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ARTICLE

Special Feature: Harnessing the NEON Data Revolution

Harnessing NEON to evaluate ecological tipping points: Opportunities, challenges, and approaches

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Abstract

The combination of continuing anthropogenic impact on ecosystems across the globe and the observation of catastrophic shifts in some systems has generated substantial interest in understanding and predicting ecological tipping points. The recent establishment and full operation of NEON has created an opportunity for researchers to access extensive datasets monitoring the composition and functioning of a wide range of ecosystems. These data may be uniquely effective for studying regime shifts and tipping points in ecological systems because of their long time horizon, spatial extent, and most importantly the coordinated monitoring of many biotic and abiotic components of focal ecosystems. The variety of these data can capture a range of potential community shifts while also monitoring an extensive set of environmental drivers. This combination is critical for assessing whether changes are a result of external forcings or internal dynamics. Here, we present an overview of regime shift dynamics; describe a variety of approaches to identify tipping points with data from time series, spatial patterns, or frequency distributions of community states across environmental conditions; and suggest a number of NEON data products that may be appropriate for such analyses.

KEYWORDS
NEON, regime shift, spatial pattern, Special Feature: Harnessing the NEON Data Revolution, time series, tipping points

INTRODUCTION

Current trajectories of ecological change have raised concerns about regime shifts (a rapid and dramatic change in the state of a system, which, in ecological contexts, is generally characterized by a shift in dominant members of a community) in a variety of ecosystems and across spatial and temporal scales. Shifts in climate, disturbance regime, or other environmental characteristics may push ecological regimes into "alternative stable states," characterized by nonlinear and potentially irreversible changes (Folke et al., 2004; Johnstone et al., 2016; Kefi et al., 2007; Scheffer et al., 1993). These regime shifts may be marked by a specific threshold or "tipping point" at which mechanisms of ecosystem resilience are exceeded, leading to substantial changes in ecosystem structure, function, or dynamics (Andersen et al., 2009; Moore, 2018; Rietkerk et al., 2004). With continued anthropogenic disturbances and accelerating climate change, strengthening our ability to identify, anticipate, and forecast ecological tipping points is crucial for navigating current and future ecosystem change (Biggs et al., 2009).

Theory around the identification and dynamics of regime shifts and tipping points has become relatively well established (Dakos et al., 2015; Ratajczak et al., 2018; Scheffer et al., 2015); however, empirical approaches have been more limited, largely because of the logistical challenges of working in complex systems. Empirical efforts have largely focused on specific systems and locations that were amenable for analysis. Because of logistical constraints, ecological data are generally collected in individual studies lacking spatial and temporal continuity and focused on a constrained set of factors expected to be drivers of community change. Each of these issues imposes certain limitations on those studies. Most critically, a number of synthesis studies (Bestelmeyer et al., 2011; Filbee-Dexter et al., 2018; Ratajczak et al., 2018; Zinnert et al., 2021) have identified long-term observational studies as a key need for identifying and exploring regime shifts and tipping point dynamics in ecosystems. With certain notable exceptions (including fast cycling planktonic communities or other microbial communities), many of the systems of greatest concern for having tipping points undergo shifts over month, year, or decadal timescales (Figure 2), and long-term monitoring is the only way to capture major transitions and to assess their persistence (Zinnert et al., 2021). Tipping points also occur in complex systems with many connected components and potential drivers of shifts. Yet, studies of regime shifts generally focus on a small number of factors that are expected to have significant influence on the transitions (e.g., Muthukrishnan et al., 2016). While this is an efficient strategy for studies with finite resources, it is also a necessarily limited one (see discussion of potential criticisms in Dudgeon et al., 2010). In some cases, and potentially most, multiple drivers act on systems simultaneously, increasing the likelihood of abrupt changes (Ratajczak et al., 2018). This includes the potential for repeated disturbances, potentially interacting with a slow long-term driver pushing the system into an alternate regime. Similarly, nonlinear or tipping point transitions, and the persistence of subsequent new regimes, are often controlled by processes in the broader ecological or social–ecological systems (Filbee-Dexter et al., 2018). Thus, understanding and observing more components of a system than only the expected driver and response variables can provide important insights into the nature of those transitions and potential mechanisms of resilience. Bestelmeyer et al. (2011) have identified certain key components for studies of tipping points (at least in a temporal context), which include long time series with data on biological responses, environmental drivers, and environmental context, with a recognition that "context is critical." Effective studies of tipping points and regime shifts, particularly if they hope to provide general insights with broad applicability, need to find strategies to collect these types of broad and rich datasets, which is likely to be a substantial challenge.

