous work (e.g., 47) this should not be considered a different ecological "regime" and hysteresis is not indicated. The frequency distribution of abundances were unimodal and, most definitively, the relationship between *N. simplex* abundance (response variable) and the PDO (driver) varied linearly with the variations in the PDO and was identical in both the warm and the cool phases of the PDO. Thus, the California Current System illustrates a case of linear tracking (49), without discrete, definable (or "preferred") system states. Such linear tracking may be common in short-lived organisms (Fig. 4) that can quickly and closely track abrupt changes in drivers.

A Coastal Benthic Ecosystem: The Southern California Rocky Reef

Data from shallow rocky reefs off the coast of Southern California provide evidence of hysteresis due to predation-mediated feedbacks. The reefs can support either a macroalgae-dominated community or one characterized by high densities (>10,000/m^2) of the filter-feeding sea cucumber, *Pachythyone rubra*. Spatially extensive sea cucumber-dominated states can persist for decades and dramatically alter reef food webs (50, 51). The loss of macroalgae leads to a reduction in micro-crustaceans and their associated fish predators (52-54).

Manuscript in review
Do not cite or distribute

Time-series data from nine sites spread along a 5-km stretch of coastline on the north shore of Santa Cruz Island illustrate the mechanisms of abrupt sea cucumber-to-macroalgae transitions (Fig. 3F, also see 51). The frequency distribution of annual sea cucumber abundance data revealed evidence of bimodality (Fig. 3H). The first transition from macroalgae to sea cucumber dominance occurred in the late 1980s and was associated with a series of years in which there were few high wave events during winter storms (Fig. 3G). High waves dislodge sea cucumbers from algal beds (50), but when winter storms are weak, sea cucumbers competitively displace algae by smothering and killing them.

Frequent, strong storms returned after 1995, but the relationship between days of high waves (driver) and sea cucumber abundance (response) disappeared and sea cucumbers continued to dominate the system (Figs. 3I, 3J). Consumption of algal spores by abundant sea cucumbers allowed this species to persist in the face of increased wave disturbance (50). This relationship switched to yet another low cucumber state when predatory sea stars colonized the system in late 2002 (SI Text S3). Thus, this case conforms to a hysteresis model in which stabilizing feedbacks conferred resilience with respect to the environmental driver.

A Polar Marine Ecosystem: The Western Antarctic Peninsula

The Western Antarctic Peninsula (WAP) provides another example of hysteresis due to the effects of multiple, interacting drivers. Since 1950, annual mean air temperature in some regions has increased by 2°C, and winter air temperature has increased by nearly 6°C (55-57) These climatic changes have caused long-term reductions in the regional extent and duration of winter sea-ice (58-60), a proximate driver of directional environmental change in the WAP marine ecosystem (61-63). One important change is poleward shifts in breeding ranges of three closely

Manuscript in review
Do not cite or distribute

related species of *Pygoscelis* penguin: the Adélie (*P. adeliae*), chinstrap (*P. antarctica*), and gentoo (*P. papua*) penguin (62, 64, 65). There is considerable debate regarding the environmental drivers of change in penguin breeding population dynamics (65-67).

Nearly 40 years of data collected from the Palmer Archipelago near Anvers Island, Antarctica (Fig. S2) illustrate abrupt declines in the Adélie penguin breeding population beginning in 1993, and abrupt increases in numbers of breeding chinstrap and gentoo penguins beginning in 2004 (Fig. 3K). Bimodality of annual abundance data was not evident (Fig. 3M), nor did temporal variance (Fig. 3N) illustrate dramatic changes before or during the observed population changes. However, analysis of the relationship between the proximate driver (sea-ice duration) and Adélie penguin breeding population size revealed that prior to the 1993 breakpoint, the abundance of this species was essentially unresponsive to variation in sea-ice duration, however after 1993 these variables were strongly and positively correlated (Fig. 3O), conforming to the hysteresis model. We did not examine driver-response relationships for chinstrap or gentoo penguins because only five data points on yearly numbers of breeding pairs have been obtained since the 2004 breakpoint. Progressive climate warming resulted in an abrupt transition operating through multiple, cascading ecological drivers and feedbacks, including reduced sea-ice duration, changes in terrestrial snowfall accumulation that affect penguin breeding biology, and feedbacks between Adélie population reductions and predator efficiency (SI Text S4).

A Semi-arid Grassland Ecosystem: The Chihuahuan Desert

Data from northern Chihuahuan Desert grasslands provide an example of hysteresis involving a strong trigger and novel feedbacks. These grasslands were dominated historically by black grama grass (*Bouteloua eriopoda*), but during the last 150 years, black grama grasslands have shifted to

Manuscript in review
Do not cite or distribute

shrublands dominated by xerophytic woody plants. Similar shifts from grasslands to shrublands have occurred in semi-arid systems throughout the world (68). Historically, black grama grass persisted through episodic droughts, and shrub cover within black grama grasslands was limited by competition for water, limited shrub seed dispersal, and possibly periodic fire (69). Heavy cattle grazing on black grama grass during drought periods is believed to have initiated the grassland-to-shrubland transition (SI Text S5). It has not been clear, however, how rapidly the initial grassland loss takes place and therefore how best to employ monitoring strategies to prevent it (23).

Time-series data on annual production of black grama grass collected during the mid-1900s from two pastures in the Jornada Experimental Range near Las Cruces, NM, USA, indicate the start of an abrupt transition in 1948. In that year, there was no grass production (Fig. 3P), and this lack of production coincided with the onset of a prolonged drought (Fig. 3Q). Several lines of evidence suggest threshold behavior in this system that conforms to the hysteresis model. First, annual production was bimodal (Fig. 3R), indicating two alternative states. Second, grass production exhibited an increase in temporal variance during the transition (Fig. 3S) associated with a series of alternating dry and wet periods (Fig. 3Q). Third, driver-response regressions show that prior to 1948, black grama production had a positive relationship to growing-season (July-September) precipitation (70). After 1948, however, this relationship weakened and overall production was low regardless of growing-season rainfall (Fig. 3T). The shift in grass production was very abrupt, never attaining previous high values after 1950. A positive feedback between soil erosion and low grass cover appears to have precluded grassland recovery after a return to higher levels of precipitation (SI Text S5).

Manuscript in review
Do not cite or distribute

Discussion

These case studies illustrate that abrupt transitions and state changes not only can be identified, but also can be understood via a suite of general concepts (Fig. 1) and relatively simple methods (SI Text S1). Although the availability of long-running time series of both drivers and responses has been limited (6, 24), long-term data now can be accessed from LTER and related sites (http://ecotrends.info), and many institutions worldwide are investing considerable resources establishing new ecological observation networks (e.g., National Ecological Observatory Network, Global Lake Ecological Observatory Network, Ocean Observatory Initiative, Paleoecological Observatory Network). The sequence of methods used here, including an objective evaluation of abrupt transitions and alternative states, examination of frequency distributions of response variables and leading indicators, and analysis of patterns and mechanisms of driver-response relationships can be applied to many of these datasets.

A common, systematic approach applied across different datasets will advance a general understanding and prediction of abrupt transitions and state changes. Such a common approach is especially important now, as abrupt, often irreversible transitions are forecast to increase as climatic change accelerates (3, 4); a coherent, integrated strategy is needed to manage and mitigate the expected state changes. Our comparative exploration of case studies also suggests some lessons for future analyses of existing data and guidance for new observation and monitoring networks embarking on long-term studies.

*Leading indicators may have limited utility***.** Mathematical modeling (71) and empirical studies conducted in temperate lake ecosystems (6) predict increased variance in the time series of biological responses prior to abrupt transitions. Many systems, however, may show no change or even decreases in variance (5). Our analysis of four different systems, three of which showed

Manuscript in review
Do not cite or distribute

clear hysteretic patterns between drivers and responses, suggest that this leading indicator must be carefully scaled to the time-scale of dynamics in the biological response variable (*e.g.*, organism lifespan; Fig. 4). Short-lived organisms can track abrupt changes in drivers closely. Thus, some transitions, such as those in the California Current krill (Figs. 3A-3E), may appear abrupt until rescaled to the short lifespan of this organism (Fig. 4). In contrast, especially when lifespan matches the dominant time scale of environmental variability (49), other transitions may appear gradual, but actually occur quite abruptly relative to the organism's lifespan (e.g., penguins: Figs 3K-3O; black grama grass: Figs 3P-3T).

To be informative, leading indicators of rising variance require many highly autocorrelated samples collected *within* the lifespan of the sentinel organism of interest. The traditional ecological emphasis on temporal trend as opposed to variance has led researchers to undervalue the importance of regularly sampled time series and fine temporal intervals. Detection of abrupt transitions and state changes require time series without missing values (or ones that can be reasonably modeled). If sampling designs capture weakly- or un-correlated measures of abundance, or if studied organisms are long-lived and transitions occur rapidly (i.e., between samples), measures of temporal variance may not be informative. In such cases, it would be worthwhile to identify faster-changing variables (6) that reflect organismal performance in populations, such as physiological status. However, if transitions are not caused by "slow" variables but instead are caused by abrupt, unpredictable triggers acting within vulnerable systems, variance-based leading indicators may provide only limited information (5). Additional evidence must be sought.

Driver-response relationships are powerful tools. Researchers should hesitate to infer response mechanisms based solely on the presence of threshold patterns in biological response

Manuscript in review
Do not cite or distribute

variables; analysis of driver-response relationships provide stronger tests of such inferences. For example, the linear tracking model (Fig. 2) may appear to have abrupt transitions when biological responses track abrupt changes in drivers, as in the California Current System (Fig. 3A-3E). Such observations have been used to suggest the existence of alternative stable states (47) that is not supported by our analysis (Fig. 3E).

Context is critical. In the four cases that we examined, the historical context and the location in which the study was conducted relative to physical processes occurring at larger spatial scales both had important consequences for the observed dynamics. The location of the CalCOFI and Palmer Station studies relative to biogeographic transition zones, the Jornada Experimental Range study on sandy soils during a period of comparatively high grazing pressure, and the Santa Cruz Island study area relative to the shifting southern range limit of sea-stars each influenced the patterns observed in their respective time-series of biological responses (SI Text S2-S5). Data on the same response variables collected at other locations or times might yield different results or reveal how large-scale forces such as ocean circulation, regional climate, physiography, or soils mediate abrupt transitions (31, 72). As case studies of abrupt transitions accumulate, researchers should ensure that spatial and temporal measurement scales of drivers and response variables are appropriately congruent and to be alert for changes in context when comparing studies.

Multiple lines of evidence can be convincing. Different kinds of state changes were identified by different analyses. Interpretations of state changes were greatly facilitated by consideration of data and observations apart from the driver and response time series. The choice of the "right" driver and the "right" response variable was based on detailed short- and long-term experiments along with ancillary information and anecdotal observations that provided important

Manuscript in review
Do not cite or distribute

clues to the interpretation of time-series data. In spite of the case-specific nature of response mechanisms, we predict that a systematic review of additional cases will reveal a limited set of classes of interactions between drivers, triggers, and responses (cf. Fig. 2). This framework can guide future investigations and promote a data-supported understanding of abrupt transitions (73).

