Detecting thresholds of ecological change in the Anthropocene

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Detecting Thresholds of Ecological Change in the Anthropocene

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Keywords

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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

> 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)

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

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 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).

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

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).

TYPOLOGY 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 1*a***). Often, however, gradual changes in the environment can lead to nonlinear responses, including threshold, unimodal, and more complex patterns (**Figure 1*b–d***). In these examples, ecological thresholds are points or zones at which relatively

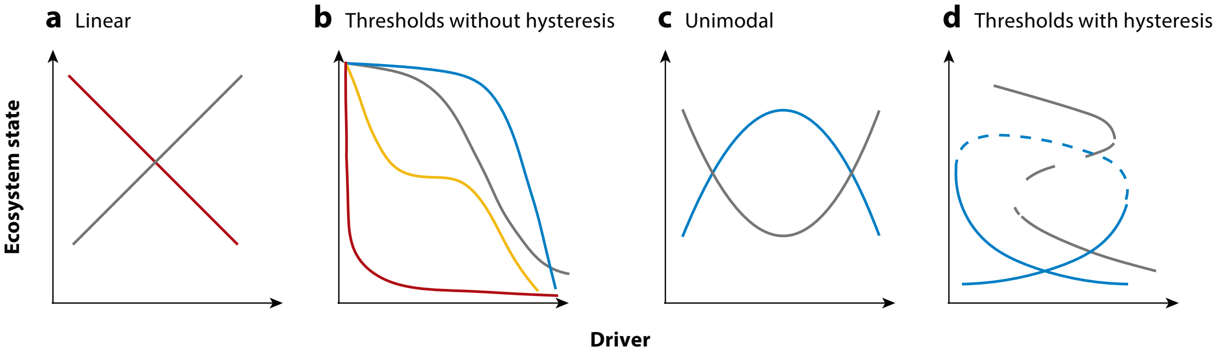


Figure 1

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 1*b***). 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.

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

Unimodal relationships are threshold-like across the range of a driver (**Figure 1*c***). 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 1*d***). 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

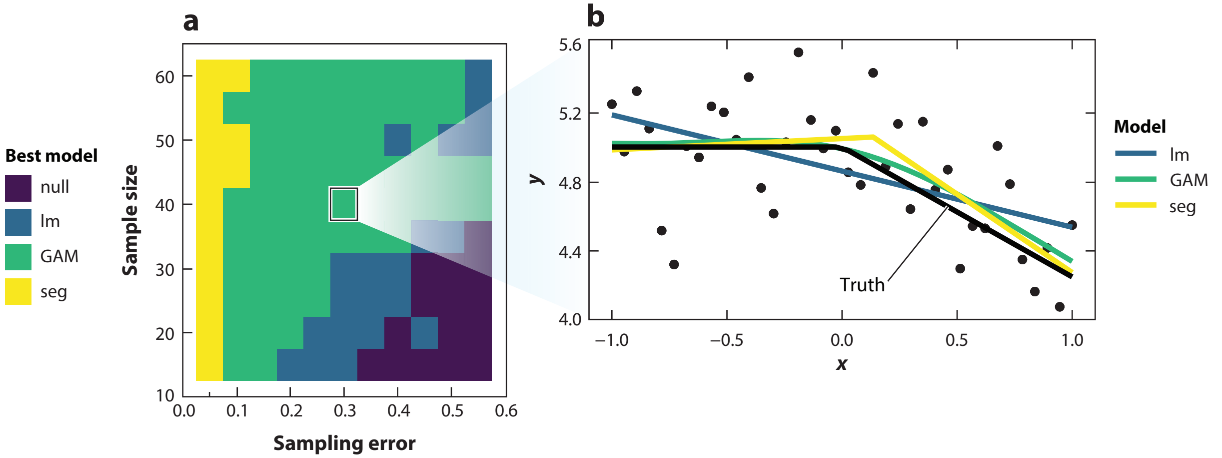


Figure 2

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 "wiggliness" 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).

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)

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 3*a***).

