

*Annual Review of Environment and Resources*  
**Detecting Thresholds of  
 Ecological Change in the  
 Anthropocene**

Rebecca Spake,<sup>1,2,3</sup> Martha Paola Barajas-Barbosa,<sup>1,4</sup>  
 Shane A. Blowes,<sup>1,4</sup> Diana E. Bowler,<sup>1,5,6</sup>  
 Corey T. Callaghan,<sup>1,7</sup> Magda Garbowski,<sup>1</sup>  
 Stephanie D. Jurburg,<sup>1,6,8</sup> Roel van Klink,<sup>1,4</sup>  
 Lotte Korell,<sup>1,6</sup> Emma Ladouceur,<sup>1,6,8</sup> Roberto Rozzi,<sup>1,9</sup>  
 Duarte S. Viana,<sup>1,10</sup> Wu-Bing Xu,<sup>1,4</sup>  
 and Jonathan M. Chase<sup>1,4</sup>

<sup>1</sup>German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany; email: R.Spake@reading.ac.uk, paola.barajas@idiv.de, shane.blowes@idiv.de, diana.e.bowler@gmail.com, corey.callaghan@idiv.de, magda.garbowski@uwo.edu, s.d.jurburg@gmail.com, roel.klink@idiv.de, lotte.korell@ufz.de, emma.ladouceur@idiv.de, roberto.rozzi@idiv.de, dviana@ebd.csic.es, wubing.xu@idiv.de, jonathan.chase@idiv.de

<sup>2</sup>School of Geography and Environmental Science, University of Southampton, Southampton, United Kingdom

<sup>3</sup>School of Biological Sciences, University of Reading, Reading, United Kingdom

<sup>4</sup>Institute of Computer Science, Martin Luther University Halle-Wittenberg, Halle, Germany

<sup>5</sup>Institute of Biodiversity, Friedrich Schiller University Jena, Jena, Germany

<sup>6</sup>Helmholtz Centre for Environmental Research – UFZ, Leipzig, Germany

<sup>7</sup>Institute of Biology, Martin Luther University Halle-Wittenberg, Halle, Germany

<sup>8</sup>Institute of Biology, Leipzig University, Leipzig, Germany

<sup>9</sup>Museum für Naturkunde – Leibniz Institute for Evolution and Biodiversity Science, Berlin, Germany

<sup>10</sup>Estación Biológica de Doñana (CSIC), Sevilla, Spain

**ANNUAL  
REVIEWS CONNECT**

[www.annualreviews.org](http://www.annualreviews.org)

- Download figures
- Navigate cited references
- Keyword search
- Explore related articles
- Share via email or social media

Annu. Rev. Environ. Resour. 2022. 47:797–821

First published as a Review in Advance on  
 September 6, 2022

The *Annual Review of Environment and Resources* is  
 online at [environ.annualreviews.org](http://environ.annualreviews.org)

<https://doi.org/10.1146/annurev-environ-112420-015910>

Copyright © 2022 by Annual Reviews. This work is licensed under a Creative Commons Attribution 4.0 International License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. See credit lines of images or other third-party material in this article for license information

**Keywords**

biodiversity, critical load, extinction threshold, nonlinear, scale, tipping point

**Abstract**

Ecological thresholds comprise relatively fast changes in ecological conditions, with respect to time or external drivers, and are an attractive concept in both scientific and policy arenas. However, there is considerable debate concerning the existence, underlying mechanisms, and generalizability of ecological thresholds across a range of ecological subdisciplines. Here, we use the general concept of scale as a unifying framework with which to systematically navigate the variability within ecological threshold research.

We review the literature to show how the observational scale adopted in any one study, defined by its organizational level, spatiotemporal grain and extent, and analytical method, can influence threshold detection and magnitude. We highlight a need for nuance in synthetic studies of thresholds, which could improve our predictive understanding of thresholds. Nuance is also needed when translating threshold concepts into policies, including threshold contingencies and uncertainties.

## Contents

INTRODUCTION .....	799
THRESHOLD RESPONSES TO FIVE KEY ANTHROPOGENIC	
DRIVERS .....	800
Harvesting .....	801
Land-Use Change .....	801
Pollution .....	801
Biological Invasions .....	801
Anthropogenic Climate Change .....	802
TYPOLOGY OF ECOLOGICAL THRESHOLD RESPONSES	
TO ENVIRONMENTAL CHANGE .....	802
DIVERSITY OF STATISTICAL MODELING APPROACHES	
FOR DETECTING ECOLOGICAL THRESHOLDS .....	803
SCALE AS A UNIFYING FRAMEWORK FOR NAVIGATING CONTEXT	
DEPENDENCE IN ECOLOGICAL THRESHOLDS .....	805
OBSERVATIONAL SCALES .....	
Organizational Level .....	805
Study Grain .....	807
Study Extent .....	808
Analytical Scale .....	808
DEMONSTRATING SCALE DEPENDENCE OF THRESHOLDS	
IN A METACOMMUNITY SIMULATION .....	809
DEMONSTRATING SCALE DEPENDENCE OF THRESHOLDS USING	
EMPIRICAL CASE STUDIES .....	810
Organizational Level .....	810
Study Grain .....	811
Study Extent .....	811
Analytical Scale .....	811
UTILITY OF THRESHOLD CONCEPTS IN POLICY .....	
Implementing Science-Based Policy Using Ecological Thresholds .....	814
TOWARD A PREDICTIVE UNDERSTANDING OF ECOLOGICAL	
THRESHOLDS THROUGH SYNTHESIS .....	814

## INTRODUCTION

More than 20% of the terrestrial surface will cross one or several . . . thresholds by 2100, which calls for immediate actions to minimize the negative impacts. . . on essential ecosystem services.

—Miguel Berdugo et al. (1, p. 787)

Global change biology needs to abandon the general expectation that system properties allow defining thresholds as a way to manage nature under global change.

—Helmut Hillebrand et al. (2, p. 1502)

The Anthropocene is characterized by substantial changes to Earth's systems brought about by the actions of humans over the past hundreds to thousands of years (3, 4). Although the impacts of humans on ecological patterns and processes are undeniable and sometimes dramatic, there is still an urgent need to quantify and understand these changes in order to forecast future changes, as well as identify avenues for sustainable use of the Earth's resources for generations to come (5, 6). There is a particular need to establish whether rates of change are relatively smooth and linear across space or time, or whether ecological thresholds are common. That is, are there transition points or zones of relatively rapid change between ecological conditions or ecosystem states, with respect to time or external drivers?

Ecological thresholds, if they exist and are common, have important implications for our basic understanding and predictions of ecosystem dynamics, as well as for developing policies that mitigate change or restore degraded ecosystems. At local scales, ecological thresholds have been implicated in, among other things, the decline (and slow recovery) of water quality, fisheries stocks, and the associated ecosystem services of freshwater (7) and marine (8) systems. Similarly, threshold responses have been observed in terrestrial ecosystems, for example where interdependent actions of fire, drought, and invasive species drive shifts between open (grass-dominated) and more closed (shrub- and tree-dominated) communities, with changes in the associated ecosystem services (1, 9). In each of these cases, scientists have used multiple lines of evidence to suggest the existence and location of ecological thresholds, and have collaborated with policymakers to develop policy and adaptive management to minimize the possibility of crossing such thresholds (10–12).

At global scales, the concepts of planetary boundaries and safe operating space explicitly assume that there are thresholds in biodiversity loss and other ecosystem functions beyond which the Earth system might collapse to a difficult—or impossible—to-recover-from—alternative state (13, 14). Thresholds concepts are also built directly into reports on the state of the planet's ecosystems, such as the report from the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) (5), and are used as tools in conservation and restoration policies (10, 15, 16).

Despite great interest in ecological thresholds from a scientific and policy perspective, we are still a long way from understanding their prevalence and predictability in the real world. There is no question that there are many important examples of threshold-like responses in nature. At the same time, some of this evidence has generated lively debate among scientists (reviewed in 12). Much of the controversy surrounding thresholds concerns their actual existence in nature (2) and, where they do exist, their underlying mechanisms and quantitative values. Any proposed threshold values are often contentious (17) and of questionable utility due to the context-dependent nature of their quantification, contingent on a host of methodological decisions, as well as the environmental context of a study (18, 19). For example, a study that compiled long-term trends in 12 coastal and estuarine ecosystems to demonstrate the frequency of fishery collapses over time (20) was met with great criticism given the methods and data used, and the extrapolation of regression results

---

**Threshold:** points or zones at which relatively rapid change occurs from one ecological condition or state to another, often in response to small, continuous changes in one or more external drivers

**Drivers:** external factors that influence the dynamics of a system without themselves being affected

---

**Critical load:** a level of pollution beyond which ecosystem states, properties, or functions are altered

to project the global collapse of all fished taxa by 2048 (21, 22). Similarly, a review of landscape ecology studies suggested that forest cover needs to be restored or maintained on at least 40% of land area in order to maintain biodiversity and the ecosystem services (23). This generic figure has been criticized, because 40% is likely not enough in some areas and too high in others, and because the size of the landscape to which this figure is applied is not easily defined (17). Indeed, a recent meta-analysis suggested that thresholds were likely to be rare in most ecosystems that using them in the policy arena could do more harm than good (2).

Understanding the contentious field surrounding ecological thresholds requires a deep dive across diverse scales of study, from single lakes (24) to entire continents (25), as well as across varying timescales from millennia (26) to more recent observations of global change within the Anthropocene (2). This review attempts to assemble and organize the ways that thresholds are context dependent using scale as a unifying framework. We first overview the different qualitative forms (typologies) of ecological thresholds. Next, we present a short review of evidence for ecological thresholds associated with important anthropogenic drivers and highlight how thresholds are used in a diversity of environmental policies. We describe ways in which empirical evidence has been used to test for ecological thresholds and then review how various forms of ecological scale, especially observational scale, can strongly influence our ability to detect and quantify them. We then illustrate scale dependencies using a simple simulation model and several empirical case studies. Finally, we conclude with a discussion about how threshold science can be used to inform policies aimed at mitigating threshold transitions and ecosystem restoration, and the challenges and opportunities that synthesis provides.

Although research on ecological thresholds is broad, spanning ecological, social, and economic disciplines (27), we narrow our scope to the following: (a) ecological response variables, i.e., the population-community continuum of ecological variables; (b) anthropogenic drivers rather than intrinsic factors and natural pulse drivers, i.e., external drivers brought about by human activities (e.g., climate change, harvesting, habitat loss); and (c) empirical patterns. Our review primarily concerns empirical approaches to detecting thresholds in nature, rather than on theoretical explorations of their mechanistic underpinnings (see, e.g., 28 for a useful introduction to this material). Finally, a note on terminology: Here, we use the term thresholds to refer to nonlinear ecological responses to drivers. We note that a diversity of terms are used in the literature (for reviews, see 9, 12, 19, 28). These include tipping points (e.g., 29), critical transitions (30), regime shifts (e.g., 31), planetary boundaries and safe operating limits (e.g., 13, 32), ecosystem collapse (12), critical loads (e.g., 33), and ecological meltdown (34).

## THRESHOLD RESPONSES TO FIVE KEY ANTHROPOGENIC DRIVERS

IPBES recognizes five categories of drivers that influence biodiversity and ecosystem processes: direct harvesting of organisms, land-/sea-use change, pollution, invasive species, and climate change (5). Threshold responses to all of these drivers have been documented (12, 19, 24, 31). Because of their intuitive appeal, policies designed to mitigate against the adverse impacts of these drivers often invoke thresholds, although the actual link to observed or observable ecological thresholds varies substantially (35). For example, threshold values might be used to prioritize ecosystems on the brink of a threshold for restoration or to define safe limits to ecosystem degradation (18, 36). However, policy thresholds may not relate to ecological thresholds but rather societal decisions or regulatory limits where a given risk of system change is deemed acceptable [e.g., limits to nitrate levels in drinking water (24)]. In this section, we review the application of threshold concepts in policies designed to mitigate against adverse impacts of the five global environmental change drivers.