Can we manage state changes? Long-term, multi-faceted datasets can provide retrospective explanations of transitions and state changes for specific cases, but can they provide useful information for pro-active management? In some cases, such as the California Current System, in which krill track the physical environment, intervention is not feasible but forecasting may eventually become so. In others, such as the Antarctic penguins or the semi-arid grasslands, the abruptness of transitions relative to organisms' lifespans (Fig. 4) suggests that management must quickly adjust to changing conditions (*e.g.*, adjust stocking rates in drought periods and establish institutions that can respond rapidly) (74). Alternatively, abrupt transitions can be managed according to the precautionary principle that acknowledges our limited ability to respond rapidly (22). In a changing climate, however, active management may be impossible. When the spatial scale over which environmental drivers act is much larger than the area we can manipulate, we may have to adapt to inevitable change. To make informed choices among these possible responses, ecologists and policymakers must commit to sustaining, renewing, and initiating observational platforms in multiple sentinel sites. The resulting data can, as we have shown, produce useful maps for navigating our changing world.

Manuscript in review
Do not cite or distribute

Materials and Methods

We used a sequence of five steps to identify abrupt transitions and characterize state changes with respect to the classes of mechanisms: i) visualization of temporal patterns in drivers and response variables; ii) locating and statistically testing one or more breakpoints in time-series of response variables; iii) statistical testing of unimodality of frequency distributions of response variables; iv) calculation of temporal variance (a leading indicator of state transitions) of response variables, and v) assessment of relationships between response variables and drivers before and after breakpoints identified in (ii) (details in SI Text S1). Contextual information used to interpret the results was derived from ancillary experimental data, expert knowledge on triggers and response mechanisms, and other natural history information (SI Text S2-S5).

Acknowledgments

Support for this work was provided by NSF LTER awards to the Ecosystems Center of the Marine Biological Laboratory at Woods Hole (08-23101), Harvard University (06-20443), New Mexico State University (06-18210), UC San Diego (04-17616), UC Santa Barbara (06-20276), the University of Wisconsin (08-22700), an NSF contract to the LTER Network Office at the University of New Mexico (08-32652), and the Natural Sciences and Engineering Research Council of Canada (NSERC). The LTER EcoTrends project, the LTER Network Office, and Laurie Chiasson at Harvard Forest supported the data synthesis efforts. The California Current System data were collected in part with the assistance of A. Townsend (Scripps Institution of Oceanography Pelagic Invertebrates Collection) and the late E. Brinton. Collection of the Southern California Rocky Reef data prior to 2000 was supported by NSF awards to RJS and SJH. The Jornada Experimental Range data collection and synthesis was supported by staff of

Manuscript in review
Do not cite or distribute

the USDA Agricultural Research Service. The authors thank Ben Baiser, Audrey Barker-Plotkin, Elizabeth Crone, Elizabeth Farnsworth, David Foster, Brian Hall, Dave Orwig, Sydne Record, Kristina Stinson, and Jack Williams for helpful discussions and comments on early versions of the manuscript.

Manuscript in review
Do not cite or distribute

References

1. Beisner BE, Haydon DT, Cuddington K (2003) Alternative stable states in ecology. *Front Ecol Environ* 1:376-382.

2. Suding KN, Gross KL, Houseman GR (2004) Alternative states and positive feedbacks in restoration ecology. *Trends Ecol Evol* 19:46-53.

3. Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well-being: Desertification Synthesis* World Resources Institute (Washington, DC).

4. Fagre DB, et al. (2009) *CCSP: Thresholds of Climate Change in Ecosystems. A report by the US Climate Change Science Program and the Subcommittee and Global Change Research* U.S. Geological Survey (Reston, VA).

5. Hastings A, Wysham DB (2010) Regime shifts in ecological systems can occur with no warning. *Ecol Lett* 13:464-472.

6. Carpenter SR, et al. (2011) Early warnings of regime shifts: a whole-ecosystem experiment. *Science* 332:1079-1082.

7. Jones HP, Schmitz OJ (2009) Rapid recovery of damaged ecosystems. *PLoS One* 4.

8. Hughes TP (1994) Catastrophes, phase-shifts, and large-scale degradation of a Caribbean coral-reef. *Science* 265:1547-1551.

9. Scheffer M, et al. (2001) Catastrophic shifts in ecosystems. *Nature* 413:591-596.

10. Groffman P, et al. (2006) Ecological thresholds: the key to successful environmental management or an important concept with no practical application? *Ecosystems* 9:1-13.

11. Lindig-Cisneros R, et al. (2003) Wetland restoration thresholds: can a degradation transition be reversed with increased effort? *Ecol Appl* 13:193-205.

12. Briske DD, Fuhlendorf SD, Smeins FE (2006) A unified framework for assessment and application of ecological thresholds. *Rangel Ecol Manag* 59:225-236.

13. Suding KN, Hobbs RJ (2009) Threshold models in restoration and conservation: a developing framework. *Trends Ecol Evol* 24:271-279.

14. Rudnick DL, Davis RE (2003) Red noise and regime shifts. *Deep-Sea Res Part I-Oceanogr Res Pap* 50:691-699.

15. Schroder A, Persson L, De Roos AM (2005) Direct experimental evidence for alternative stable states: a review. *Oikos* 110:3-19.

16. Brown JR, Archer S (1999) Shrub invasion of grassland: recruitment is continuous and not regulated by herbaceous biomass or density. *Ecology* 80:2385-2396.

Manuscript in review
Do not cite or distribute

17. Collie JS, Richardson K, Steele JH (2004) Regime shifts: can ecological theory illuminate the mechanisms? *Prog Oceanogr* 60:281-302.

18. Petraitis PS, Latham RE (1999) The importance of scale in testing the origins of alternative community states. *Ecology* 80:429-442.

19. Bertness MD, et al. (2002) Do alternate stable community states exist in the Gulf of Maine rocky intertidal zone? *Ecology* 83:3434-3448.

20. Carpenter SR, Brock WA (2006) Rising variance: a leading indicator of ecological transition. *Ecol Lett* 9:308-315.

21. Biggs R, Carpenter SR, Brock WA (2009) Spurious certainty: how ignoring measurement error and environmental heterogeneity may contribute to environmental controversies. *Bioscience* 59:65-76.

22. Contamin R, Ellison AM (2009) Indicators of regime shifts in ecological systems: what do we need to know and when do we need to know it? *Ecol Appl* 19:799-816.

23. Bestelmeyer BT (2006) Threshold concepts and their use in rangeland management and restoration: the good, the bad, and the insidious. *Restor Ecol* 14:325-329.

24. Andersen T, et al. (2009) Ecological thresholds and regime shifts: approaches to identification. *Trends Ecol Evol* 24:49-57.

25. Folke C, et al. (2004) Regime shifts, resilience, and biodiversity in ecosystem management. *Annu Rev Ecol Evol Syst* 35:557-581.

26. Nystrom M, Folke C, Moberg F (2000) Coral reef disturbance and resilience in a human-dominated environment. *Trends Ecol Evol* 15:413-417.

27. Breshears DD, et al. (2005) Regional vegetation die-off in response to global-change-type drought. *Proc Natl Acad Sci USA* 102:15144-15148.

28. Holmgren CA, Betancourt JL, Rylander KA (2006) A 36,000-yr vegetation history from the Peloncillo Mountains, southeastern Arizona, USA. *Paleogeogr Paleoclimatol Paleoecol* 240:405-422.

29. Mantua N (2004) Methods for detecting regime shifts in large marine ecosystems: a review with approaches applied to North Pacific data. *Prog Oceanogr* 60:165-182.

30. Daskalov GM, et al. (2007) Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. *Proc Natl Acad Sci USA* 104:10518-10523.

31. Rietkerk M, et al. (2004) Self-organized patchiness and catastrophic shifts in ecosystems. *Science* 305:1926-1929.

Manuscript in review
Do not cite or distribute

32. Bourbeau-Lemieux A, et al. (2011) Predator-driven component Allee effects in a wild ungulate. *Ecol Lett* 14:358-363.

33. Carpenter SR, Ludwig D, Brock WA (1999) Management of eutrophication for lakes subject to potentially irreversible change. *Ecol Appl* 9:751-771.

34. Swift TL, Hannon SJ (2010) Critical thresholds associated with habitat loss: a review of the concepts, evidence, and applications. *Biol Rev* 85:35-53.

35. He F, Hubbell SP (2011) Species-area relationships always overestimate extinction rates from habitat loss. *Nature* 473:368-371.

36. Foley JA, et al. (2003) Regime shifts in the Sahara and Sahel: interactions between ecological and climatic systems in northern Africa. *Ecosystems* 6:524-539.

37. Cook BI, Miller RL, Seager R (2009) Amplification of the North American "Dust Bowl" drought through human-induced land degradation. *Proc Natl Acad Sci USA* 106:4997-5001.

38. Peters DPC, et al. (2004) Cross-scale interactions, nonlinearities, and forecasting catastrophic events. *Proc Natl Acad Sci USA* 101:15130-15135.

39. Choy SL, O'Leary R, Mengersen K (2009) Elicitation by design in ecology: using expert opinion to inform priors for Bayesian statistical models. *Ecology* 90:265-277.

40. Genkai-Kato M, Carpenter SR (2005) Eutrophication due to phosphorus recycling in relation to lake morphometry, temperature, and macrophytes. *Ecology* 86:210-219.

41. Heffernan JB, Sponseller RA, Fisher SG (2008) Consequences of a biogeomorphic regime shift for the hyporheic zone of a Sonoran Desert stream. *Freshw Biol* 53:1954-1968.

42. Bestelmeyer BT, Ward JP, Havstad KM (2006) Soil-geomorphic heterogeneity governs patchy vegetation dynamics at an arid ecotone. *Ecology* 87:963-973.

43. Hughes TP, et al. (1999) Patterns of recruitment and abundance of corals along the Great Barrier Reef. *Nature* 397:59-63.

44. Petraitis PS, et al. (2009) Experimental confirmation of multiple community states in a marine ecosystem. *Oecologia* 161:139-148.

45. Mantua NJ, et al. (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull Amer Meteorol Soc* 78:1069-1079.

46. Brinton E, Townsend A (2003) Decadal variability in abundances of the dominant euphausiid species in southern sectors of the California Current. *Deep-Sea Res Part II-Top Stud Oceanogr* 50:2449-2472.

Manuscript in review
Do not cite or distribute

47. deYoung B, et al. (2008) Regime shifts in marine ecosystems: detection, prediction and management. *Trends Ecol Evol* 23:402-409.

48. Brinton E, et al. (1999) *Euphausiids of the World Ocean* (UNESCO Publishing, Paris).

49. Hsieh CH, Ohman MD (2006) Biological responses to environmental forcing: the linear tracking window hypothesis. *Ecology* 87:1932-1938.

50. Rassweiler A, et al. (2008) Net primary production, growth, and standing crop of *Macrocystis pyrifera* in Southern California. *Ecology* 89:2068.

51. Rassweiler A, Schmitt RJ, Holbrook SJ (2010) Triggers and maintenance of multiple shifts in the state of a natural community. *Oecologia* 164:489-498.