Large observational networks could provide a uniquely effective setting for identifying thresholds and tipping points in complex environmental systems. This idea has been discussed since the early 2000s in the context of social–ecological systems (AC-ERE, 2009) and forecasting ecological changes (MacMahon, 2006). With standardized protocols, long-term monitoring, and broad coordinated sampling of a range of biophysical parameters, NEON is well situated to support efforts that examine and predict tipping points and regime shifts. While the potential of the NEON framework to contribute to ecological transition theory and applications has been recognized (Jordan et al., 2007), NEON data and monitoring protocols have only recently reached full operation and have not yet been used to build understanding of ecological tipping points. At the time of this paper, a Web of Science search for "NEON" and ecological terms related to tipping points (e.g., "stable state" and "threshold") did not return any results, indicating this opportunity to use NEON in relation to tipping points' literature has yet to be fully realized. We believe this is largely due to the relatively recent establishment of NEON, and to a lesser degree the lack of explicit research agenda, as the NSF long-term ecological research program (NSF-LTER) has shown how other long-term monitoring efforts can yield important insights about tipping points (Zinnert et al., 2021). In the hope of motivating research focused on tipping points and regime shifts using the resources of NEON, we briefly review several types of ecological transitions and then discuss the capacity, challenges, and strengths of NEON and NEON data to investigate such transitions.

A PRIMER FOR UNDERSTANDING TIPPING POINTS AND REGIME SHIFTS

Tipping points are critical thresholds, generally of some environmental driver (e.g., precipitation, nutrient levels, or disturbance frequency), where systems change abruptly from one state (e.g., the particular composition and abundances of species or functioning of the system) to another with its own self-reinforcing feedbacks (Moore, 2018). Tipping points may occur across both spatial (Reyer et al., 2015) and temporal scales (Clements & Ozgul, 2016; Lindegren et al., 2012) and have been described in a variety of ecosystem types including coral reefs (Mumby et al., 2007; Muthukrishnan et al., 2016), forests (Hirota et al., 2011; Staver et al., 2011), freshwater ecosystems (Carpenter et al., 2011; Scheffer et al., 1993), and rangelands (Kefi et al., 2007), and are likely occur in some fashion in most ecosystems. In addition, tipping points occur in systems across a broad range of spatial scales (Reyer et al., 2015), from small ponds to planetary processes (Barnosky et al., 2012; Lenton et al., 2008). While regime shifts are believed to occur disproportionately faster in larger systems (Cooper et al., 2020), rapid change in smaller systems or across smaller scales is still quite common (Clements & Ozgul, 2016; Kramer & Drake, 2010). Understanding the role of spatial scale in regime shifts and in particular how and when local-scale processes can propagate to system-wide transitions remain important questions (Michaels et al., 2020). Regime shifts can occur in a number of different ways, and we describe three particular cases below (linear, phase shift, and alternate stable states; Figure 1). Discriminating between these scenarios can be important both to provide insight into the mechanisms that structure the system and to better inform effective management to prevent unwanted transitions or restore degraded systems (Suding & Hobbs, 2009).

The simplest transition between system states is a smooth or "linear" shift (Figure 1a). While there does not need to be a strictly linear relationship between environmental drivers and system state, it is a smooth relationship such that incremental changes in environmental conditions cause corresponding incremental changes in the system state (e.g., abundance or percent cover of a key community member). This type of transition likely indicates that changing environmental conditions push the system away from or toward the optimal conditions for some member of the system, which shifts species' relative abundances. Importantly, this type of transition occurs without a true tipping point, but a rapid community shift can occur if an environmental driver itself changes abruptly pushing the system to a different state. This would produce a change that appears to be nonlinear, but the fundamental relationship between driver and system state is still linear and no early warning signals would be observed (Dakos et al., 2015).