## Harvesting

Overexploitation occurs when populations are harvested at a faster rate than their natural recovery. Populations can collapse following reductions below critical population size thresholds, at which individual fitness declines, for example, due to Allee effects at low numbers (37), or through the selective removal of larger, faster-growing individuals (38). The collapse of the Atlantic northwest cod fishery in Canada represents the greatest decline in fish stocks in one of the world's most abundant cod stocks: In the early 1960s, cod numbered almost two billion breeding individuals but declined by 97% within a few decades (38). Overharvesting can scale up from populations to entire ecosystems via trophic cascades. For example, overfishing of predatory cod led to changes in nitrate concentrations through an indirect impact on phytoplankton (39). To prevent population and ecosystem collapses, regional catch quotas or fishing mortality rates that lead to maximum sustainable yield have been proposed. Although limits to harvesting have enabled populations to recover, apparently abundant stable marine populations are still vulnerable to collapse following small declines in intrinsic growth rates, emphasizing the need to base harvest limits on intrinsic population parameters (40). Recent advances in ecosystem-level food-web modeling enable the incorporation of trophic interactions and other direct and indirect anthropogenic drivers (41).

## Land-Use Change

Land-use changes, such as agricultural expansion and urbanization, lead to the loss and fragmentation of habitats (42). A large body of research has sought to identify extinction and biodiversity thresholds—critical values of habitat loss below which populations cannot persist due to reductions in resources or connectivity between original habitat patches (42). These concepts have sparked much debate on minimum amounts and ideal arrangements of protected areas (43) and the importance of land sparing versus land sharing (44, 45). Still, implementing thresholds into these decision-making frameworks is difficult because it depends on historical land use (46), development types and intensities (47), landscape composition (48), and other contextual variables that are difficult to quantify or disentangle.

## Pollution

Pollutants include chemicals from industrial emissions, agricultural runoff and inadequate waste management, as well as energy, such as that in the form of noise, light at night, and heat. As relatively discrete systems, lakes have been widely used by experimental and theoretical ecologists to study threshold responses to the introduction of pollutants. Cumulative inputs of nitrogen and phosphorus can lead to phytoplankton blooms that turn lakes from clear to turbid states (7). Similarly, catastrophic losses in seagrass meadows have been documented worldwide in coastal lagoons and estuaries with low tidal flushing due to the smothering effects of phytoplankton that are enhanced by nutrient loading from land (49, 50). Policies that mitigate against pollution include the delimitation of critical loads beyond which ecosystem states, properties, or functions are altered (51). Critical loads can be estimated empirically, through experimentation, the use of long-term monitoring data, spatial deposition gradients to construct dose-response relationships (52), or by using mass-balance or steady-state modeling (53). Concerns about their use in policy stem from contingency in ecological responses to deposition (15, 54, 55).

## Biological Invasions

Biological invasions impact biodiversity and ecosystem functioning across terrestrial and aquatic ecosystems (56). By altering abiotic conditions and restructuring native communities, invasive

species can drive significant changes in the abundance of key taxa and conditions that govern the balance of alternative equilibria (57). There is interest in exploiting threshold-like responses of invaders to management interventions. For example, the introduction of predatory biocontrol agents, or the use of sterile male release strategies, can induce Allee effects in invader populations under certain conditions (58), and fire and other natural disturbances can influence the success of natives relative to invaders in systems with alternative states (59).

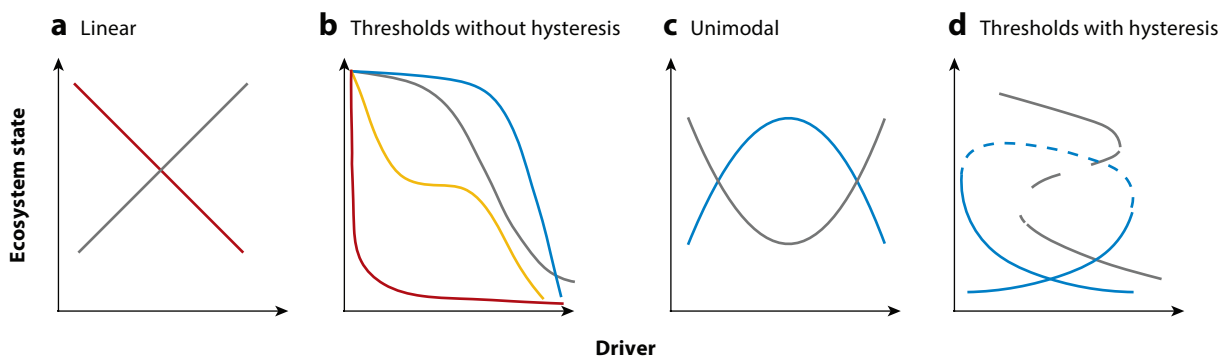
## Anthropogenic Climate Change

Considered a meta-threat due to its ability to interact with other anthropogenic drivers (12), climate change can profoundly affect populations (e.g., demography), species (e.g., distributions, phenology), and communities [e.g., relative abundances, biotic interactions, food-web structure (e.g., 60)]. Prominent examples of threshold responses to climate change include mass coral bleaching events, triggered by strong environmental perturbations (e.g., marine heatwaves), which cause corals to eject their algal symbionts and reduce to white skeletons (61). The discrepancy between the spatiotemporal scales at which climate policies are based and those at which ecological thresholds are observed is a major obstacle for the conservation of biodiversity in the face of climate change (62).

## TYOLOGY OF ECOLOGICAL THRESHOLD RESPONSES TO ENVIRONMENTAL CHANGE

An ecosystem's external conditions often change gradually with time, for example via nutrient addition and habitat fragmentation (24). Several qualitatively distinct ecological responses to such changes are possible (**Figure 1**). Here, we briefly describe four broad types of responses that can occur (see, e.g., 9, 28 and 12 for comprehensive reviews). Although ecosystems experience, and respond to, changes over time, studies can exploit environmental gradients across space, thus the *x*-axes in **Figure 1** can represent gradients in space or time.

Changes in external conditions in time or space can lead to relatively smooth, linear changes in the ecological response of interest (**Figure 1a**). Often, however, gradual changes in the environment can lead to nonlinear responses, including threshold, unimodal, and more complex patterns (**Figure 1b–d**). In these examples, ecological thresholds are points or zones at which relatively



**Figure 1**

Different responses of ecosystem state (measured as, e.g., biomass, species diversity) to changes in external conditions—drivers (e.g., nutrient loads, land-use intensity): (a) linear, (b) thresholds without hysteresis, (c) unimodal, (d) thresholds with hysteresis. Adapted from Reference 9.

rapid change occurs from one ecological condition or state to another, often in response to small, continuous changes in one or more external drivers (9).

Ecological parameters may be relatively unresponsive to drivers until conditions reach a critical value (**Figure 1b**). This type is often observed, or expected to occur, in response to a range of drivers such as land-use change, where decreases in habitat amount can reach an extinction threshold, beyond which local extirpation probability can rapidly change from near-zero to near-one (63). Similarly, increases in pollution beyond a critical load can yield threshold responses of individuals, populations, and communities in both terrestrial (52) and aquatic (16) ecosystems.

Unimodal relationships are threshold-like across the range of a driver (**Figure 1c**). Temperature is a classic example, where individual-level performance (fitness) and population size increase with temperature until an optima is reached, after which declines occur (64). As global temperatures increase, community composition may change through the loss of species now outside their climate niche and the gain of other species whose niche better matches the new climate (65). Other examples of hump-shaped responses (not without debate) include responses of plankton diversity to eutrophication in lakes and ponds (66), responses of bird diversity to urbanization (67), and studies showing highest diversity at intermediate levels of (anthropogenic) disturbance (68).

In accordance with dynamical systems theory, a third, more dramatic, nonlinear response is possible (**Figure 1d**). In such cases, ecosystems can exist in two (or more) alternative stable states, which are separated by an unstable equilibrium between basins of attraction (24, 28). Once an inflection point is traversed, hysteresis occurs, and ecosystems cannot be easily returned to the initial state by simply returning ecosystem conditions to the level before which the transition occurred (69). Sometimes these states are transient rather than equilibrial but can be maintained for a long period (70). Real-world examples include transitions between forests and savannah (71), coral and algal dominance in coral reefs (72), clear water and phytoplankton-dominated shallow lakes (7), and biocrusts and vegetation in drylands (73). Although alternative states are driven by positive feedback mechanisms (intrinsic processes such as negative density dependence), abrupt changes can also be caused by rapid, rather than gradual, changes in the external conditions (sometimes referred to as pulse, rather than press, disturbances), or from interactions among drivers without a positive feedback mechanism (12).

Although not shown in **Figure 1**, more complex responses are also possible. For example, there are numerous examples where a threshold in one part of a complex ecological system can cascade to influence threshold responses in other parts of the system (74).

## DIVERSITY OF STATISTICAL MODELING APPROACHES FOR DETECTING ECOLOGICAL THRESHOLDS

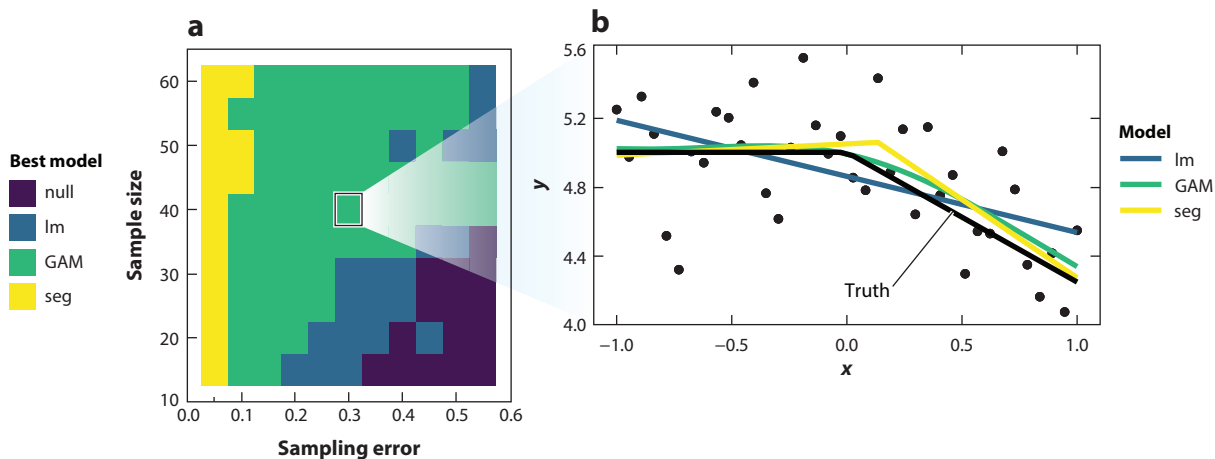
Many statistical modeling approaches can be used to detect and quantify thresholds and, more generally, to characterize nonlinearity between environmental and biodiversity response variables. Approaches range from computationally and data-intensive analyses (75) to simple post hoc decisions about threshold locations in regression outputs (e.g., value of an independent variable at a particular value of the dependent variable) (76). Different modeling approaches often concern differences in the type of threshold expected (**Figure 1**), especially whether the assumption is a sharp or gradual change and whether the transition is reversible.

Abrupt change in the slope of a relationship is also called structural change, and the locations of change are commonly called change or break points. One of the simplest tests for abrupt change is the generalized fluctuation test (77); however, piecewise or segmented regression that fits multiple parametric slopes for different regions of a relationship is more commonly used in ecology (78) (**Figure 2**). Piecewise regression is a special case of bent-cable regression models, which allow

---

**Abrupt change:** change in the mean or variability of a biodiversity variable that is fast in time or fast relative to their drivers

---



**Figure 2**

The fit of different modeling approaches to simulated data with a threshold response. (a) The best performing models (with lowest AICc) under a range of sample sizes and sampling errors (standard deviation of  $y$  around the mean). Each parameter combination was simulated 100 times and the mode of the best performing model for each combination is shown. Even though the true underlying relationship contained an abrupt threshold, the segmented model was only the best model when sampling error was low. For most of the parameter space, a smooth GAM model was the best model. (b) The black line shows the true deterministic relationship between  $x$  and  $y$ , with a threshold change of  $y$  at  $x = 0$ . Black points show observations that are sampled and deviate from the deterministic relationship due to additional variation in  $y$  around the mean (assumed to be normally distributed error). The colored lines show predictions of different models (lm, GAM, seg) fit to the observations. Abbreviations: AICc, sample-size adjusted Akaike's information criterion; GAM, generalized additive model; lm, linear regression; seg, segmented.

different kinds of transitions between different structural parts of a relationship, thereby allowing a sharp change or gradual change in the transition zone (79). Characterizing uncertainty in change point locations and/or the width of transition zones is an active area of research that has important implications for detecting ecological thresholds and using them in policy and practice (79).