52. Holbrook SJ, Schmitt RJ (1989) Resource overlap, prey dynamics and the strength of competition. *Ecology* 70:1943-1953.

53. Schmitt RJ, Holbrook SJ (1990) Contrasting effects of giant-kelp on dynamics of surfperch populations. *Oecologia* 84:419-429.

54. Schmitt RJ, Holbrook SJ (1990) Populations responses of surfperch released from competition. *Ecology* 71:1653-1665.

55. Vaughan DG, et al. (2003) Recent rapid regional climate warming on the Antarctic peninsula. *Clim Change* 60:243-274.

56. Turner J, et al. (2006) Significant warming of the Antarctic winter troposphere. *Science* 311:1914-1917.

57. Smith RC, Stammerjohn SE, Baker KS (1996) Surface air temperature variations in the Western Antarctic Peninsula. *Foundations for Ecological Research West of the Antarctic Peninsula*, eds Ross RM, Hofmann EE, & Quetin LB (American Geophysical Union, Washington, DC), Antarctic Research Series 70, pp 105-122.

58. Smith RC, Stammerjohn SE (2001) Variations of surface air temperature and sea-ice extent in the western Antarctic Peninsula region. *Ann Glaciol* 33:493-500.

59. Stammerjohn SE, et al. (2008) Trends in Antarctic annual sea ice retreat and advance and their relation to El Nino-Southern Oscillation and Southern Annular Mode variability. *J Geophys Res-Oceans* 113:Article Number C03S90.

60. Stammerjohn SE, et al. (2008) Sea ice in the western Antarctic Peninsula region: Spatio-temporal variability from ecological and climate change perspectives. *Deep-Sea Res Part II-Top Stud Oceanogr* 55:2041-2058.

61. Smith RC, Fraser WR, Stammerjohn SE (2003) Climate variability and ecological response of the marine ecosystem in the western Antarctic Peninsula (WAP) region. *Climate variability and ecosystem response at longterm ecological research sites*, eds

Manuscript in review
Do not cite or distribute

Greenland D, Goodin DG, & Smith RC (Oxford University Press., New York, NY), pp 158–173.

62. Ducklow HW, et al. (2007) Marine pelagic ecosystems: the west Antarctic peninsula. *Philos Trans R Soc B-Biol Sci* 362:67-94.

63. Moline MA, et al. (2008) High latitude changes in ice dynamics and their impact on polar marine ecosystems. *Ann NY Acad Sci* 1134:267-319.

64. Forcada J, et al. (2006) Contrasting population changes in sympatric penguin species in association with climate warming. *Glob Change Biol* 12:411-423.

65. Forcada J, Trathan PN (2009) Penguin responses to climate change in the Southern Ocean. *Glob Change Biol* 15:1618–1630.

66. Patterson DL, Easter-Pilcher AL, Fraser WR (2003) The effects of human activity and environmental variability on long-term changes in Adelie penguin populations at Palmer Station, Antarctica. *Antarctic Biology in a Global Context*, eds Huiskes AHL, Gieskes WWC, Rozema J, Schorno RML, van der Vies SM, & Wolf WJ (Backhuys Publishers, Leiden), pp 301–307.

67. Trivelpiece WZ, et al. (2011) Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *Proc Natl Acad Sci USA* 108:7625-7628.

68. Archer S (1995) Tree-grass dynamics in a prosopis-thornscrub savanna parkland - reconstructing the past and predicting the future. *Ecoscience* 2:83-99.

69. Peters DPC, Gibbens RP (2006) Plant communities in the Jornada Basin: the dynamic landscape. *Structure and Function of a Chihuahuan Desert Ecosystem: The Jornada Basin Long-Term Ecological Research Site*, eds Havstad KM, Huenneke LF, & Schlesinger WH (Oxford University Press, New York, NY), pp 211-231.

70. Nelson EW (1934) *The influence of precipitation and grazing upon black grama grass range. Technical Bulletin* (Washington D.C.).

71. Scheffer M, et al. (2009) Early-warning signals for critical transitions. *Nature* 461:53-59.

72. Williams JW, Blois JL, Shuman BN (2011) Extrinsic and intrinsic forcing of abrupt ecological change: case studies from the late Quaternary. *J Ecol* 99:664-677.

73. Walker B, Meyers JA (2004) Thresholds in ecological and social-ecological systems: a developing database. *Ecol Soc* 9.

74. Meze-Hausken E, Patt A, Fritz S (2009) Reducing climate risk for micro-insurance providers in Africa: a case study of Ethiopia. *Glob Environ Change-Human Policy Dimens* 19:66-73.

Manuscript in review
Do not cite or distribute

Figure legends

Figure 1. A conceptual model of the relationships between the elements of abrupt transitions and analytical approaches used to investigate them.

Figure 2. Three classes of driver-response relationships and analytical indicators of transitions and state changes. The top row (**A**) illustrates time series of driver and response variables in linear tracking, threshold, and hysteretic systems. The second row (**B**) illustrates that the frequency distribution of the observations should shift from unimodal to bimodal when a threshold or hysteretic change occurs. The third row (**C**) illustrates how one leading indicator, the variance of the time series, should differ among the three classes of driver-response relationships. As the transition becomes more abrupt and the post-transition state becomes more distinctive from the pre-transition state, the variance should become more peaked at the transition point. The bottom row (**D**) illustrates changes in the driver-response relationships from linear (in the linear tracking class) to nonlinear (in the threshold class) to hysteretic.

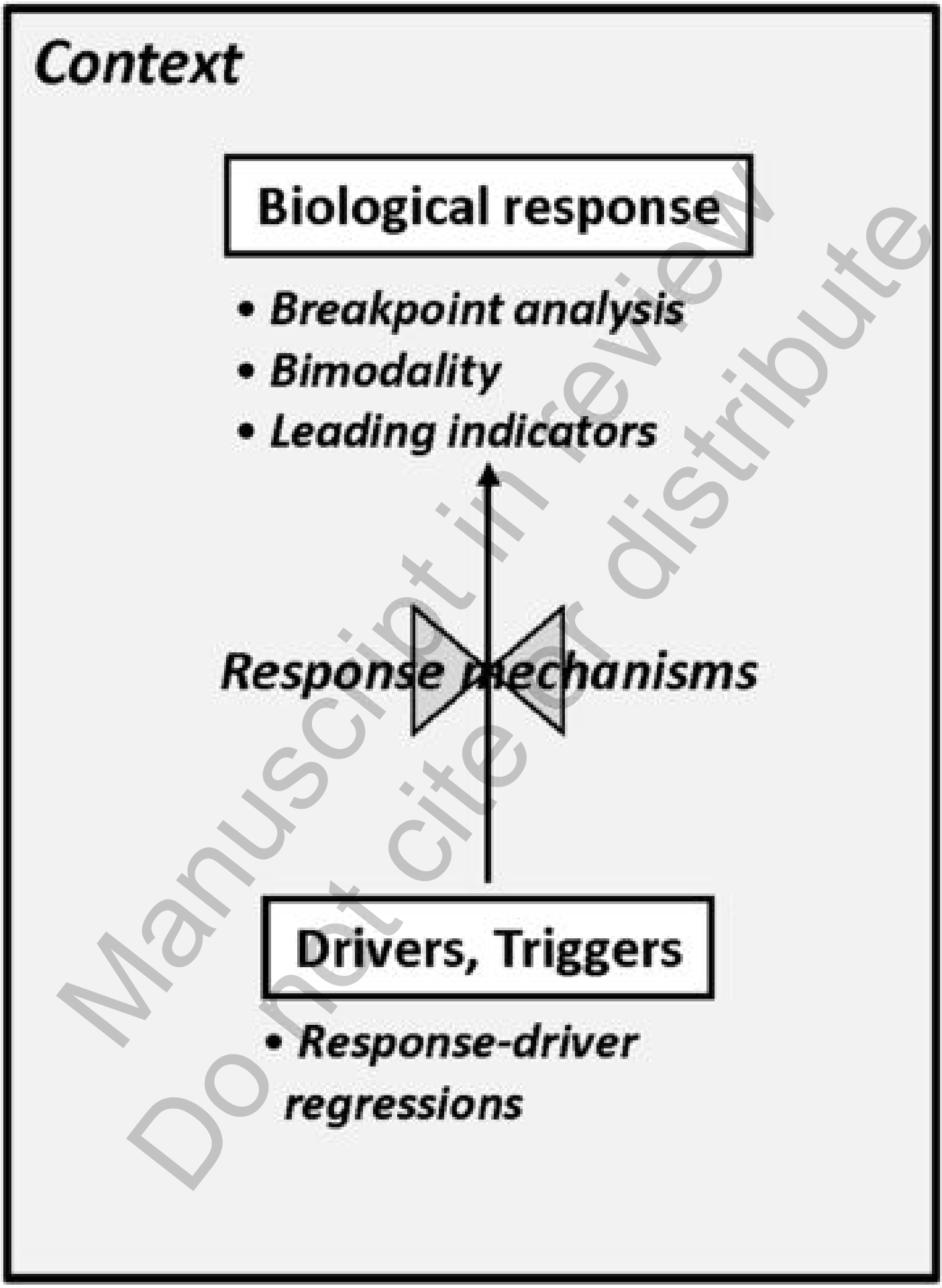
Figure 3. Results of analyses for the California Current System (**A-E**), the Southern California Rocky Reef (**F-J**), the Western Antarctic Peninsula (**K-O**), and the Northern Chihuahuan Desert (**P-T**). In all cases, the biological responses are scaled in standard deviation units (see SI Text S1). In the time series of biological responses (**A, F, K, P**), the observed data are shown as points, the time series (which include modeled values) as grey lines connecting the points, and the locally weighted regression (loess) illustrating the temporal pattern as a solid black line. The three species of penguins in the Western Antarctic Peninsula (**K**) are illustrated in three colors