Alternatively, systems can respond nonlinearly to changing environmental conditions. Regime shifts can occur when relatively minor changes in environmental drivers push the system over a critical tipping point. As systems cross these tipping points, the change in system state is much larger than would be expected from the magnitude of change in the environmental driver (Scheffer, 2009). Tipping points can be observed in two types of systems: systems in which a single equilibrium state exists for any given environmental condition (Figure 1b) and systems with the potential for multiple stable equilibria (Figure 1c). Tipping points in systems with a single equilibrium state at every environmental condition are associated with environmental constraints on species, such as their physiological limits (e.g., coral bleaching and mortality in response to elevated water temperatures; Hoegh-Guldberg, 1999) or the environmental conditions where the competitive dominance of different species flips, allowing for the competitive exclusion of a species (e.g., plant zonation along salinity gradients; Emery et al., 2001; Levine et al., 2003) and a sharp change in relative abundances. Systems with multiple stable equilibria are likely to have strong positive feedbacks and high connectedness between components, such that shifts are propagated or accelerated by internal mechanisms (Scheffer et al., 2012). When the system crosses a tipping point, it shifts to an alternate regime with its own set of self-reinforcing processes that draw the system toward the new equilibrium state (Folke et al., 2004; Scheffer et al., 2001). For example, in semiarid grazing systems the presence of plants above a critical abundance can also increase rates of water infiltration supporting continued increases of plant abundance and pulling the system toward a vegetated state (Rietkerk & van de Koppel, 1997). These mechanisms also make the system resistant to recovery such that the tipping point for the system to return to its initial condition is different from the first tipping point (i.e., the system exhibits hysteresis; red circles in Figure 1c). As systems approach tipping points, theory indicates that they may present a number of potential "early warning signals" such as

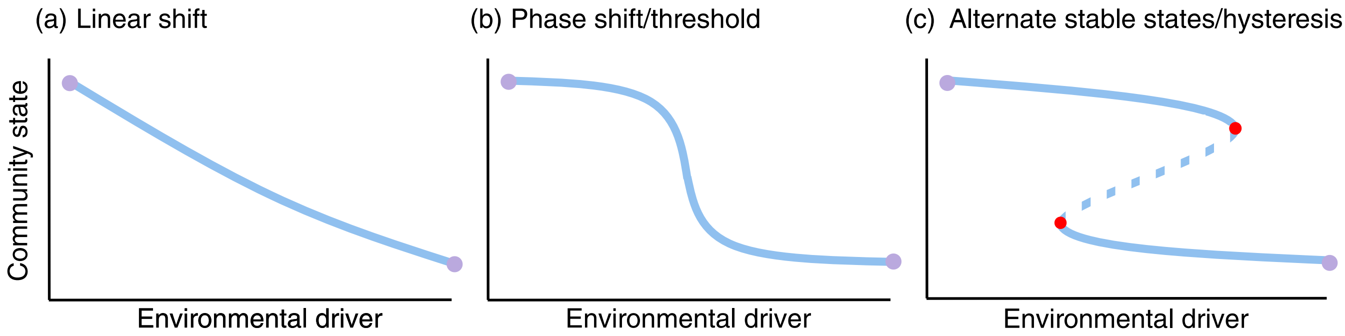

FIGURE 1 Different potential relationships between environmental drivers and system states. In systems with a linear relationship (a), a rapid transition can only occur if the environmental driver also changes rapidly. In systems with phase shifts (b) or alternate stable states (c), rapid changes in community state can occur with a small change in the environmental driver at the tipping points

critical slowing down, increased variance, and spatial autocorrelation that are generally associated with a breakdown in the processes that pull the system back toward its stable equilibrium state (Dakos et al., 2015).

Finally, a change in system state may be triggered either by internal or external drivers. External drivers can initiate a regime shift by shifting conditions to a point where a different community member is able to establish or become dominant (or equivalently where a current dominant species is no longer able to persist). For example, shifts in precipitation have driven transitions between vegetated and desert regimes in the Sahara and Sahel (Foley et al., 2003). An internal component of the system can also naturally, or stochastically, move beyond a critical threshold such that feedback mechanisms can no longer return the system to the prior equilibrium state or they accelerate the system toward an alternate state. This can be seen in systems with Allee effects where the likelihood of extinction increases when a population drops below a critical threshold (Kramer & Drake, 2010). Alternatively, bark beetles have been empirically demonstrated to reach an outbreak threshold in western US forests when the beetle population size is large enough to overwhelm constraints otherwise imposed by stand-level composition and configuration of host tree species (Raffa et al., 2008). This outbreak threshold demarcates the difference between endemic beetle populations, where beetles reproduce in and kill only weakened trees, and epidemic populations, where beetles cause widespread mortality even to trees that would otherwise be resistant in nonoutbreak conditions.