Generalized additive models (GAMs) are increasingly used in ecology, including in threshold research, since they model nonlinear relationships in a flexible way (80) (Figure 2). Ficetola & Denoël (76) found that 27% of reviewed papers used GAMs to investigate species' habitat extinction thresholds. A GAM's effective degrees of freedom determines the "wiggleness" or nonlinearity of the modeled relationship; however, there is no standard approach to test for an abrupt transition characteristic of a threshold. Analysis of the derivatives of the fitted relationship can identify regions of rapid change, as well as inflection points, when the second derivative of the fitted relationship changes sign (80).

Clustering or partitioning techniques do not directly model nonlinearity, but rather split a dataset into groups, where the locations of the splits can be interpreted as thresholds. Similarly, tests for multimodality of a biodiversity response variable, for example, using Hartigan's dip test statistic, have been used to provide support for threshold responses (2). Cluster analysis has been applied to time series, including paleoecological, in which chronological clustering defines time periods of similar states and time points of transitions (81). Regression trees split a dataset using recursive partitioning and can identify thresholds from multiple environmental pressures acting on an ecological response at the same time. Other studies have used regression trees to define thresholds of nutrient concentrations for freshwater pollution monitoring (82). Threshold Indicator Taxa Analysis is another technique most commonly used in freshwater studies (53), which combines regression trees with indicator taxa analysis.



Empirically testing for more complex thresholds, such as hysteresis, is more complicated than simply testing for nonlinearity. One indicator of hysteresis that has been examined by ecologists is state- or time-dependent driver-response relationships, for instance, if the relationship differs before and after a state change (81, 83, 84). Su et al. (81) used a 65-year lake ecosystem dataset to show how relationships between environmental stressors and taxa responses were different following an abrupt change in the mid-1980s, consistent with hysteresis. The predictive promise of early-warning signals that occur prior to abrupt change has led to a range of possible metrics being proposed (84). These early-warning signals include increasing variance, autocorrelation or skewness of a biodiversity response, as well as slower recovery of a system to its original state following disturbance (84, 85). Rarely do ecologists have sufficient data to make these metrics useful in practice (86); however, this is still an active area of research (81, 84).

## SCALE AS A UNIFYING FRAMEWORK FOR NAVIGATING CONTEXT DEPENDENCE IN ECOLOGICAL THRESHOLDS

The problem of pattern and scale is the central problem in ecology, unifying population biology and ecosystem science and marrying basic and applied ecology.

—Simon A. Levin (87, p. 1943)

The scale dependence of ecological patterns, processes, and their relationships has been a central theme in ecology for decades (87–89). Although conceived as a problem (87), scale also lends itself as a unifying framework with which to navigate apparent context dependencies, including in ecological thresholds. A range of conceptualizations of scale have been proposed, collated by Wu & Li (90) into a framework (**Figure 3**) describing aspects of scale along three dimensions: space, time, and organizational level (**Figure 3a**).

Within each dimension, three fundamental scales can be operationalized: intrinsic, observational, and policy scales (**Figure 3b**). The intrinsic scale concerns the spatial and temporal scales at which organisms respond to changes in their environment. In space, such scales are determined by life-history characteristics such as body size, mobility, and dispersal distances (91). The timing of responses to environmental change might depend on an organism's generation time, dispersal and colonization ability, and dormancy periods. Our ability to detect ecological thresholds will depend on the degree of alignment between the scales intrinsic to the phenomenon under study and the observational scale used to sample ecological phenomena and construct analytical models. Often, the appropriate scales of observation for measuring ecological responses are unknown a priori, necessitating multiscale analysis (92).

We distinguish four components of observational scale, which correspond to decisions that researchers either make or are restricted to, given logistical or computational constraints (**Figure 3c**). These are (*a*) organizational level, the metric used to represent ecological change (i.e., the number of species or the biomass in a system); (*b*) study grain, describing the resolution of individual observation units in space and time (and also the intervals between them); (*c*) study extent, its total areal size, and its duration; and (*d*) analytical scale, concerning how models are fitted to data. We acknowledge that any separation of scale components is a human construct and that components are not independent of one another.

## OBSERVATIONAL SCALES

### Organizational Level

The choice of organizational level can explain some context dependencies in threshold research. Here, organizational level concerns the selected response variable used to quantify threshold

---

**Early-warning signals:** system metrics that indicate a system is approaching an abrupt change or a critical transition

**Organizational level:** level of biological organization that ranges from individuals, population, communities, and ecosystems to biomes

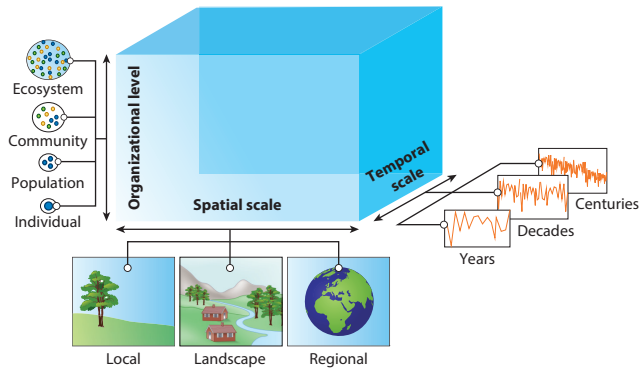
**Intrinsic scale:** the scale at which an ecological pattern or process truly operates

**Grain:** sampling size of the individual units of observation, e.g., a quadrat (spatial grain) or sample duration (temporal grain)

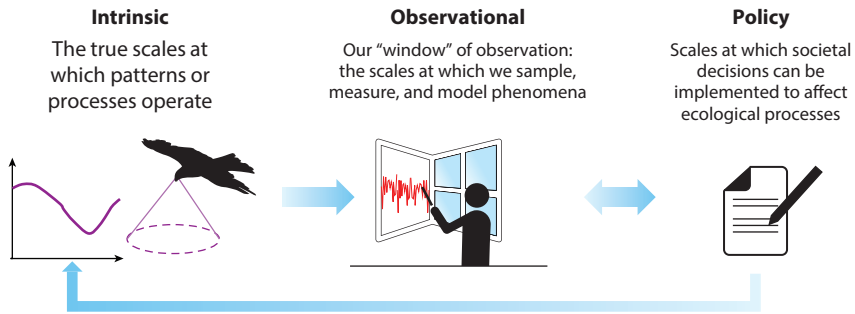
**Extent:** total area sampled of a study (spatial extent) or total time window of observations (temporal extent)

---

**a** Dimensions of scale



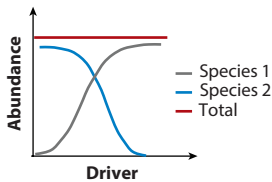
**b** Intrinsic, observational, and policy scales



**c** Components of observational scale

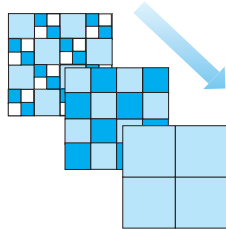
**Organizational level**

The response variable, whether measured at the population or (meta-) community level, can determine the strength and shape of threshold responses.



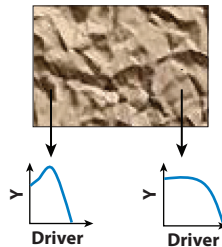
**Study grain**

The size of sampling units and their intervals in space and time can change the strength of observed relationships.



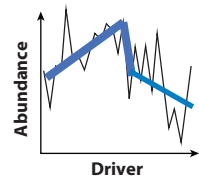
**Study extent**

The aerial size and duration of a study can determine the range and arrangement of environmental drivers. Confounding and contingency among drivers can determine the threshold responses.



**Analytical scale**

Analytical decisions influence the detection and value of thresholds, including how data are transformed during model fitting, and how confounding and contingencies are dealt with.



*(Caption appears on following page)*

### Figure 3 (Figure appears on preceding page)

Scale as a unifying framework to explain the context dependence of ecological patterns and processes. (a) Threshold research takes place in three dimensions: time, space, and organization. (b) Within each dimension, our ability to detect ecological thresholds will depend on the degree of alignment between the scales intrinsic to the phenomenon under study and the scale imposed by the observer, that is, the observational scale used to sample ecological phenomena and construct analytical models. The scales at which inferences are drawn are then transferred to policy scales to affect ecological processes. (c) Observation scales concern the organizational level, grain, extent, and analytical scales imposed by the researcher. Adapted from Wu & Li (90).

responses, and ranges from individuals to populations of species to communities and ecosystems (**Figure 3a**). Because thresholds may be apparent in some metrics and not others, it is generally recommended that multiple metrics be analyzed (9, 19).

At the species level, the vast majority of taxa are rare and have highly variable occurrence probabilities across samples, making it challenging to discern threshold responses to environmental gradients (93). Species that are relatively common have been used to estimate habitat amount thresholds below which occurrence is unlikely. In general, we can expect generalist species to show weaker threshold responses to the amounts of specific habitat types than specialists (94) but more broadly for species' characteristics to influence threshold responses (95).

At the community level, aggregate measures capture changes in summary properties, such as total abundance, biomass, and species richness, and are considered less sensitive to environmental change, and thus thresholds, than compositional measures, such as turnover and species-level abundances (46). This is because, for example, differences in species' responses to change (e.g., niche differentiation) can compensate or buffer against changes in aggregate, community-level metrics (**Figure 3c**). Hence, abrupt changes in aggregate metrics can depend on the degree of interspecific variation in species' response and are more likely observed if the species have similar responses (96).

### Study Grain

Grain size defines the size of individual sampling units used to measure both response variables (e.g., plot size to measure abundance or diversity) and predictor variables (size of the landscape unit within which drivers are measured). In time, grain concerns the duration of observations to yield an individual sample. In many cases, the grain might be determined by the availability of biodiversity and environmental data, or computing resources. A range of mechanisms are responsible for grain dependence of ecological patterns and processes but generally arise because different grains yield different degrees of alignment between sampling and intrinsic (or characteristic) scales of the ecological process. Most studies only test the effect of predictors at one or a few discrete grain sizes; however, new methods are being developed to characterize species responses over a more continuous range of possible grain sizes (92), which may help to more accurately determine threshold values.

The importance of temporal grain is well-established in paleoecological studies that seek to identify the historical timing of abrupt ecological change via the reconstruction of past ecological communities. Such time series are vulnerable to unequal sampling intervals, due to compaction and changes in sedimentation rates over time (97). Using subsampling of simulated and real datasets, numerous studies have shown that increases in temporal grain size and interval can diminish both the autocorrelation and variance signals that indicate early-warning signals of flickering and critical slowing down, and the apparent timing of abrupt change in species composition (98, 99). Grain sensitivity hinders the comparison of rates of compositional change both within and between time series. However, compositional metrics that are robust to unequal intervals are available (26, 100), as well as modeling approaches that incorporate uncertainties in time point estimation (101).

Spatial grain-size dependence has been long recognized in studies that seek to characterize extinction thresholds. In these studies, habitat amount is typically measured in multiple buffer or grain sizes surrounding a focal point, which give rise to variability in the strength of habitat-occupancy relationships. The grain size at which observed relationships are strongest is considered the most appropriate for quantifying threshold responses (102). However, observed relationships can also be sensitive to the grain size of the land cover maps used to measure habitat amount and influence the estimated habitat threshold value (103).