Manuscript in review
Do not cite or distribute

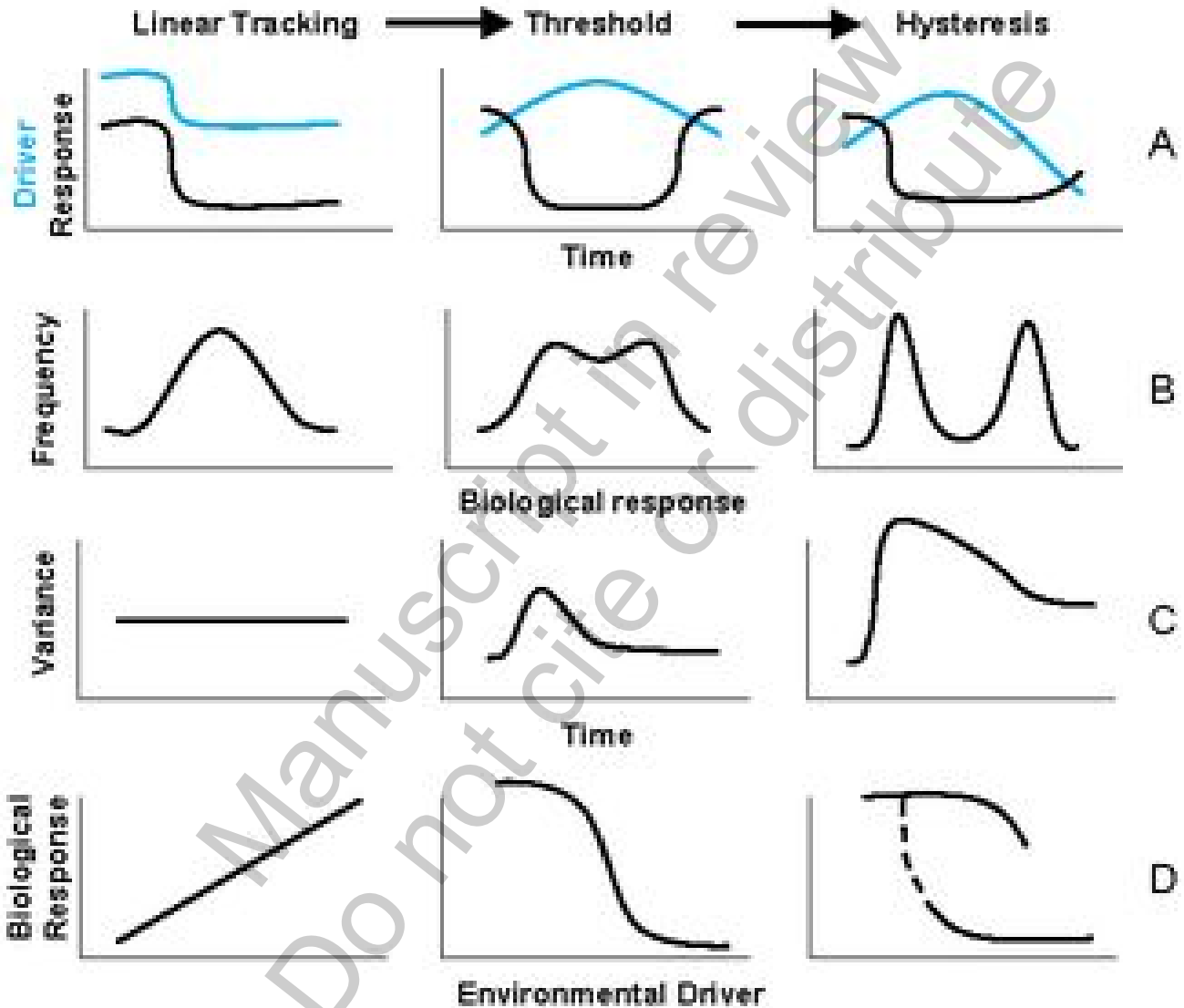
(Adélie penguins in black, chinstrap penguins in orange, gentoo penguins in blue). The two pastures in the Chihuahuan Desert (**P**) are illustrated in black (Pasture 2) and orange (Pasture 9). Breakpoints identified using CUSUM, RSS, and BIC are identified with arrows on the *x*-axis. The potential alternate state begins the year *after* the breakpoint. In the time series of drivers (**B, G, L, Q**), the observed data are shown as points and the time series as grey lines connecting the points. There are no missing values in the time series of drivers. The frequency distributions (**C, H, M, R**) are all equivalently scaled, and all bins are the same width (0.5 SD units). The probability density function of the observations is overlain on the histogram. Similarly, the time series of variance (**D, I, N, S**) are all equivalently scaled, and breakpoints again are identified. Colors in **M** and **N**, and **R** and **S**, indicate different species of penguins or pastures, as in **K** and **P**. Finally, the relationships between drivers and response (**E, J, O. T**) are illustrated for the initial state (solid symbols, black lines) and post-transition state (open symbols, grey lines). For the California Current System (**E**), data from the third state are combined with those from the first state (negative phase of the PDO). For the Southern California Rocky Reef (**J**), only data from the first and second states are shown (see SI Text S3 for additional detail on the third state of this system).

Figure 4. The time series of the biological responses from each case study rescaled to the maximum life span of each organism. Each tick on the *x*-axis indicates one lifespan (value in parentheses).

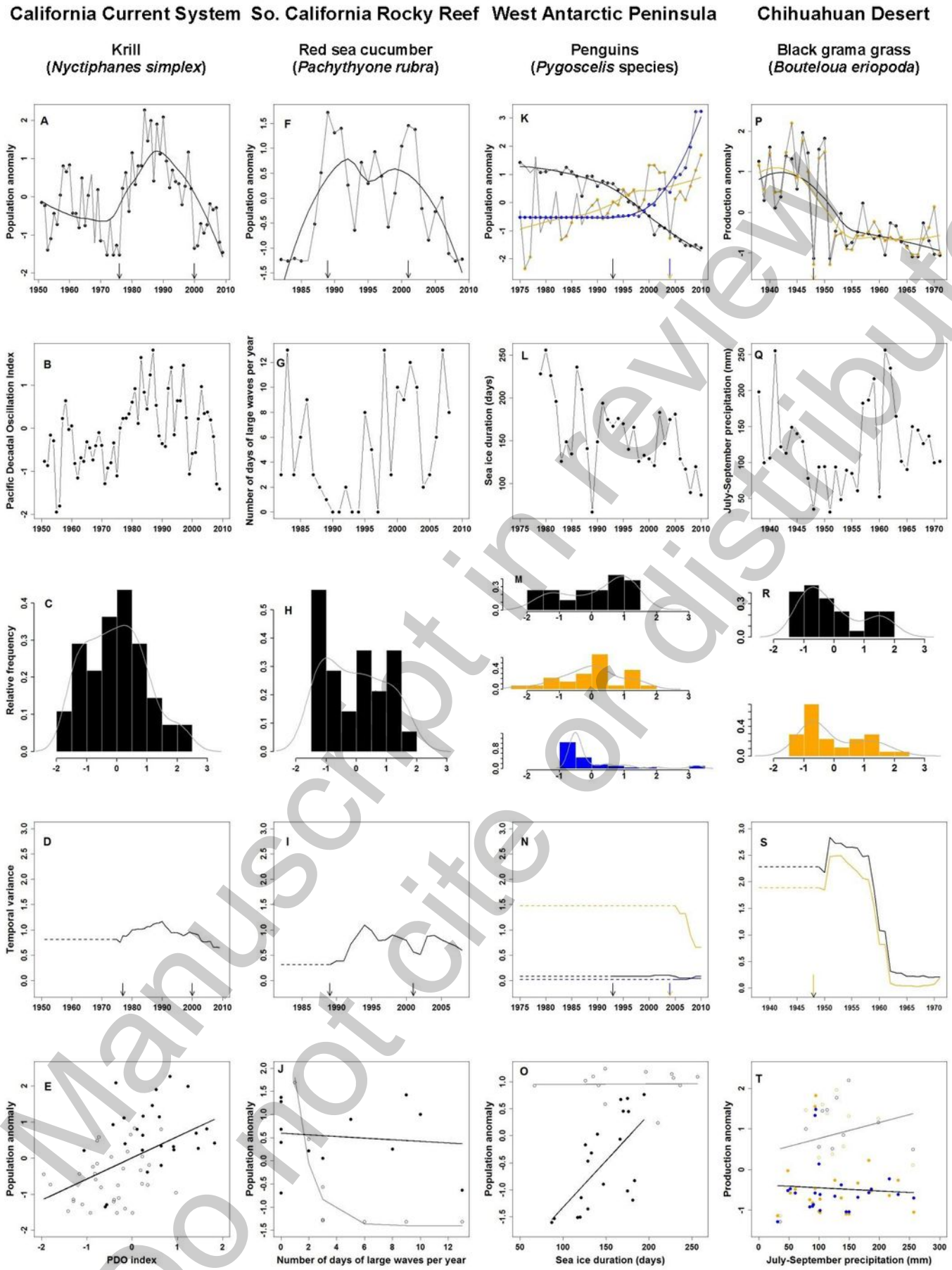
Manuscript in review
Do not cite or distribute



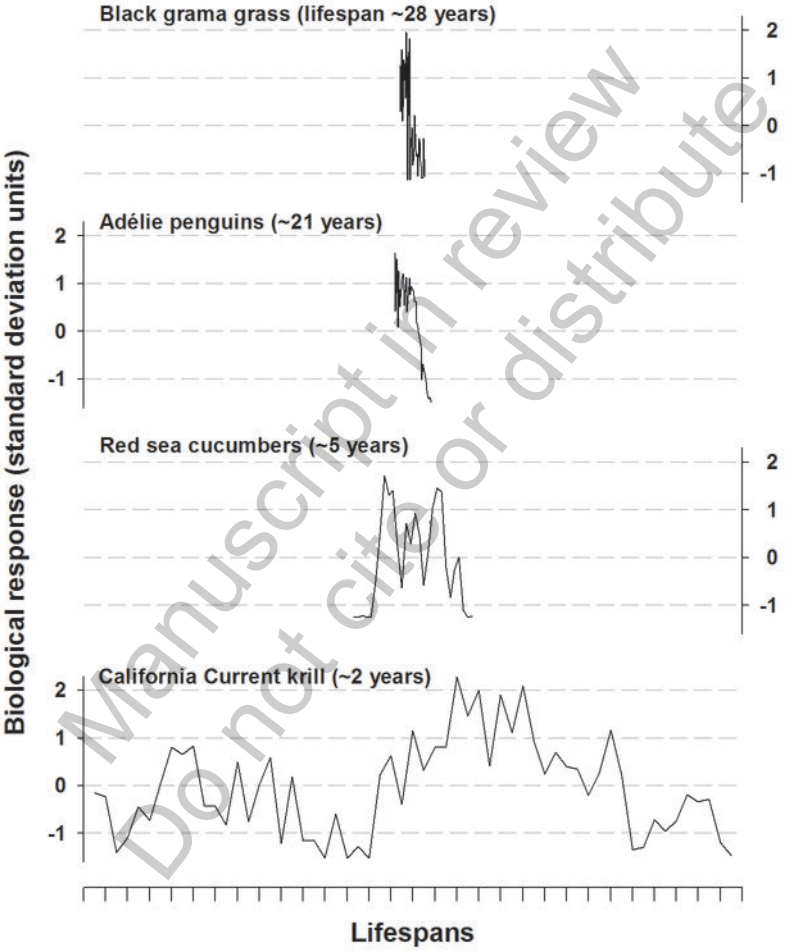
Manuscript in review
Do not cite or distribute



Manuscript in review
Do not cite or distribute



Manuscript in review
Do not cite or distribute



Manuscript in review
Do not cite or distribute

Supporting Information

SI Text S1: Common analytical methods

We applied five sequential steps to identify abrupt transitions and characterize state changes in four ecological systems: i) visualization of temporal patterns in drivers and response variables; ii) locating and testing breakpoints in time series of response variables; iii) visual inspection of frequency distributions of response variables; iv) calculation of temporal variance (a leading indicator of state transitions) of response variables, and v) assessment of relationships between response variables and drivers before and after breakpoints identified in (ii). Datasets and associated metadata are archived on, and publicly available from, the Harvard Forest Data Archive (http://harvardforest.fas.harvard.edu/data/archive.html), dataset HF170. All data manipulation and statistical analyses were performed using base and user-contributed functions in the R-language environment (1), as detailed below.