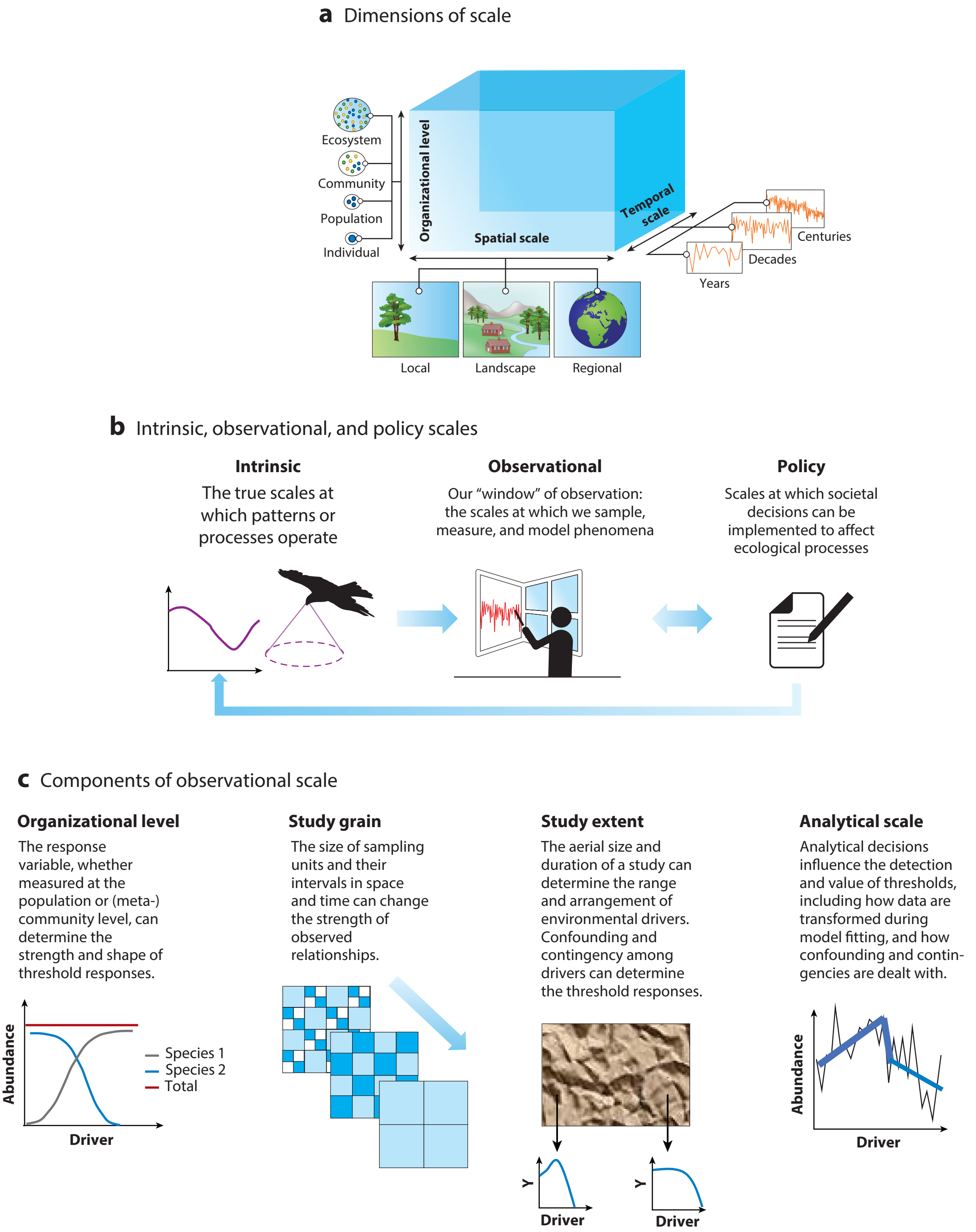
Within each dimension, three fundamental scales can be operationalized: intrinsic, observational, and policy scales (**Figure 3*b***). The intrinsic scale concerns the spatial and temporal scales at which organisms respond to changes in their environment. In space, such scales are determined by life-history 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 3*c***). 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



Intrinsic
The true scales at which patterns or processes operate

Observational
Our "window" of observation: the scales at which we sample, measure, and model phenomena

Policy
Scales at which societal decisions can be implemented to affect ecological processes

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 3*a***). 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 3*c***). 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

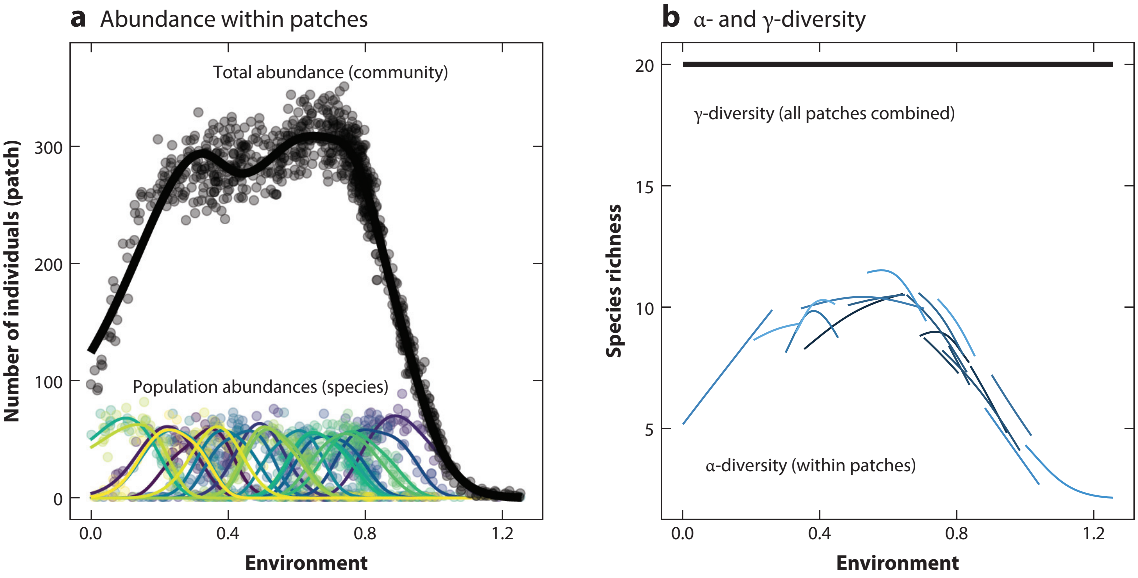


Figure 4

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 4*a*** 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 4*b***). 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 5*a*** (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 ~10% urbanization (see also **Supplemental Table 1**). In contrast, when all taxa are aggregated, the relationship between macroinvertebrate abundance and urbanization is weak (**Figure 5*a***, 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).