Species richness can be measured at multiple grains, aggregated into local-scale observations (often called alpha diversity) to regional-scale observations (often called gamma diversity), and the choice of grain for analysis can influence the detection of thresholds. For example, Kupsch et al. (104) found that species richness of birds in Afrotropical agroforestry was relatively constant when measured as the number of species in a sampling block, until a threshold of 42% forest cover, after which bird diversity significantly declined. However, when measured at smaller-grain sampling points, no such threshold was observed.

### Study Extent

Extent describes the size of the study area encompassed by all sampling units in space, and the duration of sampling in time. Sampling the full potential range of a predictor variable is important for detecting nonlinear relationships, including thresholds, and failure to do so by individual studies may explain discrepancies among their findings (105).

Study durations must be sufficient to detect threshold responses that exhibit time lags. For example, extinction debts (delayed species extinctions in response to ecosystem perturbations) can lead to the persistence of populations for extended periods below expected extinction thresholds, even if a species is expected to go deterministically extinct (106). If studies do not consider extinction debts, or use methods that do not reliably detect them, extinction debts and threshold responses will likely go underreported (107). In addition to the range, the frequency and spacing of samples along the range can influence the likelihood of false detection of thresholds (type I errors) and estimates of threshold values (108). Bruel & White (109) showed that subsampling approaches that employ equally spaced sampling across variable ranges can inaccurately estimate the timing or location of abrupt change when insufficient samples are taken close to the true change point location.

In addition to a focal driver of interest, as the spatial and/or temporal extent of a study increases, other abiotic variables (e.g., climate or resource availability) that were constant at smaller extents become variable at larger extents. As a result, we can no longer assume homogeneous ecological responses—including threshold responses—to anthropogenic drivers. For example, Simkin et al. (25) demonstrated variable sensitivities of plant communities to atmospheric nitrogen deposition across the United States due to moderation by climate and edaphic factors, consequently affecting critical loads of nitrogen at which species losses begin. Such contingencies highlight the need for either sampling or analytical designs to recognize contingency and confounding among multiple drivers acting at multiple scales (110).

### Analytical Scale

Analytical decisions can strongly affect the identification and quantification of threshold and nonlinear biodiversity responses. These include whether sampling or observation error is taken into account (111), how confounding and contingency in ecological effects are dealt with, and the scale of modeling [e.g., whether additive or logarithmic (112)].

Ecological data are inherently noisy, with implications for threshold detection and magnitude. Abrupt change in a noisy time series may be often indistinguishable from random sampling

variation (113). Regression-to-mean effects can lead to smaller following larger extreme values due to random variation, even if no biological threshold has been crossed. Statistical tools such as state-space threshold models have been developed that account for observation processes that generate the sampling variation to better characterize the true underlying biological threshold response (e.g., 111, 114).

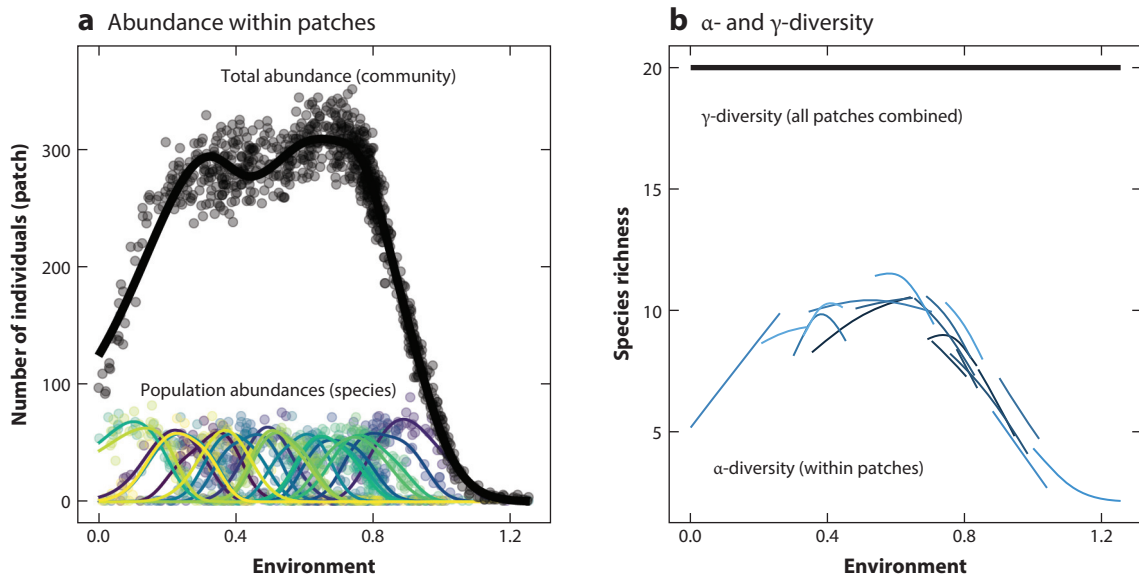
Contingencies of thresholds can be examined in statistical models that include multiple drivers and their interactions. Outputs can be used to characterize spatial variation in threshold responses, and target management or restoration efforts to ecosystems at greatest risk of abrupt change (110). Threshold studies vary in model complexity, ranging from simple univariate responses to a single driver, to multiple regression models that explicitly incorporate confounders and interactions among drivers. A further complexity is that environmental drivers are often confounded; for example, forest loss to agriculture typically correlates with climate, topography, and soil fertility. Failing to account for confounding variation in study or analytical designs could lead to misattribution or the obscuring of threshold responses (115). Causal inference or counterfactual thinking approaches can also be used to increase the internal validity of studies attributing threshold responses to hypothesized environmental drivers (116). For example, observational studies can be made to emulate randomized experiments, through the use of statistical matching methods that impose similar covariate distributions across the range of a focal driver of interest (see 117), while structural equation modeling provides the means for evaluating proposed hypotheses against data (118).

The analytical scale of effect estimation may also dictate whether threshold responses are detected. For metrics such as species abundance and richness, researchers can model effects on additive scales or multiplicative (e.g., logarithmic) scales. Often these choices are made based on statistical reasoning. For example, abundance is often modeled with a log link function because it ensures that the model predictions are sensible, i.e., remain above zero. However, choices based on statistical grounds might differ from choices that would be made based on biological grounds (112). Importantly, a nonlinear relationship on the additive scale can be linearized on the log-scale; however, studies rarely acknowledge this in interpretation of modeled relationships (e.g., 119). Arguably, many cases where biodiversity thresholds may exist on an arithmetic scale could have been overlooked on a log scale. For example, in the synthetic analysis by Hillebrand et al. (2), comparisons were made using log-response ratios, which might explain why they found little evidence for threshold responses to global change factors.

## **DEMONSTRATING SCALE DEPENDENCE OF THRESHOLDS IN A METACOMMUNITY SIMULATION**

In this section, we illustrate two types of scale dependence that influence threshold detection—organizational scale and spatial extent—using a metacommunity model that incorporates density-independent abiotic responses, density-dependent competitive interactions, and dispersal (120). We simulated a metacommunity composed of 20 functionally different species across 20 habitat patches distributed across an environmentally heterogeneous region. After allowing an equilibrium to be reached, each patch was subjected to an environmental pressure (e.g., warming or nutrient release) that increased linearly over 800 time steps, with varying rates in each patch. The purpose of the simulation is to illustrate three of the concepts described above (organization, grain, and extent), and thus we do not explore multiple parameter values. Thompson et al. (120) provide details of the simulation.

To demonstrate the scale dependence of threshold responses, we recorded abundances at the finest organizational, spatial, and temporal grain possible, corresponding to individual species



**Figure 4**

Metacommunity simulations illustrating how organizational scale and spatial extent can influence the detection of thresholds. (*a*) Total community abundance (*black*) and abundances of different species (different colors) summed within patches; (*b*) local- (alpha-) and regional- (gamma-) scale species richness plotted along the environmental gradient.

abundances, in each patch, at each time step. This allowed us to aggregate the results at different organizational scales (i.e., single species' population abundances and total community abundance) and at different spatial grains (i.e., patch-level alpha diversity and regional gamma diversity). **Figure 4a** shows the abundances of individual species and the total community abundance within patches across the full extent of the environmental gradient. Species' population abundances exhibit hump-shaped responses, as specified in the simulation, each centered on species' environmental optima. Total community abundance also shows an approximately hump-shaped relationship across the whole gradient. However, choosing either population- or community-level responses for any section of the environmental gradient (i.e., a restricted extent of the driver) would influence whether threshold responses are detected. Similarly, when species richness is calculated at the regional grain (i.e., all patches combined), there is no variation in richness across the gradient (**Figure 4b**). In contrast, we observe a variety of functional responses of richness at the grain of the patch in response to the environmental gradient, including linear, hump-shaped relationships and abrupt changes.

## DEMONSTRATING SCALE DEPENDENCE OF THRESHOLDS USING EMPIRICAL CASE STUDIES

Here we present analyses from published studies that detected threshold responses across an anthropogenic gradient. We then adopt a different scale of observation to reanalyze these data and demonstrate scale influences on threshold detection.

### Organizational Level

Morse et al. (121) quantified the response of stream macroinvertebrate communities to a gradient of catchment urbanization. The study set out to identify a threshold level of urbanization above

which an abrupt change might be observed in a range of species- and community-level metrics. **Figure 5a** (left panel) shows a strong threshold response of Ephemeroptera (mayflies), a classical indicator group due to their low tolerance of stream pollutants, with abrupt reductions in densities beyond  $\sim 10\%$  urbanization (see also **Supplemental Table 1**). In contrast, when all taxa are aggregated, the relationship between macroinvertebrate abundance and urbanization is weak (**Figure 5a**, right panel). This is because other taxa increased in abundance with increasing urbanization, representing a common situation of “winners and losers” averaging out at the community level (122).

### Study Grain

In a study examining the effects of the introduction of a predatory fish (see 123, 124 for study details), local species richness measured within individual ponds declined only slightly (**Figure 5b**, left panel), despite considerable temporal turnover of fauna in ponds to which fish were introduced. However, a strong threshold-like decline in richness is observed at the regional scale (the sum of species in five ponds in a spatial block) after the introduction of the fish (**Figure 5b**, right panel). This pattern is a result of fish- (i.e., predator-) driven biotic homogenization of pond communities, resulting in lowered beta diversity across space. Hence, it is important to explore grain dependence in threshold responses of biodiversity to anthropogenic drivers (125).