Prior to any analyses, observations of response variables were standardized: $z_i = \frac{(x_i - \bar{x})}{\mathrm{sd}(x)}$. By working in standard-deviation units, data and analyses were comparable across the studies. The response and driver variables were unique to each of the four case studies (Figure 3) and time series ranged from 28 to 59 years long. The time series of the responses in each case study included missing data, so modeled values were used in place of missing values. Modeled values were generated from a normal distribution with the mean and variance equal to the running mean and variance, respectively, of the standardized measured values bracketing the missing value(s). For example, in a time series running from 1970 – 2010, if observations were missing for 1975 – 1978 and 1980, the modeled values would be sampled from $N(\mathrm{mean}[z_{1974}, z_{1979}, z_{1981}], \mathrm{SD}[z_{1974}, z_{1979}, z_{1981}])$. Below, we use $\{z_i\}$ to refer to the time series that includes both observed and modeled response variables in standard deviation units.

Manuscript in review
Do not cite or distribute

Temporal patterns in responses were visualized by fitting a locally weighted scatterplot smoother (LOESS) (2) to $\{z_i\}$. The smoothed curve was fit using the *loess* function in the R *stats* library. Default settings were used: a weighted least-squares fit to a fraction of the points in a moving window that spanned ¾ of the points. The weighting function for each point was proportional to the cube of the distance to each point in the moving window. The curve is fit using a low-degree polynomial to a subset of the data using a weighted least squares method (2) (Cleveland and Devlin 1988).

Breakpoints in $\{z_i\}$ were identified using the *strucchange* package (3). First, the time series was detrended by differencing using the *diff* function in the R *base* library. A detrended time series of standardized observations has slope equal to zero, and if there is no breakpoint in the time series, the intercept also would be equal to zero. Breakpoints are years after which the intercept of the detrended time series changes significantly, and detection of one or more breakpoints would suggest that an abrupt transition may have occurred. A combination of three approaches was used to detect breakpoints and to determine the number of breakpoints in the $\{z_i\}$ for each case study. First, a cumulative sum (CUSUM) plot summarized the cumulative sums of differences between each value and the overall mean. A breakpoint was indicated by a sudden change in direction of the CUSUM plot. Because CUSUM plots are "jagged" and can indicate many directional changes, residual sums of squares (RSS) and the Bayesian Information Criterion (BIC) were used to identify the number of breakpoints that significantly improved the fit of the CUSUM model (3). Finally, we examined the statistical significance of each breakpoint identified from RSS and BIC using an F statistic (based on the Chow test statistic) (3). CUSUM, RSS, and BIC plots all indicated either one or two breakpoints in each of the case studies.

Manuscript in review
Do not cite or distribute

Because changes in response variables exceeded two standard-deviation units only in the case of the gentoo penguins, however, F-statistics were significant only at the $\alpha = 0.1$ level.

Histograms and density smoothers of $\{z_i\}$ were plotted to determine if the frequency distribution was unimodal or bimodal. Departures from unimodality were tested using Hartigan's dip test (4) as implemented in the *dip* function in the R *diptest* library. This test is very conservative – the distribution of the test statistic is based on asymptotic and empirical samples relative to a uniform distribution. A table of quantiles (*P*-values) is provided in the file qDiptab in the R *diptest* library. The power of the test (for $\alpha = 0.05$) is 80% when sample size = 50; since our sample sizes (excluding missing values) ranged from 27-55, we accepted *P*-values ≤ 0.10 as statistically significant evidence for departure from unimodality. The linear tracking model should yield a unimodal distribution of $\{z_i\}$, whereas a threshold or hysteresis model should yield a bimodal distribution of $\{z_i\}$ (see Fig. 2).

Changes in temporal variance of $\{z_i\}$ were assessed because abrupt increases in variance have been demonstrated to be a leading indicator of abrupt transitions in the hysteresis model (5). We calculated changes in temporal variance of the differenced time series using the *rollapply* function in the R *zoo* library. The window size used for each case study was the shortest time-interval between breakpoints in the time series; window sizes ranged from seven to 30 years. The temporal variance for years prior to the onset of our moving window could not be calculated (as the number of points available was less than the window size); we indicate those years with dotted lines in Figs 3D, 3I, 3N, and 3S. We note that using temporal variance as a leading indicator works best for very long time series (>> 50 observations) of temporally autocorrelated data sampled at high frequency. Real ecological data, such as those analyzed here, are of relatively short duration (< 50 observations), and ecologists generally attempt to minimize

Manuscript in review
Do not cite or distribute

temporal autocorrelation by sampling less frequently. If the threshold response occurs *within* the lifespan of the organism, but sampling frequency is on the same time-scale as organism lifespan or generation time (*cf.* Fig. 4), a state change or threshold response may not be detected. Finally, if observation errors are relatively large or if multiple linear and non-linear processes interact and mute the response variables, changes in variance may not be detected even though state changes have occurred (6-8).

Finally, relationships between response and driver variables were examined for the data overall and for data partitioned into before and after breakpoints. For the California Current System data, the data were partitioned into sets when the PDO was either negative (before the first breakpoint and after the second breakpoint) or positive (in between the two breakpoints). For the Southern California Rocky Reef data, we only examined the data before the first breakpoint and after the first, but before the second, breakpoint (only three values for the driver variable were available after the second breakpoint). For the Western Antarctic Peninsula data, we only examined the data for Adélie penguins, because there were too few data for chinstrap or gentoo penguins after their 2004 breakpoints. We used linear (*lm*) and non-linear (*nls*) regression in the R *stats* library to model the relationships between responses and drivers. The expectation for the linear tracking model was that there would be similar response-driver relationships before and after the breakpoint(s), and the expectation for the hysteresis model was that there would be different response-driver relationships before and after the breakpoint(s). For example, a different slope and intercept for a linear regression fitting response-driver relationships or a non-linear *versus* linear fit for data and after the identified breakpoint would support the hysteresis model (9, 10).

Manuscript in review
Do not cite or distribute

SI Text S2: Detail on the California Current System case study

To assess the likely mechanism underlying the relationship between variations in the California Current euphausiid (krill) *Nyctiphanes simplex* and the Pacific Decadal Oscillation (PDO) first shown by (11) and re-examined in this paper (Figs. 3A-E), we analyzed the life-history structure of *N. simplex* from 1951 to 2009. Zooplankton were sampled in the upper 210 m or 140 m of the water column using 0.5-mm mesh plankton nets (12) and analyzed by E. Brinton. The stations used in the analysis were from Southern California reported in (13): the California Cooperative Oceanic Fisheries Investigations (CalCOFI) lines 80 through 93, from shore to station 70, springtime cruises, and night-time samples only. This station pattern differs slightly from that used by (11). Annual averages of the Pacific Decadal Oscillation (14) were obtained from the monthly values posted at: http://jisao.washington.edu/pdo/ PDO.latest.

Counts of krill during these 48 years were available for four life-history stages: calyptopis, furcilia, juveniles, and adults. The proportional composition of each stage (Fig. S1) was used to differentiate between two primary means by which changes in the physical environment, as represented by the PDO, might have influenced euphausiid abundance: altered advection of organisms into or out of the study region, and altered in situ changes in water column conditions (*e.g.*, temperature, food, predators) that can affect population growth of *N. simplex*.

The primary breeding center of *N. simplex* is located off Baja California (15), to the south of our study site. Abrupt increases in advection of organisms into our region from the south, reflecting individuals introduced from a population showing regular recruitment in a favorable habitat, would have rapidly increased the proportion of younger individuals (calyptopis larvae) in the population. Conversely, if conditions changed favorably in situ, without corresponding

Manuscript in review
Do not cite or distribute

changes in advection, the contribution of calyptopis larvae would have increased more gradually over time. Finally, if in situ conditions for *N. simplex* deteriorated without a corresponding change in advection, there should have been a decline in relative abundance of larval stages due to reduced egg production by adults.

Inspection of Fig. S1 relative to the two abrupt transitions identified in the population time series (Fig. 3A) suggested that altered advection was the more plausible hypothesis. The 1976-77 abrupt increase in total abundance of *N. simplex* was accompanied by a simultaneous increase in the proportion of larvae, without a temporally lagged response. The explanatory power of the PDO for the temporal variability in *N. simplex* is corroborated by modeling variations in *N. simplex* as an autoregressive (AR-1) process related only to present and one previous state of the PDO, which shows excellent agreement with observations (Di Lorenzo and Ohman, unpubl. data).

Furthermore, the rapid decline in total abundance in 1999-2000 was not accompanied by a gradual diminution in contribution by larvae. Rather, the proportion of larvae remained roughly constant, although production was intermittent. Hence, we conclude that the predominant mechanism underlying rapid changes in the euphausiid-PDO time series was the introduction or flushing out of individuals through altered transport. Once introduced into the study site, *N. simplex* were able to reproduce and survive for extended periods of time because of more favorable conditions in situ, but the rapid increases/decreases in abundance were initiated by altered advection. Further support for this interpretation comes from observations of responses by *N. simplex* to major El Niño events. These events typically have resulted only in transient increases in abundance of *N. simplex* (Figs. 3A, 3B, see also 11) initiated by transport from the south. The unusual El Niño of 2009-2010 was not accompanied by changes in *N. simplex*

Manuscript in review
Do not cite or distribute

abundance because this particular event propagated through atmospheric teleconnections rather than through altered ocean advection (16).

SI Text S3: Detail on the Southern California Rocky Reef case study

We used data on abundance of red sea cucumbers (*Pachythyone rubra)* from nine sites on the north shore of Santa Cruz Island, CA. Sites were situated along a 5 km stretch of coastline (centered on 34.05°N, 119.737°W), with six sites established in 1982 and three more added in 1989 (for a complete description of the sites see 17, 18). Sampling was usually annual between September and November; in some instances not all sites were sampled every year. Sites were similar in depth, slope, exposure and initial benthic community structure. At each site there were two fixed 40 m transects, one each along the 6-m and 9-m isobath. The percent cover of *P. rubra*, understory macroalgae (mainly species in the genera *Eisenia*, *Laurencia*, *Gelidium*, *Rhodymenia*, *Codium* and *Corallina*), sea urchins, and *Macrocystis pyrifera* were estimated using point-contact methods (eight randomly located points per meter per transect). The sea-star *Pycnopodia helianthoides* was counted in a 2-m wide swath centered on each transect. Abundance of *P. rubra* was estimated as the average percent cover across all transects sampled in each year. Similarly, abundance of *P. helianthoides* was estimated as the mean density across all transects sampled in each year.

Data on wave heights were taken from buoys operated by the National Oceanic and Atmospheric Administration (www.ndbc.noaa.gov). Because no single buoy operated without interruption between 1982 and 2008, data from three buoys were combined. The East Santa Barbara buoy (No. 46053) is located nearest to the sites where organismal cover and abundance data were collected (23 km NNW of the study sites) and, therefore, wave heights recorded at this

Manuscript in review
Do not cite or distribute

buoy were used when available. On days when data were not available from the East Santa Barbara buoy, data from the Point Arguello and Santa Maria buoys (Nos. 46023 and 46011, ~135 km NW of the monitoring sites) were used to estimate wave height and water temperature in the east channel. Estimates were made based on linear regressions developed from days when all three buoys were operational (19).