Supplemental Material >

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 5*b***, 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 5*b***, 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

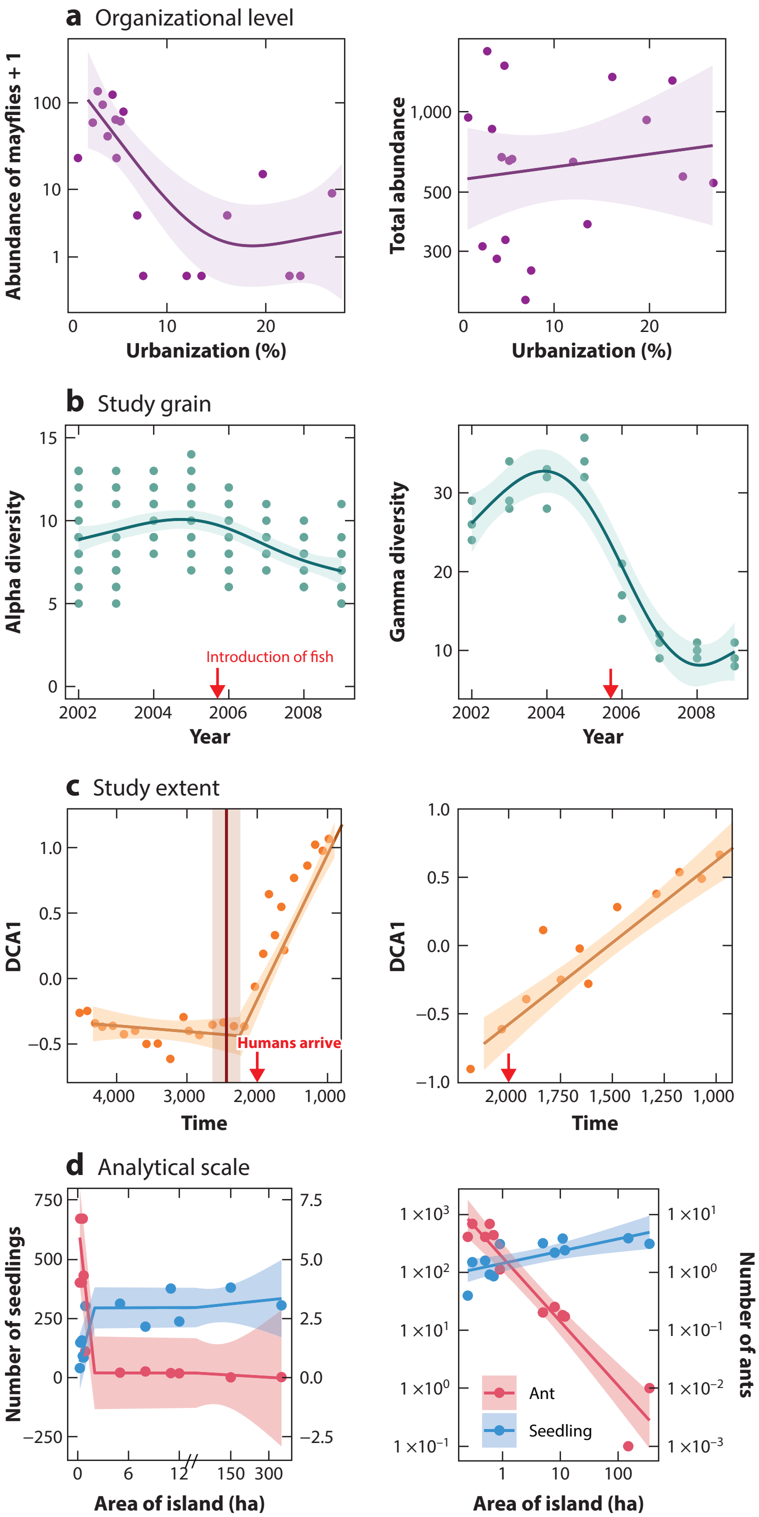
We demonstrate the influence of temporal extent on the detection of abrupt change in plant community composition turnover using a well-sampled paleoecological time series (small grain, short intervals, and long duration) from Tenerife in the Canary Islands (data from 26). The abrupt change in community turnover rates following colonization by humans (**Figure 5*c***, left panel) is no longer detectable when the time series (before human arrival) was reduced in temporal extent (**Figure 5*c***, 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 ~1 hectare (**Figure 5*d***, left panel), whereas the abruptness is no longer evident and the trend is linear when analyzed on the log scale (**Figure 5*d***, 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.

Supplemental Material >

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 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 synthesis 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.

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