### Study Extent

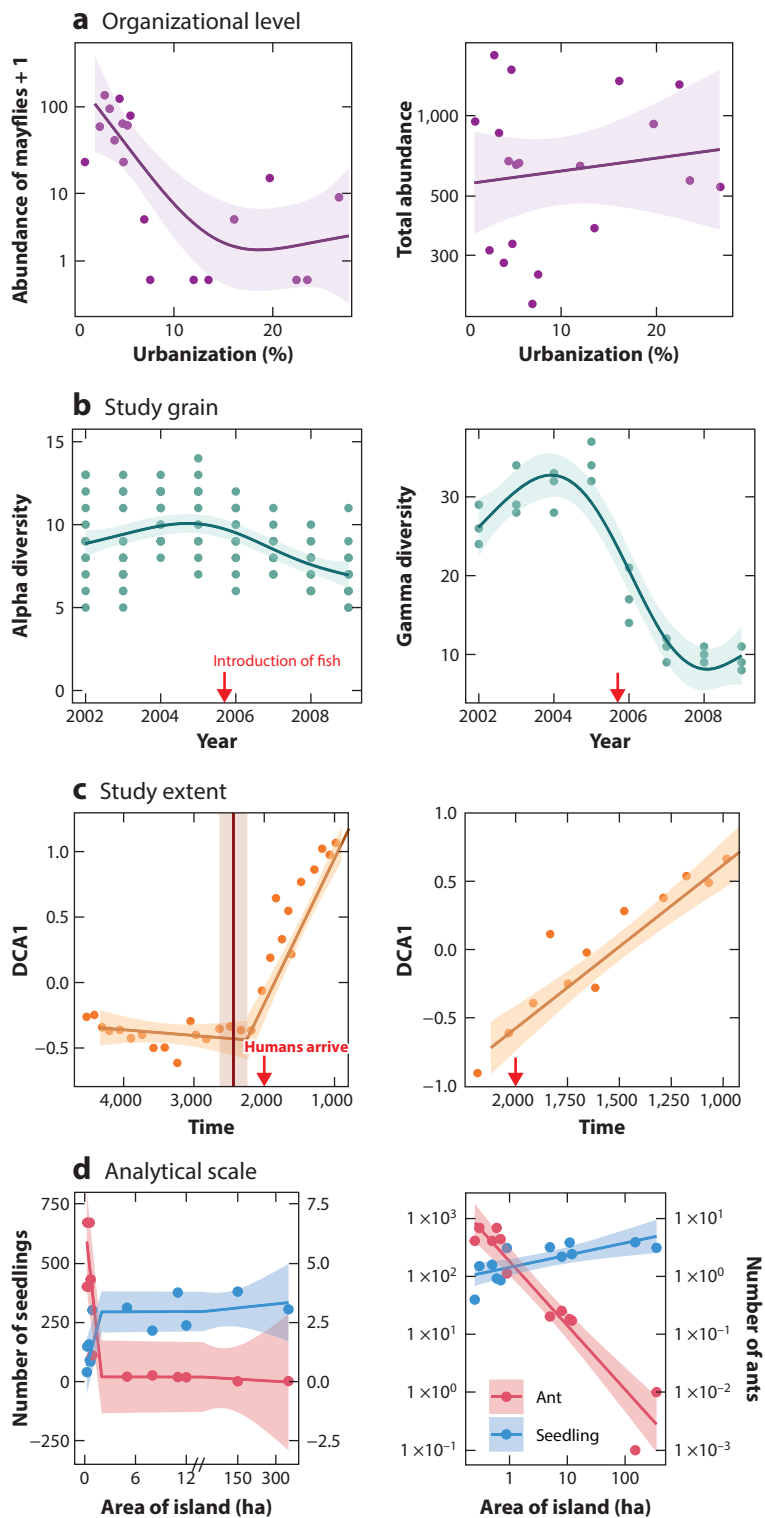
We demonstrate the influence of temporal extent on the detection of abrupt change in plant community composition turnover using a well-sampled paleoecological time series (small grain, short intervals, and long duration) from Tenerife in the Canary Islands (data from 26). The abrupt change in community turnover rates following colonization by humans (**Figure 5c**, left panel) is no longer detectable when the time series (before human arrival) was reduced in temporal extent (**Figure 5c**, right panel). This emphasizes the importance of time series length for potential baselines (i.e., prior to humans) for detecting impacts (126).

### Analytical Scale

Here we illustrate how analytical scale can influence threshold detection, using data from a study that documented abrupt changes in food-web structure on habitat islands created by a hydroelectric impoundment in Venezuela. Terborgh et al. (34) found that while larger islands had a mostly full complement of vertebrate predators, populations of these large mammals could not persist on the smaller islands, allowing smaller herbivores and seed predators to flourish and limiting the recruitment of tree seedlings. When examined on the additive scale, abrupt changes in absolute densities of leaf-cutter ants and seedlings are apparent when islands are less than  $\sim 1$  hectare (**Figure 5d**, left panel), whereas the abruptness is no longer evident and the trend is linear when analyzed on the log scale (**Figure 5d**, right panel). While noting that log-transformation can obscure a nonlinear (threshold-like) response may seem somewhat trivial, it highlights why threshold-type responses may be rare in some synthetic analyses where nonlinear transformations (e.g., log response ratios) are applied (e.g., 2).

## UTILITY OF THRESHOLD CONCEPTS IN POLICY

Broadly, threshold concepts are used to minimize adverse changes to ecosystems, by specifying acceptable levels of human activities (conservation thresholds) (18), or to reverse change, by guiding the restoration of species, populations, and ecosystem processes to some desired past state



(Caption appears on following page)



**Figure 5** (Figure appears on preceding page)

Empirical examples of scale dependence in detecting ecological thresholds. For each example, we fitted a linear model, a generalized additive model, and a segmented regression and plotted the best-supported model. Solid lines show the fitted relationships, and shading shows the 95% confidence intervals. (a) Organizational level: abundance of mayflies and total abundance of stream macroinvertebrates in response to different degrees of catchment urbanization (percent total impervious surface area; referred to here as urbanization %) (data from 116). (b) Study grain: changes in local and regional species richness of macroinvertebrates and amphibians in experimental ponds after introduction of a predatory fish (data from the same experiment as 124). (c) Study extent: detection of thresholds in the rate of palynological compositional turnover for Tenerife from a complete and a truncated sedimentary sequence (data from 26). The *x*-axis represents calibrated years before 1950. The *y*-axis represents the ordination axis 1 score of a detrended correspondence analysis (DCA1). The vertical red line indicates the detected threshold. (d) Analytical scale: density of leaf-cutter ants and tree seedling changes in islands of different size that were formed following the creation of a hydroelectric impoundment in Venezuela (data from 34). The data were analyzed and visualized on numerical scale and on a log scale. See **Supplemental Table 1** for results of model comparison.

(restoration thresholds) (36). Here we review issues that arise when threshold concepts are uncritically applied in these two approaches and outline how scale dependencies could be considered in the future.

Examples of conservation thresholds include fishery harvest quota, extinction thresholds, and critical loads of pollutant deposition. Their use is controversial given confusion about (a) whether values relate to abrupt or gradual change, (b) the risks and consequences of transgressing the threshold, (c) potential restoration costs following threshold transgression, (d) the organizational, spatial, and temporal scales at which thresholds are realized, and (e) interactions among environmental drivers (18). There is a clear need to understand the mechanistic basis underlying various threshold types observed (**Figure 1**) in order for appropriate policy responses to be developed (127).

Applications of habitat extinction and biodiversity thresholds estimated in localized case studies must consider whether land-use patterns in a region are confounded with abiotic gradients and other habitat attributes, including configuration and quality (128). Patterns of habitat loss are not random and yield fragments that are not of uniform quality. Failure to account for correlates of vegetation extent risks the prescription of erroneous area-based conservation targets in human-modified environments (35, 115). In addition to confounding, contingencies or complex interactions among abiotic and biotic variables may lead to modifications of extinction thresholds. Simmonds et al. (129) found that these contingencies are unpredictable and suggested that generalizing threshold existence and values, and incorporating them into landscape management, requires that (a) these interactions are identified and understood in a range of landscapes and (b) the confounding effect of such interactions is controlled for in analyses of threshold responses to natural land cover.

The prescription of thresholds will be hampered by climate change, which can modify multiple abiotic and biotic components of ecosystems and interact with other anthropogenic drivers (12). Threshold uncertainties and contingencies with climate change must be carefully communicated using multiple scenarios. For example, Winter et al. (130) used age-structured population models to show how fishing-induced Allee effects change with climate scenarios. Once contingencies are quantified, interactive web tools and maps that dynamically update in response to user-specified contextual factors or scenarios can be used to apply more localized, context-dependent threshold values (131).

Threshold concepts are used in ecological restoration to understand why recovery is failing and identify appropriate restoration interventions (132). For example, restoration can be slow

**Supplemental Material** >

due to stabilizing feedback processes or ongoing disturbances (133). Restoration interventions can involve the simple removal of anthropogenic pressures, or facilitate the recovery of intrinsic processes, such as interactions between organisms or dispersal across human-modified landscapes. However, restoring ecosystems to predisturbance levels may be exceedingly difficult or unattainable even with intensive restoration interventions (134) and, as a result, an increasingly widespread, yet debated, view is that future novel ecosystems can instead be targeted in a changed world (135, 136).

### **Implementing Science-Based Policy Using Ecological Thresholds**

It is clear that the context dependence of ecological thresholds undermines the use of threshold concepts, and their specific values, across policy contexts. Rather than providing policymakers with “magic bullets” (137) (e.g., how much habitat is enough?), scientists can inform policies by identifying the mechanisms through which thresholds may or may not arise (137). Kelly et al. (10) and Foley et al. (11) reviewed the implementation of threshold concepts in a range of policy contexts and identified three features that determine their usefulness, which we expand on here. First, timely and consistent monitoring of appropriate ecosystem response variables can allow better quantification of possible early-warning signals, such as rising variance or autocorrelation in key community parameters. This requires that monitoring is carried out using appropriate response metrics (organizational levels), spatiotemporal grains and extents, and analytical scales. If these are not known a priori, then multiple scales should be adopted in early monitoring stages. Second, adaptive policies that explicitly consider the possibility of a threshold transgression and respond to early warnings are more effective than reactive management in systems where restoration would be extremely difficult. Finally, knowledge of the mechanisms that underlie ecological thresholds can inform policies by identifying the appropriate scales at which specific drivers should be managed and measured in future monitoring efforts. For example, in relatively small or discrete ecosystems, such as shallow lakes and coastal lagoons, drivers of change are relatively tractable because local inputs can be regulated. However, processes and drivers operating at larger scales, such as regional nutrient inputs, can overwhelm the effects of local intervention and require multilateral policy reforms.

### **TOWARD A PREDICTIVE UNDERSTANDING OF ECOLOGICAL THRESHOLDS THROUGH SYNTHESIS**

Synthesis allows us to extend the scope of inference of individual studies, for example by increasing the length of an anthropogenic gradient sampled in any one study. Moreover, by virtue of its comparative lens, synthesis could help reconcile idiosyncrasies in threshold research, for example, by assessing the relative prevalence of threshold versus gradual ecological responses to global change (2), evaluating the correspondence between abrupt changes to island flora and human arrival (26), or contrasting tropical versus temperate habitat extinction threshold values (138).

Hillebrand et al. (2) combined data from 36 meta-analyses—which together included more than 4,600 studies conducted in terrestrial, aquatic, and marine systems—to assess the prevalence of threshold responses to a range of environmental pressures. Despite evidence for strong responses of ecosystem variables to environmental pressure across the compiled datasets (e.g., biomass production in response to fertilization), they concluded that threshold transgressions were rare (2). Rather, they found that ecological responses were gradual, with significant variation across studies, and concluded that thresholds are unlikely to be detected because of noise and complex interactions of multiple pressures and responses (see, however, 139 for objections to the overall

conclusions). However, as discussed above, the primary analyses used by Hillebrand et al. were based on log-response ratios, which are less likely to detect threshold-like changes across studies with varying baselines. In future syntheses, scale could provide a unifying framework with which to disentangle these complexities and yield more targeted analyses and nuanced generalizations about when and where thresholds are more or less likely to emerge.

Future lines of inquiry that could improve our predictive understanding of thresholds include whether drivers are shared or distinct across different ecosystems, organizational levels, or biomes (19). The synthesis of long-term, distributed field studies that sample broad environmental gradients (especially extremes) could be used to characterize their interactions with climatic and biogeographic gradients. Currently, however, quantitative synthesis is challenged by the diversity of scales employed by primary studies, in addition to variation in baseline states (19). Caution must be exercised to avoid misattributing contingencies in threshold values to systematic differences in grain and extent across groups of studies. The archival of raw, site-level data could permit the application of uniform analytical approaches, including causal inference, and modeling of contingencies (140). The scale of effect size estimation must also be carefully considered (e.g., avoiding effect sizes that linearize nonlinear relationships, such as log response ratios, when modeling driver-response relationships). In sum, synthesis of ecological thresholds will require the development of appropriate data and analyses that explicitly account for the different domains of scale we have reviewed here. We must take care not to overgeneralize across domains of scale that we know are critically important in determining processes and patterns in ecology.