To quantify wave intensity, we calculated the number of days each year when maximum significant wave height exceeded 3.25 m. October 1 was the cut-off between years, because biological sampling typically occurred near this date. We chose 3.25 m as our definition of a large storm because previous experiments revealed that the competitive effects of algae on *P. rubra* abundance only occurred when waves exceeded this height (19, 20). We did not include wave data from the summer period of each year (May through September), because summer swells typically come from a southerly direction and the northern shores of the Channel Islands, where our sites are located, are sheltered from these waves.

One challenge in analyzing state changes is that there can be more than two states. In this case study, an exclusive focus on *P. rubra* initially suggested only two states: prior to 1987 the sea cucumbers were nearly absent, from 1987 to 2002 they were very abundant although variable, and after 2002 they returned to their low density state, approaching the densities initially observed in the early 1980s (Figs. 3F, 3J). However, when other invertebrates were considered, it became apparent that the post-2002 low abundance state was not equivalent to the pre-1987 state. Rather, the post-2002 system consists of different species and is maintained by a new mechanism – predation. The third state was initiated by the sudden arrival of the predatory sea star, *P. helianthoides*, a mobile and voracious predator, with well-established potential to decimate echinoderm populations (21, 22). In 2003 when sea stars first became abundant they

Manuscript in review
Do not cite or distribute

were typically large – 35 cm or more across – suggesting that they immigrated into these sites, either from deeper water or from the western end of the island where they have been previously observed (23).

The role of sea stars in the initiation and maintenance of the third state illustrates that an interaction between multiple environmental factors triggered the post-1987 shift into the high *P. rubra* state. The absence of predators alone was not sufficient to have caused this shift; before 1987, *P. rubra* was rare even though predators were absent. Similarly, it is unlikely that low waves could have triggered a shift into the high density state if *P. helianthoides* had been present, because the sea stars exert strong top-down control on *P. rubra* abundance. Our results underscore the complex nature of state changes. Different mechanisms can initiate, maintain, or end a state, and interactions between multiple drivers may be necessary to trigger shifts in states.

SI Text S4: Detail on the Western Antarctic Peninsula case study

Species comprising polar marine systems have evolved life histories associated with the presence or absence of sea-ice, often broadly termed sea-ice obligate or sea-ice intolerant species, respectively (24-26). *Pygoscelis* penguins of the Western Antarctic Peninsula (WAP, Fig. S2) integrate environmental variability over large spatio-temporal scales due to their longevity and spatially extensive foraging (27). Relationships between environmental drivers and penguin population dynamics (Figs. 3K, 3L, 3O) reflect life history integration of this variability, and the abundance and distribution of these species provided some of the earliest evidence of rapid climate-induced change in the WAP (26, 28-34). Physical oceanographic processes occurring along the WAP are important proximate drivers of changes in regional climatology (25, 35-38). Interactions between climate phases and physical oceanography has resulted in displacement of

Manuscript in review
Do not cite or distribute

the cold, dry polar climate that historically dominated the region by a warm, moist sub-Antarctic system characteristic of the northern WAP and Scotia Arc (25).

Penguin population data in this case study span nearly four decades, a period during which sea-ice extent decreased by 50% and sea-ice duration decreased by 85 days (39, 40). Number of breeding pairs of *Pygoscelis* penguins has been estimated annually since the mid-1970's from surveys of nesting individuals on seven islands within 15 km of Palmer Station, a US scientific research station located on Anvers Island (Fig. S2). Most of the data used in these analyses were based on numbers obtained immediately following peak clutch completion (November-December). In the few years where this peak was missed due to weather and sea-ice conditions hindering island access, the next survey conducted closest to this period was used. During 1980, 1984, 1985 and 1988, regional totals were estimated from partial surveys *(i.e.,* data from islands not surveyed were estimated based on percent increases or decreases on adjacent islands that were surveyed). Analyses to examine relationships between sea-ice duration and Adélie penguin population response were lagged by four years to account for delayed reproductive maturity of these species (41), however, results were qualitatively similar for lags equal to zero and five. Following (40), annual sea-ice duration was based on the number of days that elapsed between the first day of advance and the first day of retreat for the Palmer LTER study region near Anvers Island (Figure S2); an "ice year" begins in mid-February of year y and ended in mid-February of year $y+1$.

Since 1975, the breeding population of the true Antarctic, sea-ice obligate, Adélie penguin (41) along the Palmer Archipelago has declined by 85% (Fig. 3K). The breakpoint in Adélie population dynamics occurred in 1993 (Fig. 3K); this response is temporally consistent, given the species lag in reproductive maturity, with the poorest sea-ice conditions evident in the

Manuscript in review
Do not cite or distribute

remote sensing record (40, 42) and the lowest abundance of Antarctic krill (*Euphausia superba*) in the contemporary WAP record (42) that occurred in 1990. Krill is the current dominant prey not only of Adélie penguins along the Palmer Archipelago, but also of sub-Antarctic, sea-ice-intolerant chinstrap and gentoo penguins (cf. 28, 33, 42, 43) species whose breeding populations increased dramatically beginning in 2004. Although it has been hypothesized that krill abundance is a primary driver of the population dynamics of all three *Pygoscelis* species (29, 33), their contrasting population dynamics along the Palmer Archipelago do not support this general hypothesis. For example, chinstrap and gentoo penguin established local founder colonies in 1975 and 1993, respectively (Fig. 3K). Although several lines of evidence suggest that krill has important nutritional impacts on reproduction and survival of these penguins, these impacts, both positive and negative, are ultimately mediated by species-specific life history affinities to sea-ice (25, 28, 29).

An additional key environmental driver in this system appears to be increased snowfall due to escalating oceanic venting of moisture resulting from reduced winter sea-ice conditions (44-47). This increased snowfall affects penguin demography via two response mechanisms. First, heavy spring snow eventually floods nests and drowns chicks (46, 47). Adélie penguins are particularly vulnerable to flooding because their breeding phenology is highly synchronized, and they initiate egg production earlier than the other *Pygoscelis* species, when snow accumulations peak (43, 44). In contrast, gentoo penguins have a much more plastic breeding phenology, and along with chinstraps, typically breed 3-4 weeks later than Adélie penguins (25, 43). Second, brown skuas (*Catharacta lonnbergi*), territorial avian predators, prey on penguin eggs and chicks. As the size of Adélie colonies declines within skua territories due to snowfall, penguins become progressively more vulnerable to skua depredation. Once colonies have decreased to ~50

Manuscript in review
Do not cite or distribute

breeding pairs, skuas appear to locally extirpate these colonies by annually consuming all penguin eggs and chicks (46, 47). As with the sea cucumbers and sea stars, different mechanisms can initiate, maintain, or end penguin population states.

SI Text S5: Detail on the Chihuahuan Desert case study

"*December closed a year which in many respects was the most disastrous in Jornada history. With a total rainfall of less than four inches* [100 mm] *for the whole year, practically no current forage was produced, either of perennial grasses or weeds. It was so dry in fact, that the hardy perennial shrubs such as creosotebush and tarbush did not even leaf out. The strong southwesterly winds of December have already told a partial tale of the damage done, the drought caused deterioration of the range. After two such windstorms in the month, the sand lies drifted and in windrows everywhere. The roads are blown level full, making it difficult in places to trace their course. Any place subjected in the past to extra trampling such as fence corners and also along fencelines, is now scoured clean down to the sub-soil. The top soil gouged out in these spots has been deposited on adjacent grassed range, covering large areas. The wind erosion has been double acting in its destructive effect, blowing out or cutting down grass plants in one place and covering them completely in another nearby. It is certainly heartbreaking to see what was recently good black grama range subjected to such treatment after all the years of protective effort.*"

Fred Ares, Superintendent, Jornada Monthly Report, December 1951

Manuscript in review
Do not cite or distribute

This case pertains to the sandy soils (typic aridic, thermic, coarse-loamy Calcids, Cambids, and Argids) of southern New Mexico, west Texas (USA) and northern Chihuahua states (Mexico), where mean annual precipitation is ~250-350 mm. In these areas, state changes from grasslands to shrublands are among the best recognized of terrestrial transitions (9), but there is considerable debate about their underlying causes and timing. A combination of overgrazing and drought is thought to have caused the transition by shifting the interaction of competition and physical processes in favor of shrubland (i.e., the so-called teeter-totter model of 48). This simple model belies a more complex, multi-staged process that we have recently revealed by analyzing historical and long-term data. This evolving "multi-stage model" breaks up the grassland-shrubland transition into a series of stages, including: loss of dominant grass cover in discrete areas (stage I); invasion or expansion of shrubs within low-grass cover conditions (stage II); and lateral expansion of soil erosion, grassland loss, and expansion of shrub populations (stage III) (49, 50).

Black grama grass (*Bouteloua eriopoda*) initially is the dominant plant and ground cover (> 60%), with very few or no shrubs. It persists in the face of periodic droughts, grows and sets seed reliably, and stabilizes surface soil horizons, and may competitively exclude shrubs (51). In contrast, other perennial grass species have lower canopy cover, die out during droughts, and coexist with shrubs (52-55).

Data for this case study were obtained from annual reports archived between 1938 and 1972 at the Jornada Experimental Range. Production of black grama grass (lbs/acre) was extracted from tables in these reports for pastures 2 and 9, which were dominated by this species. Estimates were based on an annually varying number of 15-m long × 10-cm wide transects. Transects were added until the standard error of the estimate was within 10% of mean production

Manuscript in review
Do not cite or distribute

value. On each transect, 100 plants were measured and the height of grazed and ungrazed tillers was recorded. Standing crop of different perennial grass species was estimated by clipping all aboveground grass parts, air-drying them, and weighing them (Jornada Forage Crop Report, 1942, Jornada archives). Areas of each pasture that were not dominated by black grama grass (due to variation in soils) were excluded from sampling. A utilization scale (56) was used to estimate the percent of grazing use for each species, which was averaged over hundreds of plants (Fig. S3). Utilization values equaled the percentage of the recommended biomass removed (35% at that time), and were determined from a "large number of transects" randomly placed throughout each pasture in each year; values over 100% (*i.e.*, more than 100% of the 35% recommended use) indicated overgrazing. Precipitation data were from the West Well rain gauge of the USDA Rain Gauge Network (http://usda-ars.nmsu.edu/data_long-term-datasets.html), which lay at the southwest and northwest corners of pastures 2 and 9, respectively. We paired growth year black grama grass production (measured in fall) with the monsoonal rainfall totals (July-September) of that same year. Known limitations of the data include: 1) a lack of precise spatial relationships between production, patchy rainfall, and pasture utilization; and 2) complex relationships between intra- and interannual rainfall and plant production that are not reflected in the data (57, 58).

The state change data reflect the loss of black grama grass cover in discrete areas (*i.e.*, stage I of the "multi-stage model"). The observed state change was initiated by severe drought years occurring during a period with intermittently high levels of utilization (cattle grazing; Fig. S3). Years of very low summer (July-September) rainfall led to years of relatively low black grama production (Figs. 3P, 3Q, 3T). The failure to reduce livestock numbers during those years led to overgrazing, and successive years of overgrazing (measured as high utilization values)

Manuscript in review
Do not cite or distribute

were followed by years of reduced black grama grass production (Fig. S3). That dry, extremely windy conditions occurring in low grass cover conditions could initiate extensive, severe soil erosion and subsequent collapse of black grama grassland became widely appreciated in the early 1950s (see also (59)). These data, however, reveal how rapidly (over 2 years) these effects can lead to persistent reductions in black grama.