## SUMMARY POINTS

1. Thresholds in ecological responses to anthropogenic drivers are an attractive concept for both scientific research and policy decisions, but there are controversies surrounding their existence, detection, mechanisms, and generalizability.
2. We broadly define thresholds as a point of relatively abrupt change in a nonlinear relationship between a driver and its ecological response.
3. Many analytical approaches are available to detect thresholds, including segmented regression, generalized additive models, clustering or partitioning analysis, and complex methods that test for hysteresis.
4. Thresholds are observed in many systems for all the big five anthropogenic stressors (harvesting, land-/sea-use change, pollution, invasive species, and climate change), but not always.
5. Threshold concepts have been embraced by policies that aim to mitigate against these drivers, yet their effectiveness as a management tool has been questioned.
6. We show how scale can serve as a unifying framework to reconcile context dependencies in threshold research. Threshold detection generally depends on the degree of alignment between the intrinsic scales of the organisms under study and the scales of observation imposed by the researcher, and these are framed by organizational levels, grains, extents, and analytical decisions within the analysis.
7. The diversity of observation scales used in primary studies makes synthesizing threshold research challenging, but such synthesis could improve our predictive understanding of thresholds and their utility in environmental policies.

## FUTURE ISSUES

1. Can causal inference approaches to the design and analysis (e.g., statistical matching, structural equation modeling) of observational studies strengthen the attribution of threshold responses to specific drivers?
2. Long-term, distributed field studies that sample large environmental gradients (particularly extremes) could be used to better sample environmental gradients and understand their interactions with climatic and biogeographic gradients.
3. Better linkage between theoretical models, experimental studies, and empirical studies is needed to understand what biological features promote or impede a threshold response in real-world systems.
4. Novel synthesis approaches are needed to carefully account for the differences in observation scales of separate studies and datasets to better characterize the mean and variation in thresholds (in terms of existence, magnitude, and location) among taxa and environments.
5. Interdisciplinary approaches are needed to ensure the appropriate transfer of the findings from threshold research, as well as to develop ways to communicate their contingency and uncertainty.

## DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

## ACKNOWLEDGMENTS

All coauthors gratefully acknowledge the support of iDiv, funded by the German Research Foundation (DFG–FZT 118, 202548816).

## LITERATURE CITED

1. Berdugo M, Delgado-Baquerizo M, Soliveres S, Hernández-Clemente R, Zhao Y, et al. 2020. Global ecosystem thresholds driven by aridity. *Science* 367(6479):787–90
2. Hillebrand H, Donohue I, Harpole WS, Hodapp D, Kucera M, et al. 2020. Thresholds for ecological responses to global change do not emerge from empirical data. *Nat. Ecol. Evol.* 4(11):1502–9
3. Ruddiman WF. 2013. The Anthropocene. *Annu. Rev. Earth Planet. Sci.* 41:45–68
4. Malhi Y. 2017. The concept of the Anthropocene. *Annu. Rev. Environ. Resour.* 42:77–104
5. Díaz S, Settele J, Brondízio ES, Ngo HT, Agard J, et al. 2019. Pervasive human-driven decline of life on Earth points to the need for transformative change. *Science* 366(6471):1–10
6. Leclère D, Obersteiner M, Barrett M, Butchart SHM, Chaudhary A, et al. 2020. Bending the curve of terrestrial biodiversity needs an integrated strategy. *Nature* 585(7826):551–56
7. Scheffer M, Jeppesen E. 2007. Regime shifts in shallow lakes. *Ecosystems* 10(1):1–3
8. de Young B, Barange M, Beaugrand G, Harris R, Perry RI, et al. 2008. Regime shifts in marine ecosystems: detection, prediction and management. *Trends Ecol. Evol.* 23(7):402–9
9. Ratajczak Z, Carpenter SR, Ives AR, Kucharik CJ, Ramiadantsoa T, et al. 2018. Abrupt change in ecological systems: inference and diagnosis. *Trends Ecol. Evol.* 33(7):513–26
10. Kelly RP, Erickson AL, Mease LA, Battista W, Kittinger JN, Fujita R. 2015. Embracing thresholds for better environmental management. *Philos. Trans. R. Soc. B.* 370(1659):20130276

11. Foley MM, Martone RG, Fox MD, Kappel CV, Mease LA, et al. 2015. Using ecological thresholds to inform resource management: current options and future possibilities. *Front. Mar. Sci.* 2(95):1–12
12. Newton AC. 2021. *Ecosystem Collapse and Recovery*. Cambridge, UK: Cambridge Univ. Press
13. Rockström J, Steffen W, Noone K, Persson Å, Chapin FS, et al. 2009. A safe operating space for humanity. *Nature* 461(7263):472–75
14. Lade SJ, Steffen W, de Vries W, Carpenter SR, Donges JF, et al. 2020. Human impacts on planetary boundaries amplified by Earth system interactions. *Nat. Sustain.* 3(2):119–28
15. Groffman PM, Baron JS, Blett T, Gold AJ, Goodman I, et al. 2006. Ecological thresholds: The key to successful environmental management or an important concept with no practical application? *Ecosystems* 9:1–13
16. Dodds WK, Clements WH, Gido K, Hilderbrand RH, King RS. 2010. Thresholds, breakpoints, and nonlinearity in freshwaters as related to management. *J. North Am. Benthol. Soc.* 29(3):988–97
17. Banks-Leite C, Larrosa C, Carrasco LR, Tambosi LR, Milner-Gulland EJ. 2021. The suggestion that landscapes should contain 40% of forest cover lacks evidence and is problematic. *Ecol. Lett.* 24(5):1112–13
18. Johnson CJ. 2013. Identifying ecological thresholds for regulating human activity: Effective conservation or wishful thinking? *Biol. Conserv.* 168:57–65
19. Turner MG, Calder WJ, Cumming GS, Hughes TP, Jentsch A, et al. 2020. Climate change, ecosystems and abrupt change: science priorities. *Philos. Trans. R. Soc. B.* 375(1794):20190105
20. Worm B, Barbier EB, Beaumont N, Duffy JE, Folke C, et al. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314(5800):787–90
21. Daan N, Gislason H, Pope JG, Rice JC. 2011. Apocalypse in world fisheries? The reports of their death are greatly exaggerated. *ICES J. Mar. Sci.* 68(7):1375–78
22. Pauly D, Hilborn R, Branch TA. 2013. Fisheries: Does catch reflect abundance? *Nature* 494(7437):303–6
23. Arroyo-Rodríguez V, Fahrig L, Tabarelli M, Watling JI, Tischendorf L, et al. 2020. Designing optimal human-modified landscapes for forest biodiversity conservation. *Ecol. Lett.* 23(9):1404–20
24. Scheffer M, Carpenter S, Foley JA, Folke C, Walker B. 2001. Catastrophic shifts in ecosystems. *Nature* 413(6856):591–96
25. Simkin SM, Allen EB, Bowman WD, Clark CM, Belnap J, et al. 2016. Conditional vulnerability of plant diversity to atmospheric nitrogen deposition across the United States. *PNAS* 113(15):4086–91
26. Nogué S, Santos AMC, Birks HJB, Björck S, Castilla-Beltrán A, et al. 2021. The human dimension of biodiversity changes on islands. *Science* 372(6541):488–91
27. Biggs R, Peterson GD, Rocha JC. 2018. The Regime Shifts Database: a framework for analyzing regime shifts in social-ecological systems. *Ecol. Soc.* 23(3):9
28. Scheffer M, Bascompte J, Brock WA, Brovkin V, Carpenter SR, et al. 2009. Early-warning signals for critical transitions. *Nature* 461(7260):53–59
29. Brook BW, Ellis EC, Perring MP, Mackay AW, Blomqvist L. 2013. Does the terrestrial biosphere have planetary tipping points? *Trends Ecol. Evol.* 28(7):396–401
30. Scheffer M, Carpenter SR, Lenton TM, Bascompte J, Brock W, et al. 2012. Anticipating critical transitions. *Science* 338(6105):344–48
31. Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, et al. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annu. Rev. Ecol. Evol. Syst.* 35:557–81
32. Mace GM, Reyers B, Alkemade R, Biggs R, Chapin FS III, et al. 2014. Approaches to defining a planetary boundary for biodiversity. *Glob. Environ. Change* 28:289–97
33. Burns DA, Blett T, Haeuber R, Pardo LH. 2008. Critical loads as a policy tool for protecting ecosystems from the effects of air pollutants. *Front. Ecol. Environ.* 6(3):156–59
34. Terborgh J, Lopez L, Nuñez P, Rao M, Shahabuddin G, et al. 2001. Ecological meltdown in predator-free forest fragments. *Science* 294(5548):1923–26
35. Lindenmayer DB, Luck G. 2005. Synthesis: thresholds in conservation and management. *Biol. Conserv.* 124(3):351–54
36. Suding KN, Hobbs RJ. 2009. Threshold models in restoration and conservation: a developing framework. *Trends Ecol. Evol.* 24(5):271–79
37. Hilker FM, Liz E. 2020. Threshold harvesting as a conservation or exploitation strategy in population management. *Theoret. Ecol.* 13:519–536

38. Hutchings JA, Reynolds JD. 2004. Marine fish population collapses: consequences for recovery and extinction risk. *Bioscience* 54(4):297–309
39. Frank KT, Petrie B, Choi JS, Leggett WC. 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science* 308(5728):1621–23
40. Silva WTAF, Bottagisio E, Härkönen T, Galatius A, Olsen MT, Harding KC. 2021. Risk for over-exploiting a seemingly stable seal population: influence of multiple stressors and hunting. *Ecosphere* 12(1):e03343
41. Houk P, Cuetos-Bueno J, Kerr AM, McCann K. 2018. Linking fishing pressure with ecosystem thresholds and food web stability on coral reefs. *Ecol. Monogr.* 88(1):109–19
42. Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.* 34:487–515
43. Fahrig L, Watling JI, Arnillas CA, Arroyo-Rodríguez V, Jörgen-Hickfang T, et al. 2021. Resolving the SLOSS dilemma for biodiversity conservation: a research agenda. *Biol. Rev.* 97(1):99–104
44. Kremen C. 2015. Reframing the land-sparing/land-sharing debate for biodiversity conservation. *Ann. N. Y. Acad. Sci.* 1355(1):52–76
45. Fischer J, Abson DJ, Butsic V, Chappell MJ, Ekroos J, et al. 2014. Land sparing versus land sharing: moving forward. *Conserv. Lett.* 7(3):149–57
46. Chen K, Olden JD. 2020. Threshold responses of riverine fish communities to land use conversion across regions of the world. *Glob. Change Biol.* 26(9):4952–65
47. Felipe-Lucia MR, Soliveres S, Penone C, Fischer M, Ammer C, et al. 2020. Land-use intensity alters networks between biodiversity, ecosystem functions, and services. *PNAS* 117(45):28140–49
48. Wies G, Arzeta SN, Ramos MM. 2021. Critical ecological thresholds for conservation of tropical rainforest in Human Modified Landscapes. *Biol. Conserv.* 255:109023
49. Hughes BB, Eby R, Van Dyke E, Tinker MT, Marks CI, et al. 2013. Recovery of a top predator mediates negative eutrophic effects on seagrass. *PNAS* 110(38):15313–18
50. Burkholder JAM, Tomasko DA, Touchette BW. 2007. Seagrasses and eutrophication. *J. Exp. Mar. Bio. Ecol.* 350(1–2):46–72
51. Kelly MG, Phillips G, Teixeira H, Várbiro G, Salas Herrero F, et al. 2022. Establishing ecologically-relevant nutrient thresholds: a tool-kit with guidance on its use. *Sci. Total Environ.* 807(Pt. 3):150977
52. Payne RJ, Dise NB, Stevens CJ, Gowing DJ, others. 2013. Impact of nitrogen deposition at the species level. *PNAS* 110(3):984–87
53. Pardo LH, Fenn ME, Goodale CL, Geiser LH, Driscoll CT, et al. 2011. Effects of nitrogen deposition and empirical nitrogen critical loads for ecoregions of the United States. *Ecol. Appl.* 21(8):3049–82
54. Wilkins K, Clark C, Aherne J. 2022. Ecological thresholds under atmospheric nitrogen deposition for 1200 herbaceous species and 24 communities across the US. *Glob. Change Biol.* 28(7):2381–95
55. Lovett GM. 2013. Critical issues for critical loads. *PNAS* 110(3):808–9
56. Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, et al. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol. Lett.* 14(7):702–8
57. Reynolds SA, Aldridge DC. 2021. Global impacts of invasive species on the tipping points of shallow lakes. *Glob. Change Biol.* 27(3):6129–38
58. Taylor CM, Hastings A. 2005. Allee effects in biological invasions. *Ecol. Lett.* 8(8):895–908
59. Crandall R, Knight TM. 2015. Positive frequency dependence undermines the success of restoration using historical disturbance regimes. *Ecol. Lett.* 18(9):883–91
60. Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F. 2012. Impacts of climate change on the future of biodiversity. *Ecol. Lett.* 15(4):365–77
61. Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG, Anderson KD, et al. 2017. Global warming and recurrent mass bleaching of corals. *Nature* 543(7645):373–77
62. Montoya JM, Donohue I, Pimm SL. 2018. Planetary boundaries for biodiversity: implausible science, pernicious policies. *Trends Ecol. Evol.* 33(2):71–73
63. Banks-Leite C, Pardini R, Tambosi LR, Pearse WD, Bueno AA, et al. 2014. Using ecological thresholds to evaluate the costs and benefits of set-asides in a biodiversity hotspot. *Science* 345(6200):1041–45
64. Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, et al. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *PNAS* 105(18):6668–72

65. Bonachela JA, Burrows MT, Pinsky ML. 2021. Shape of species climate response curves affects community response to climate change. *Ecol. Lett.* 24(4):708–18
66. Dodson SI, Arnott SE, Cottingham KL. 2000. The relationship in lake communities between primary productivity and species richness. *Ecology* 81(10):2662–79
67. Callaghan CT, Bino G, Major RE, Martin JM, Lyons MB, Kingsford RT. 2019. Heterogeneous urban green areas are bird diversity hotspots: insights using continental-scale citizen science data. *Landscape Ecol.* 34(6):1231–46
68. Yuan ZY, Jiao F, Li YH, Kallenbach RL. 2016. Anthropogenic disturbances are key to maintaining the biodiversity of grasslands. *Sci. Rep.* 6(1):1–8
69. Beisner BE, Haydon DT, Cuddington K. 2003. Alternative stable states in ecology. *Front. Ecol. Environ.* 1(7):376–82
70. Fukami T, Nakajima M. 2011. Community assembly: Alternative stable states or alternative transient states? *Ecol. Lett.* 14(10):973–84
71. Staver AC, Archibald S, Levin SA. 2011. The global extent and determinants of savanna and forest as alternative biome states. *Science* 334(6053):230–32
72. Mumby PJ, Hastings A, Edwards HJ. 2007. Thresholds and the resilience of Caribbean coral reefs. *Nature* 450(7166):98–101
73. Chen N, Yu K, Jia R, Teng J, Zhao C. 2020. Biocrust as one of multiple stable states in global drylands. *Sci. Adv.* 6(39):eaay3763
74. Rocha JC, Peterson G, Bodin Ö, Levin S. 2018. Cascading regime shifts within and across scales. *Science* 362(6421):1379–83
75. Barry D, Hartigan JA. 1993. A Bayesian analysis for change point problems. *J. Am. Stat. Assoc.* 88(421):309–19
76. Ficetola GF, Denoël M. 2009. Ecological thresholds: an assessment of methods to identify abrupt changes in species–habitat relationships. *Ecography* 32(6):1075–84
77. Leisch F, Hornik K, Kuan C-M. 2000. Monitoring structural changes with the generalized fluctuation test. *Econom. Theory.* 16(6):835–54
78. Toms JD, Lesperance ML. 2003. Piecewise regression: a tool for identifying ecological thresholds. *Ecology* 84(8):2034–41
79. Yin D, Leroux SJ, He F. 2017. Methods and models for identifying thresholds of habitat loss. *Ecography* 40(1):131–43
80. Samhouri JF, Andrews KS, Fay G, Harvey CJ, Hazen EL, et al. 2017. Defining ecosystem thresholds for human activities and environmental pressures in the California Current. *Ecosphere* 8(6):e01860
81. Su H, Wang R, Feng Y, Li Y, Li Y, et al. 2021. Long-term empirical evidence, early warning signals and multiple drivers of regime shifts in a lake ecosystem. *J. Ecol.* 109(9):3182–94
82. Poikane S, Várbró G, Kelly MG, Birk S, Phillips G. 2021. Estimating river nutrient concentrations consistent with good ecological condition: more stringent nutrient thresholds needed. *Ecol. Indic.* 121:107017
83. Bestelmeyer BT, Ellison AM, Fraser WR, Gorman KB, Holbrook SJ, et al. 2011. Analysis of abrupt transitions in ecological systems. *Ecosphere* 2(12):1–26
84. Litzow MA, Hunsicker ME. 2016. Early warning signals, nonlinearity, and signs of hysteresis in real ecosystems. *Ecosphere* 7(12):e01614
85. Schmitt RJ, Holbrook SJ, Davis SL, Brooks AJ, Adam TC. 2019. Experimental support for alternative attractors on coral reefs. *PNAS* 116(10):4372–81
86. Boettiger C, Hastings A. 2012. Quantifying limits to detection of early warning for critical transitions. *J. R. Soc. Interface* 9(75):2527–39
87. Levin SA. 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology* 73(6):1943–67
88. Allen TF, Starr T. 1982. *Hierarchy: Perspectives for Ecological Complexity*. Chicago: Univ. Chicago Press
89. Chave J. 2013. The problem of pattern and scale in ecology: What have we learned in 20 years? *Ecol. Lett.* 16:4–16
90. Wu J, Li H. 2006. Concepts of scale and scaling. In *Scaling and Uncertainty Analysis in Ecology: Methods and Applications*, ed. J Wu, KB Jones, H Li, OL Loucks, pp. 3–15. Dordrecht, Neth.: Springer

91. Jackson HB, Fahrig L. 2012. What size is a biologically relevant landscape? *Landscape Ecol.* 27(7):929–41
92. Chandler R, Hepinstall-Cymerman J. 2016. Estimating the spatial scales of landscape effects on abundance. *Landscape Ecol.* 31(6):1383–94
93. Baker ME, King RS. 2010. A new method for detecting and interpreting biodiversity and ecological community thresholds. *Methods Ecol. Evol.* 1(1):25–37
94. With KA, Crist TO. 1995. Critical thresholds in species' responses to landscape structure. *Ecology* 76(8):2446–59
95. Aspin TWH, Khamis K, Matthews TJ, Milner AM, O'Callaghan MJ, et al. 2019. Extreme drought pushes stream invertebrate communities over functional thresholds. *Glob. Change Biol.* 25(1):230–44
96. Trisos CH, Merow C, Pigot AL. 2020. The projected timing of abrupt ecological disruption from climate change. *Nature* 580(7804):496–501
97. Carstensen J, Telford RJ, Birks HJB. 2013. Diatom flickering prior to regime shift. *Nature* 498(7455):E11–12
98. Taranu ZE, Carpenter SR, Frossard V, Jenny J-P, Thomas Z, et al. 2018. Can we detect ecosystem critical transitions and signals of changing resilience from paleo-ecological records? *Ecosphere* 9(10):e02438
99. Anderson L, Wahl DB, Bhattacharya T. 2022. Understanding rates of change: a case study using fossil pollen records from California to assess the potential for and challenges to a regional data synthesis. *Quat. Int.* 621:26–36
100. Doncaster CP, Alonso Chávez V, Viguier C, Wang R, Zhang E, et al. 2016. Early warning of critical transitions in biodiversity from compositional disorder. *Ecology* 97(11):3079–90
101. Mottl O, Grytes J-A, Seddon AWR, Steinbauer MJ, Bhatta KP, et al. 2021. Rate-of-change analysis in palaeoecology revisited: a new approach. *Rev. Palaeobot. Palynol.* 293:104483
102. Holland JD, Bert DG, Fahrig L. 2004. Determining the spatial scale of species' response to habitat. *Bioscience* 54(3):227–33
103. Lechner AM, Langford WT, Jones SD, Bekessy SA, Gordon A. 2012. Investigating species–environment relationships at multiple scales: differentiating between intrinsic scale and the modifiable areal unit problem. *Ecol. Complex.* 11:91–102
104. Kupsch D, Vendras E, Ocampo-Ariza C, Batáry P, Motombi FN, et al. 2019. High critical forest habitat thresholds of native bird communities in Afrotropical agroforestry landscapes. *Biol. Conserv.* 230:20–28
105. Eigenbrod F, Hecnar SJ, Fahrig L. 2011. Sub-optimal study design has major impacts on landscape-scale inference. *Biol. Conserv.* 144(1):298–305
106. Viana DS, Granados JE, Fandos P, Pérez JM, Cano-Manuel FJ, et al. 2018. Linking seasonal home range size with habitat selection and movement in a mountain ungulate. *Mov. Ecol.* 6(1):1–11
107. Ridding LE, Newton AC, Keith SA, Walls RM, Diaz A, et al. 2021. Inconsistent detection of extinction debts using different methods. *Ecography* 44(1):33–43
108. Daily JP, Hitt NP, Smith DR, Snyder CD. 2012. Experimental and environmental factors affect spurious detection of ecological thresholds. *Ecology* 93(1):17–23
109. Bruel R, White ER. 2021. Sampling requirements and approaches to detect ecosystem shifts. *Ecol. Indic.* 121:107096
110. Spake R, Bellamy C, Graham L, Watts K, Wilson T, et al. 2019. An analytical framework for spatially targeted management of natural capital. *Nat. Sustain.* 2(2):90–97
111. Durant JM, Ono K, Stenseth NC, Langanen Ø. 2020. Nonlinearity in interspecific interactions in response to climate change: cod and haddock as an example. *Glob. Change Biol.* 26(10):5554–63
112. Xiao X, White EP, Hooten MB, Durham SL. 2011. On the use of log-transformation versus nonlinear regression for analyzing biological power laws. *Ecology* 92(10):1887–94
113. Andersen T, Carstensen J, Hernandez-Garcia E, Duarte CM. 2009. Ecological thresholds and regime shifts: approaches to identification. *Trends Ecol. Evol.* 24(1):49–57
114. Thomson JR, Kimmerer WJ, Brown LR, Newman KB, Mac Nally R, et al. 2010. Bayesian change point analysis of abundance trends for pelagic fishes in the upper San Francisco Estuary. *Ecol. Appl.* 20(5):1431–48
115. Simmonds JS, van Rensburg BJ, Maron M. 2017. Non-random patterns of vegetation clearing and potential biases in studies of habitat area effects. *Landscape Ecol.* 32(4):729–43