Manuscript in review
Do not cite or distribute

References

1. R Development Core Team (2011) http://www.r-project.org/.

2. Cleveland WS, Devlin SJ (1988) Locally weighted regression - an approach to regression-analysis by local fitting. *J Am Stat Assoc* 83:596-610.

3. Zeileis A, et al. (2002) strucchange: An R package for testing for structural change in linear regression models. *J Stat Softw* 7:1-38.

4. Hartigan JA, Hartigan PM (1985) The dip test of unimodality. *Ann Stat* 13:70-84.

5. Carpenter SR, Brock WA (2006) Rising variance: a leading indicator of ecological transition. *Ecol Lett* 9:308-315.

6. Scheffer M, et al. (2009) Early-warning signals for critical transitions. *Nature* 461:53-59.

7. Brock WA, Carpenter SR (2010) Interacting regime shifts in ecosystems: implication for early warnings. *Ecol Monogr* 80:353-367.

8. Carpenter SR, et al. (2011) Early warnings of regime shifts: a whole-ecosystem experiment. *Science* 332:1079-1082.

9. Scheffer M, Carpenter SR (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends Ecol Evol* 18:648-656.

10. Bai YF, et al. (2010) Tradeoffs and thresholds in the effects of nitrogen addition on biodiversity and ecosystem functioning: evidence from inner Mongolia Grasslands. *Glob Change Biol* 16:358-372.

11. Brinton E, Townsend A (2003) Decadal variability in abundances of the dominant euphausiid species in southern sectors of the California Current. *Deep-Sea Res Part II-Top Stud Oceanogr* 50:2449-2472.

12. Ohman MD, Smith PE (1995) *A comparison of zooplankton sampling methods in the CalCOFI time series* pp 153-158.

13. Lavaniegos BE, Ohman MD (2007) Coherence of long-term variations of zooplankton in two sectors of the California Current System. *Prog Oceanogr* 75:42-69.

14. Mantua NJ, et al. (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull Amer Meteorol Soc* 78:1069-1079.

15. Brinton E, et al. (1999) *Euphausiids of the World Ocean* (UNESCO Publishing, Paris).

16. Todd RE, et al. (2011) Underwater gliders reveal rapid arrival of El Nino effects off California's coast. *Geophys Res Lett* 38.

17. Holbrook SJ, Schmitt RJ (1989) Resource overlap, prey dynamics and the strength of competition. *Ecology* 70:1943-1953.

Manuscript in review
Do not cite or distribute

18. Schmitt RJ, Holbrook SJ (1986) Seasonally fluctuating resources and temporal variability of interspecific competition. *Oecologia* 69:1-11.

19. Rassweiler A, et al. (2008) Net primary production, growth, and standing crop of *Macrocystis pyrifera* in Southern California. *Ecology* 89:2068.

20. Rassweiler A, Schmitt RJ, Holbrook SJ (2010) Triggers and maintenance of multiple shifts in the state of a natural community. *Oecologia* 164:489-498.

21. Mauzey KP, Birkelan.C, Dayton PK (1968) Feeding behavior of asteroids and escape responses of their prey in Puget Sound region. *Ecology* 49:603-&.

22. Pearse JS, Hines AH (1987) Long-term population-dynamics of sea-urchins in a central California kelp forest - rare recruitment and rapid decline. *Mar Ecol-Prog Ser* 39:275-283.

23. Eckert GL (2007) Spatial patchiness in the sea cucumber *Pachythyone rubra* in the California Channel Islands. *J Exp Mar Biol Ecol* 348:121-132.

24. Moline MA, et al. (2008) High latitude changes in ice dynamics and their impact on polar marine ecosystems. *Ann N Y Acad Sci* 1134:267-319.

25. Ducklow HW, et al. (2007) Marine pelagic ecosystems: the west Antarctic peninsula. *Philos Trans R Soc B-Biol Sci* 362:67-94.

26. Siniff DB, et al. (2008) Projecting the effects of environmental change on Antarctic seals. *Antarct Sci* 20:425-435.

27. Fraser WR, Trivelpiece WZ (1996) Factors controlling the distribution of seabirds: winter-summer heterogeneity in the distribution of Adelie penguin populations. *Foundations for ecological research west of the Antarctic Peninsula*, eds Ross RM, Hoffman EE, & Quetin LB (American Geophysical Union, Washington, D.C.), 70, pp 257-272.

28. Fraser WR, et al. (1992) Increases in Antarctic penguin populations - reduced competition with whales or a loss of sea ice due to environmental warming. *Polar Biol* 11:525-531.

29. Forcada J, Trathan PN (2009) Penguin responses to climate change in the Southern Ocean. *Glob Change Biol* 15:1618–1630.

30. Forcada J, et al. (2006) Contrasting population changes in sympatric penguin species in association with climate warming. *Glob Change Biol* 12:411-423.

31. Gorman KB, et al. (2010) A new high-latitude record for the macaroni penguin (*Eudyptes chrysolophus*) at Avian Island, Antarctica. *Polar Biol* 33:1155-1158.

Manuscript in review
Do not cite or distribute

32. Trathan PN, Fretwell PT, Stonehouse B (2011) First recorded loss of an emperor penguin colony in the recent period of Antarctic regional warming: implications for other colonies. *PLoS One* 6:e14738.

33. Trivelpiece WZ, et al. (2011) Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *Proc Natl Acad Sci USA* 108:7625-7628.

34. Woehler EJ, et al. (2001) *A Statistical Assessment of the Status and Trends of Antarctic and subAntarctic Seabirds.* Scientific Committee on Antarctic Research (Cambridge).

35. Thompson DWJ, Solomon S (2002) Interpretation of recent Southern Hemisphere climate change. *Science* 296:895-899.

36. Marshall GJ, et al. (2004) Causes of exceptional atmospheric circulation changes in the Southern Hemisphere. *Geophys Res Lett* 31:L14205.

37. Martinson DG, et al. (2008) Western Antarctic Peninsula physical oceanography and spatio-temporal variability. *Deep-Sea Res Part II-Top Stud Oceanogr* 55:1964-1987.

38. Meredith MP, et al. (2008) On the interannual variability of ocean temperatures around South Georgia, Southern Ocean: Forcing by El Nino/Southern Oscillation and the Southern Annular Mode. *Deep-Sea Res Part II-Top Stud Oceanogr* 55:2007-2022.

39. Smith RC, Fraser WR, Stammerjohn SE (2003) Climate variability and ecological response of the marine ecosystem in the western Antarctic Peninsula (WAP) region. *Climate variability and ecosystem response at longterm ecological research sites*, eds Greenland D, Goodin DG, & Smith RC (Oxford University Press., New York, NY), pp 158–173.

40. Stammerjohn SE, et al. (2008) Trends in Antarctic annual sea ice retreat and advance and their relation to El Nino-Southern Oscillation and Southern Annular Mode variability. *J Geophys Res-Oceans* 113:Article Number C03S90.

41. Ainley DG (2002) *The Adélie Penguin: Bellwether of Climate Change* (Columbia University Press, New York) p 310.

42. Fraser WR, Hofmann EE (2003) A predator's perspective on causal links between climate change, physical forcing and ecosystem response. *Mar Ecol-Prog Ser* 265:1-15.

43. Williams TD (1995) *The penguins: Spheniscidae* (Oxford University Press, New York, NY).

44. Massom RA, et al. (2006) Extreme anomalous atmospheric circulation in the West Antarctic Peninsula region in Austral Spring and Summer 2001/02, and its profound impact on sea ice and biota. *J Clim* 19:3544-3571.

Manuscript in review
Do not cite or distribute

45. Thompson LG, et al. (1994) Climate since AD1510 on Dyer Plateau, Antarctic Penninsula - evidence for recent climate change. *Annals of Glaciology, Vol 20, 1994 - Proceedings of the Fifth International Symposium on Antarctic Glaciology*, Annals of Glaciology, ed Morris EM (Int Glaciological Soc, Cambridge), 20, pp 420-426.

46. Fraser WR, Patterson DL (1997) Human disturbance and long-term changes in Adelie penguin populations: a natural experiment at Palmer Station, Antarctic Peninsula. *Antarctic communities: species, structure and survival, scientific committee for Antarctic research (SCAR), sixth biological symposium*, eds Battaglia B, Valencia J, & Walton DWH (Cambridge University Press, New York, NY), pp 445–452.

47. Patterson DL, Easter-Pilcher AL, Fraser WR (2003) The effects of human activity and environmental variability on long-term changes in Adelie penguin populations at Palmer Station, Antarctica. *Antarctic Biology in a Global Context*, eds Huiskes AHL, Gieskes WWC, Rozema J, Schorno RML, van der Vies SM, & Wolf WJ (Backhuys Publishers, Leiden), pp 301–307.

48. Schlesinger WH, et al. (1990) Biological feedbacks in global desertification. *Science* 247:1043-1048.

49. Peters DPC, et al. (2006) Disentangling complex landscapes: new insights into arid and semiarid system dynamics. *Bioscience* 56:491-501.

50. Bestelmeyer BT, Goolsby DP, Archer SR (2011) Spatial patterns in state-and-transition models: a missing link to land management? *J Appl Ecol* 48:746-757.

51. Herbel CH, Gibbens RP (1996) Post-drought vegetation dynamics on arid rangelands in southern New Mexico. *New Mexico Agricultural Experiment Station Bulletin* 776.

52. Nelson EW (1934) *The influence of precipitation and grazing upon black grama grass range. Technical Bulletin* (Washington D.C.).

53. Herbel CH, Ares FN, Wright RA (1972) Drought effects on a semidesert grassland range. *Ecology* 53:1084-1093.

54. Gibbens RP, Beck RF (1987) Increase in number of dominant plants and dominance classes on a grassland in the northern Chihuahuan Desert. *J Range Manag* 40:136-139.

55. Herrick JE, et al. (2002) Application of soil quality to monitoring and management: Paradigms from rangeland ecology. *Agron J* 94:3-11.

56. Lommasson T, Jensen C (1943) Determining utilization of range grasses by height-weight tables. *J For* 41:589-593.

57. Schwinning S, Sala OE (2004) Hierarchy of responses to resource pulses in semi-arid ecosystems. *Oecologia* 141:211-220.

Manuscript in review
Do not cite or distribute

58. Yahdjian L, Sala OE (2006) Vegetation structure constrains primary production response to water availability in the Patagonian steppe. *Ecology* 87:952-962.

59. Okin GS, Gillette DA, Herrick JE (2006) Multi-scale controls on and consequences of aeolian processes in landscape change in arid and semi-arid environments. *J Arid Environ* 65:253-275.

Manuscript in review
Do not cite or distribute

Figure Legends

Figure S1. Time series of life-history stages (calyptopis, furcilia, juveniles, and adults) of the euphausiid *Nyctiphanes simplex* from the Southern California sector of the California Current System. Illustrated are the proportions each life-history stage of total *N. simplex* springtime abundance, night-time samples only, averaged over the region sampled (M.D. Ohman and E. Brinton, unpubl. data).

Figure S2. The Western Antarctica Peninsula (WAP). Lower left box shows the WAP relative to other regions of the Antarctic. Upper right box shows the Palmer LTER study area near Anvers Island. Data from penguin colonies used in these analyses are located on islands within the Palmer Archipelago that are shaded in yellow. The location of Palmer Station is shaded in gray. Image generated from base maps provided by the National Snow and Ice Data Center's map server A-CAP: The Antarctic Cryosphere Access Portal (http://nsidc.org/agdc/acap/).

Figure S3. The time series of black grama grass (*Bouteloua eripopoda*) production plotted along with utilization for one pasture (Pasture 2). Pasture 9 exhibited a similar pattern. Note the high utilization in 1951, coinciding with the onset of extensive soil erosion noted in the Jornada monthly report in December 1951.

Manuscript in review
Do not cite or distribute

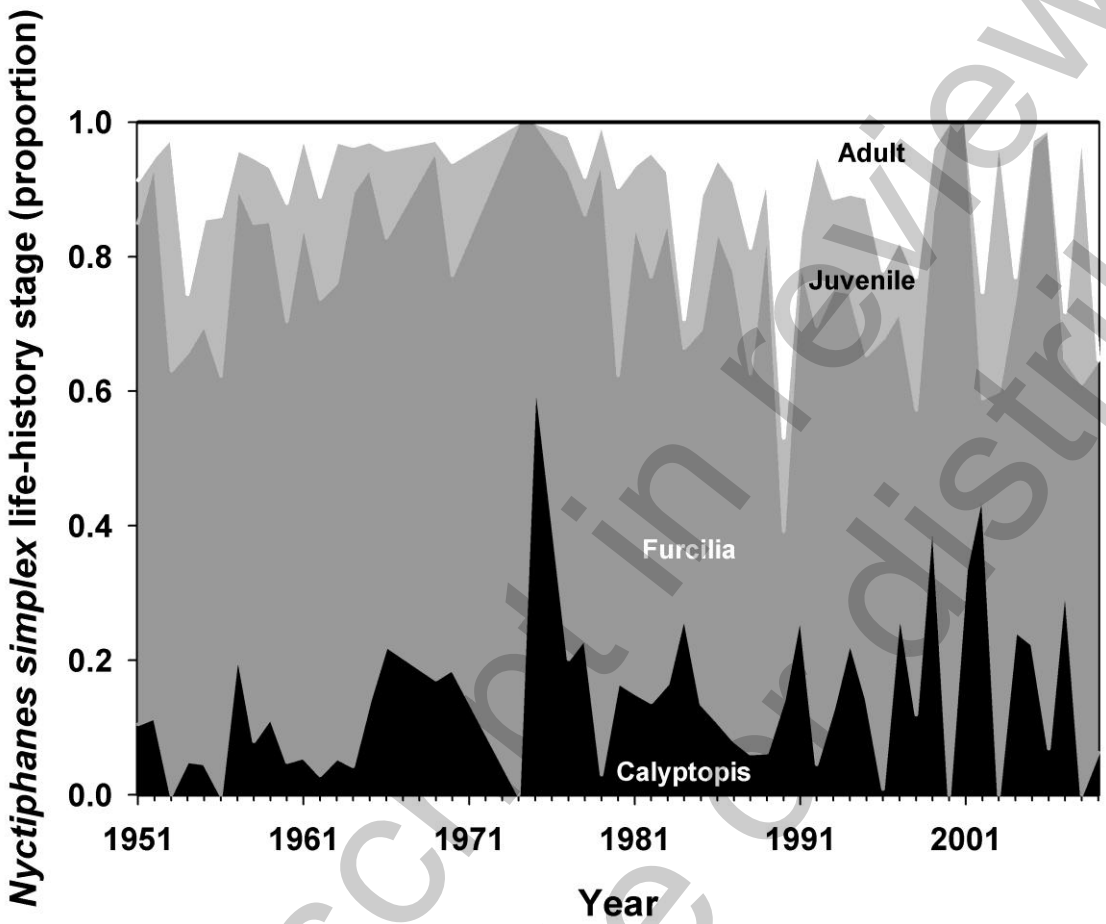


Figure S1.

Manuscript in review
Do not cite or distribute

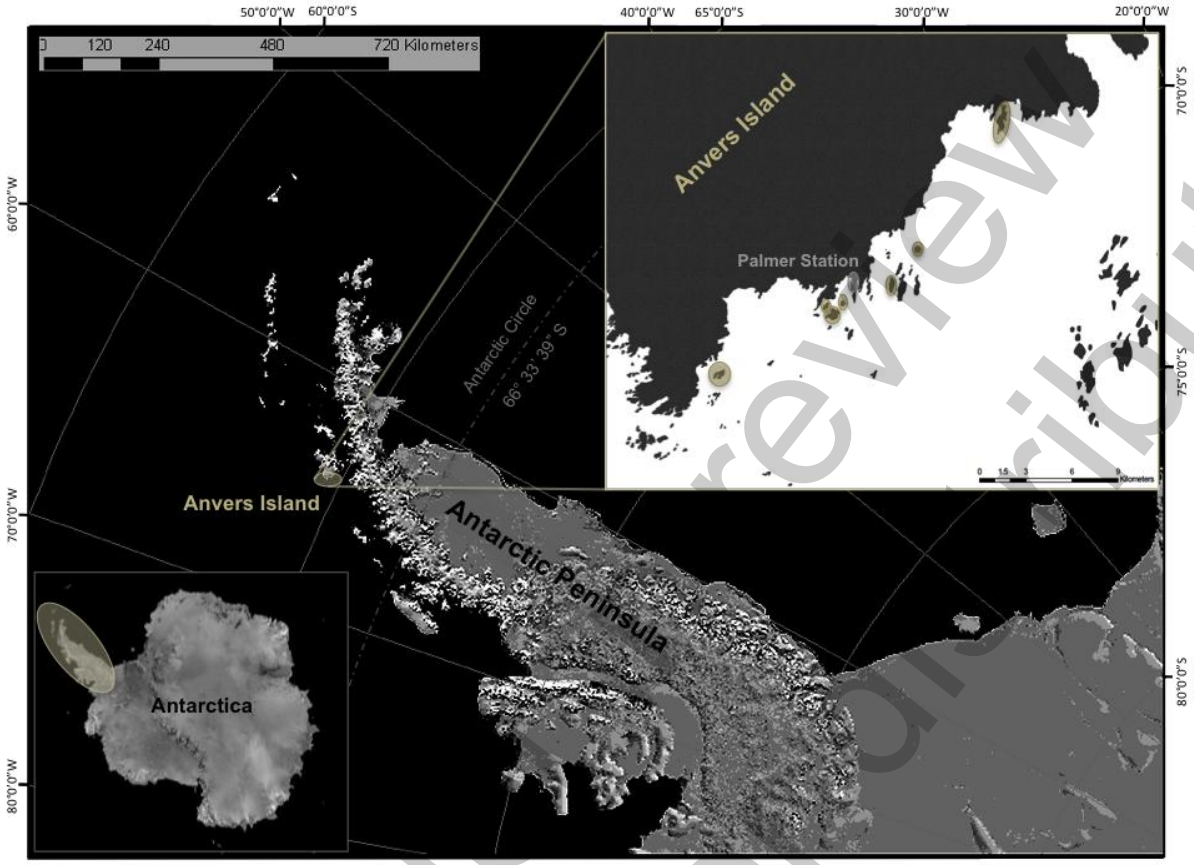


Figure S2.

Manuscript under review
Do not cite or distribute

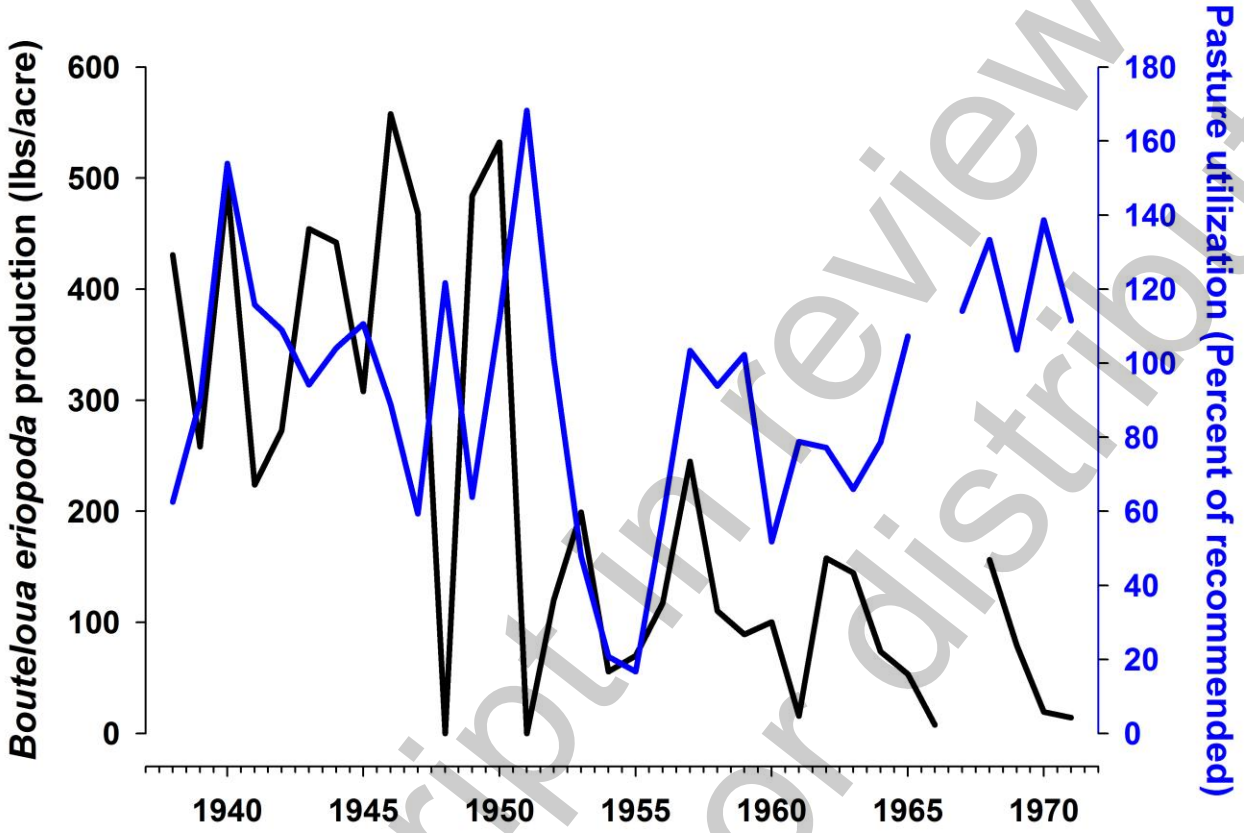


Figure S3.

Manuscript review
Do not cite or distribute