116. Ferraro PJ, Sanchirico JN, Smith MD. 2019. Causal inference in coupled human and natural systems. *PNAS* 116(12):5311–18
117. Stuart EA. 2010. Matching methods for causal inference: a review and a look forward. *Stat. Sci.* 25(1):1–21
118. Grace JB, Irvine KM. 2020. Scientist's guide to developing explanatory statistical models using causal analysis principles. *Ecology* 101(4):e02962
119. Griffen BD, Belgrad BA, Cannizzo ZJ, Knotts ER, Hancock ER. 2016. Rethinking our approach to multiple stressor studies in marine environments. *Mar. Ecol. Prog. Ser.* 543:273–81
120. Thompson PL, Guzman LM, De Meester L, Horváth Z, Ptacnik R, et al. 2020. A process-based metacommunity framework linking local and regional scale community ecology. *Ecol. Lett.* 23(9):1314–29
121. Morse CC, Huryn AD, Cronan C. 2003. Impervious surface area as a predictor of the effects of urbanization on stream insect communities in Maine, USA. *Environ. Monit. Assess.* 89(1):95–127
122. Dornelas M, Gotelli NJ, Shimadzu H, Moyes F, Magurran AE, McGill BJ. 2019. A balance of winners and losers in the Anthropocene. *Ecol. Lett.* 22(5):847–54
123. Chase JM, Biro EG, Ryberg WA, Smith KG. 2009. Predators temper the relative importance of stochastic processes in the assembly of prey metacommunities. *Ecol. Lett.* 12(11):1210–18
124. Chase JM. 2010. Stochastic community assembly causes higher biodiversity in more productive environments. *Science* 328(5984):1388–91
125. Chase JM, McGill BJ, Thompson PL, Antão LH, Bates AE, et al. 2019. Species richness change across spatial scales. *Oikos* 128(8):1079–91
126. Bull JW, Gordon A, Law EA, Suttle KB, Milner-Gulland EJ. 2014. Importance of baseline specification in evaluating conservation interventions and achieving no net loss of biodiversity. *Conserv. Biol.* 28(3):799–809
127. Watson SCL, Grandfield FGC, Herbert RJH, Newton AC. 2018. Detecting ecological thresholds and tipping points in the natural capital assets of a protected coastal ecosystem. *Estuar. Coast. Shelf Sci.* 215:112–23
128. Mace GM, Hails RS, Cryle P, Harlow J, Clarke SJ. 2015. Towards a risk register for natural capital. *J. Appl. Ecol.* 52(3):641–53
129. Simmonds JS, van Rensburg BJ, Tulloch AIT, Maron M. 2019. Landscape-specific thresholds in the relationship between species richness and natural land cover. *J. Appl. Ecol.* 56(4):1019–29
130. Winter A-M, Richter A, Eikeset AM. 2020. Implications of Allee effects for fisheries management in a changing climate: evidence from Atlantic cod. *Ecol. Appl.* 30(1):e01994
131. Spake R, Bellamy C, Gill R, Watts K, Wilson T, et al. 2020. Forest damage by deer depends on cross-scale interactions between climate, deer density and landscape structure. *J. Appl. Ecol.* 57:1376–90
132. Brudvig LA, Barak RS, Bauer JT, Caughlin TT, Laughlin DC, et al. 2017. Interpreting variation to advance predictive restoration science. *J. Appl. Ecol.* 54(4):1018–27
133. Kéfi S, Holmgren M, Scheffer M. 2016. When can positive interactions cause alternative stable states in ecosystems? *Funct. Ecol.* 30(1):88–97
134. Wiens JA, Hobbs RJ. 2015. Integrating conservation and restoration in a changing world. *Bioscience* 65(3):302–12
135. Hobbs RJ, Higgs E, Harris JA. 2009. Novel ecosystems: implications for conservation and restoration. *Trends Ecol. Evol.* 24(11):599–605
136. Gardner CJ, Bullock JM. 2021. In the climate emergency, conservation must become survival ecology. *Front. Conserv. Sci.* 2:659912
137. Huggett AJ. 2005. The concept and utility of 'ecological thresholds' in biodiversity conservation. *Biol. Conserv.* 124(3):301–10
138. Melo I, Ochoa-Quintero JM, de Oliveira Roque F, Dalsgaard B. 2018. A review of threshold responses of birds to landscape changes across the world. *J. Field Ornithol.* 89(4):303–14
139. Lade SJ, Wang-Erlandsson L, Staal A, Rocha JC. 2021. Empirical pressure-response relations can benefit assessment of safe operating spaces. *Nat. Ecol. Evol.* 5:1078–79
140. Ladouceur E, Shackelford N, Bouazza K, Brudvig L, Bucharova A, et al. 2022. Knowledge sharing for shared success in the decade on ecosystem restoration. *Ecol. Solut. Evid.* 3(1):e12117



# Contents

The Great Intergenerational Robbery: A Call for Concerted Action Against Environmental Crises <i>Asbok Gadgil, Thomas P. Tomich, Arun Agrawal, Jeremy Allouche, Inês M.L. Azevedo, Mohamed I. Bakarr, Gilberto M. Jannuzzi, Diana Liverman, Yadvinder Malhi, Stephen Polasky, Joyashree Roy, Diana Ürge-Vorsatz, and Yanxin Wang</i> .....	1
<b>I. Integrative Themes and Emerging Concerns</b>	
A New Dark Age? Truth, Trust, and Environmental Science <i>Torbjørn Gundersen, Donya Alinejad, T.Y. Branch, Bobby Duffy, Kirstie Hewlett, Cathrine Holst, Susan Owens, Folco Panizza, Silje Maria Tellmann, José van Dijk, and Maria Baghramian</i> .....	5
Biodiversity: Concepts, Patterns, Trends, and Perspectives <i>Sandra Díaz and Yadvinder Malhi</i> .....	31
COVID-19 and the Environment: Short-Run and Potential Long-Run Impacts <i>Noah S. Diffenbaugh</i> .....	65
Shepherding Sub-Saharan Africa's Wildlife Through Peak Anthropogenic Pressure Toward a Green Anthropocene <i>P.A. Lindsey, S.H. Anderson, A. Dickman, P. Gandiwa, S. Harper, A.B. Morakinyo, N. Nyambe, M. O'Brien-Onyeka, C. Packer, A.H. Parker, A.S. Robson, Alice Rubweza, E.A. Sogbobossou, K.W. Steiner, and P.N. Tumenta</i> .....	91
The Role of Nature-Based Solutions in Supporting Social-Ecological Resilience for Climate Change Adaptation <i>Beth Turner, Tabia Devisscher, Nicole Chabaneix, Stephen Woroniecki, Christian Messier, and Nathalie Seddon</i> .....	123
Feminist Ecologies <i>Diana Ojeda, Padini Nirmal, Dianne Rocheleau, and Jody Emel</i> .....	149
Sustainability in Health Care <i>Howard Hu, Gary Cohen, Bhavna Sharma, Hao Yin, and Rob McConnell</i> .....	173

Indoor Air Pollution and Health: Bridging Perspectives from Developing and Developed Countries <i>Ajay Pillarisetti, Wenlu Ye, and Sourangsu Chowdhury</i> .....	197
--	-----

## II. Earth's Life Support Systems

State of the World's Birds <i>Alexander C. Lees, Lucy Haskell, Tris Allinson, Simeon B. Bezeng, Ian J. Burfield, Luis Miguel Renjifo, Kenneth V. Rosenberg, Asbwin Viswanathan, and Stuart H.M. Butchart</i> .....	231
Grassy Ecosystems in the Anthropocene <i>Nicola Stevens, William Bond, Angelica Feurdean, and Caroline E.R. Lehmann</i> .....	261
Anticipating the Future of the World's Ocean <i>Casey C. O'Hara and Benjamin S. Halpern</i> .....	291
The Ocean Carbon Cycle <i>Tim DeVries</i> .....	317
Permafrost and Climate Change: Carbon Cycle Feedbacks From the Warming Arctic <i>Edward A.G. Schuur, Benjamin W. Abbott, Roisin Commane, Jessica Ernakovich, Eugenie Euskirchen, Gustaf Hugelius, Guido Grosse, Miriam Jones, Charlie Koven, Victor Lesbyk, David Lawrence, Michael M. Loranty, Marguerite Mauritz, David Olefeldt, Susan Natali, Heidi Rodenbizer, Verity Salmon, Christina Schädel, Jens Strauss, Claire Treat, and Merritt Turetsky</i> .....	343

## III. Human Use of the Environment and Resources

Environmental Impacts of Artificial Light at Night <i>Kevin J. Gaston and Alejandro Sánchez de Miguel</i> .....	373
Agrochemicals, Environment, and Human Health <i>P. Indira Devi, M. Manjula, and R.V. Bhavani</i> .....	399
The Future of Tourism in the Anthropocene <i>A. Holden, T. Jamal, and F. Burini</i> .....	423
Sustainable Cooling in a Warming World: Technologies, Cultures, and Circularity <i>Radhika Khosla, Renaldi Renaldi, Antonella Mazzone, Caitlin McElroy, and Giovanni Palafox-Alcantar</i> .....	449

<p>Digitalization and the Anthropocene  <i>Felix Creutzig, Daron Acemoglu, Xuemei Bai, Paul N. Edwards,  Marie Josefine Hintz, Lynn H. Kaack, Siir Kilkis, Stefanie Kunkel,  Amy Luers, Nikola Milojevic-Dupont, Dave Rejeski, Jürgen Renn,  David Rohnick, Christoph Rosol, Daniela Russ, Thomas Turnbull,  Elena Verdolini, Felix Wagner, Charlie Wilson, Aicha Zekar,  and Marius Zumbald</i> .....</p>	479
<p>Food System Resilience: Concepts, Issues, and Challenges  <i>Monika Zurek, John Ingram, Angelina Sanderson Bellamy, Conor Goold,  Christopher Lyon, Peter Alexander, Andrew Barnes, Daniel P. Bebbler,  Tom D. Breeze, Ann Bruce, Lisa M. Collins, Jessica Davies, Bob Doherty,  Jonathan Ensor, Sofia C. Franco, Andrea Gatto, Tim Hess, Chrysa Lamprinoupolou,  Lingxuan Liu, Magnus Merkle, Lisa Norton, Tom Oliver, Jeff Ollerton,  Simon Potts, Mark S. Reed, Chloe Sutcliffe, and Paul J.A. Withers</i> .....</p>	511
<p><b>IV. Management and Governance of Resources and Environment</b></p>	
<p>The Concept of Adaptation  <i>Ben Orlove</i> .....</p>	535
<p>Transnational Social Movements: Environmentalist, Indigenous, and  Agrarian Visions for Planetary Futures  <i>Carwil Bjork-James, Melissa Checker, and Marc Edelman</i> .....</p>	583
<p>Transnational Corporations, Biosphere Stewardship, and Sustainable  Futures  <i>H. Österblom, J. Bebbington, R. Blasiak, M. Sobkowiak, and C. Folke</i> .....</p>	609
<p>Community Monitoring of Natural Resource Systems and the  Environment  <i>Finn Danielsen, Hajo Eicken, Mikkel Funder, Noor Johnson, Olivia Lee,  Ida Theilade, Dimitrios Argyriou, and Neil D. Burgess</i> .....</p>	637
<p>Contemporary Populism and the Environment  <i>Andrew Ofstehage, Wendy Wolford, and Saturnino M. Borrás Jr.</i> .....</p>	671
<p>How Stimulating Is a Green Stimulus? The Economic Attributes of  Green Fiscal Spending  <i>Brian O’Callaghan, Nigel Yau, and Cameron Hepburn</i> .....</p>	697
<p><b>V. Methods and Indicators</b></p>	
<p>Why People Do What They Do: An Interdisciplinary Synthesis of  Human Action Theories  <i>Harold N. Eyster, Terre Satterfield, and Kai M.A. Chan</i> .....</p>	725

Carbon Leakage, Consumption, and Trade <i>Michael Grubb, Nino David Jordan, Edgar Hertwich, Karsten Neuboff, Kasturi Das, Kausbik Ranjan Bandyopadhyay, Harro van Asselt, Misato Sato, Ranran Wang, William A. Pizer, and Hyungna Ob</i> .....	753
Detecting Thresholds of Ecological Change in the Anthropocene <i>Rebecca Spake, Martha Paola Barajas-Barbosa, Shane A. Blowes, Diana E. Bowler, Corey T. Callaghan, Magda Garbowski, Stephanie D. Jurburg, Roel van Klink, Lotte Korell, Emma Ladouceur, Roberto Rozzi, Duarte S. Viana, Wu-Bing Xu, and Jonathan M. Chase</i> .....	797
Remote Sensing the Ocean Biosphere <i>Sam Purkis and Ved Chirayath</i> .....	823
Net Zero: Science, Origins, and Implications <i>Myles R. Allen, Pierre Friedlingstein, Cécile A. J. Girardin, Stuart Jenkins, Yadvinder Malhi, Eli Mitchell-Larson, Glen P. Peters, and Lavanya Rajamani</i> .....	849

## Indexes

Cumulative Index of Contributing Authors, Volumes 38–47 .....	889
Cumulative Index of Article Titles, Volumes 38–47 .....	897

## Errata

An online log of corrections to *Annual Review of Environment and Resources* articles may be found at <http://www.annualreviews.org/errata/environ>