To be able to characterize, detect, and forecast tipping points in systems with regime shifts, several challenges need to be addressed. First, baseline data are needed to identify "normal" variability, expected relationships between change in drivers and state variables, or changes indicative of coming tipping points. Second, coordinated measurements of both drivers and responses within a given system remain uncommon, particularly at the spatial and temporal resolution necessary for prediction or anticipation, except in specific studies designed to collect data related to tipping points (e.g., Wilkinson et al., 2018). Even in these studies, environmental data collection is generally focused on a limited number of parameters expected to be relevant to the transitions or mechanisms being considered. Limited effort is expended on other potential drivers for transitions, such that it is generally not possible to exclude alternate explanations that unobserved factors drove a transition in a linear manner (see Dudgeon et al., 2010). Finally, contingencies and ecosystem details play a significant role in whether and when those systems undergo major transitions, and thus, there is a need for system or even site-level patterns to evaluate early warning signs (e.g., critical slowing down and increasing variance; Turner et al., 2020).

Here, we discuss the potential use of NEON and the variety of data products being produced to identify or predict ecological tipping points, and we propose a series of recommendations for evaluating and anticipating nonlinear ecological change within systems. Specifically, we provide recommendations to bridge the gap between NEON resources currently available and the data needed to fully investigate the dynamics of tipping points. Developing a framework for using NEON resources to understand, evaluate, and predict tipping points in previously stable or increasingly unstable ecosystems will be crucial to anticipating future widespread or potentially irreversible ecological change and to guide the management of those systems.

USING NEON TO STUDY TIPPING POINTS IN NATURAL SYSTEMS

NEON's consistent tracking of a variety of community variables under a standardized monitoring protocol over the organization's 30-year time horizon creates the opportunity to capture transitions when they occur across a number of systems and scales (Keller et al., 2008). These data are particularly useful for unexpected transitions, which would not otherwise have a monitoring plan in place to capture them. Much of the previous work discussing ecological transitions in natural systems has identified tipping points by tracking biotic and community parameters and identifying periods of rapid change in time series. However, if relevant environmental factors are not measured in tandem, this strategy is incompatible with identifying the underlying drivers of ecological transitions or elucidating the relationships between those drivers and the biotic variables of interest (Dakos et al., 2015). An additional challenge for identifying tipping points from observational data is that tipping points are often a result of the complexity of ecological systems (i.e., a large number of species and their interactions; Moore, 2018) and complex, community-wide data may not be collected in studies targeting a specific ecological outcome. NEON can help meet these challenges by collecting a wide range of data that allows us to look at the role of and covariance between environmental drivers and community patterns by capturing both of these variable types concurrently with standardized approaches. With the timescale of the NEON project and the diversity of data that are collected, it is feasible to generate a baseline for spatial variance and heterogeneity at multiple scales in both environmental and community parameters, allowing us to identify deviations from those baselines. This wealth of data can also be used to develop and parameterize models for predicting future change and state shifts.

NEON and the role of scale in ecological tipping points

A variety of systems with potential ecological tipping points are encompassed within NEON sites (Figure 2).

The ability to use the NEON infrastructure to identify and study these tipping points depends on a match between collected data and the spatial and temporal scales necessary to observe ecological dynamics and transitions. Already, some NEON data have been collected in ecological contexts where transitions are more rapid or can be observed from spatial signatures rather than time series, making these datasets feasible for tipping point detection. Examples of fast time series include microbial communities in managed landscapes, lake or river water quality, soil N cycling, and infectious disease (e.g., Lyme disease in ticks), and spatial patterns can be seen in the establishment of vegetation in arid ecosystems or woody encroachment into grasslands (Figure 2, within the blue dashed box). However, the ecological dynamics that are relevant to tipping points in many systems of interest operate on longer timescales or across large spatial scales, such as fire-catalyzed transitions among forest communities and ecosystem-level impacts from bark beetle outbreaks in western North America, as well as the resulting implications for coarse woody debris and carbon dynamics (Figure 2, outside the blue dashed box). The current extent of NEON data is unlikely to be sufficient to evaluate tipping points in systems where regime shifts occur across broader spatial and temporal scales. However, time series will expand over the planned lifetime of NEON, increasing the potential of observing shifts in a larger variety of ecosystem types. Additionally, many datasets currently exist at or near NEON core sites (e.g., satellite data) that could be used to expand the spatial or temporal scope of NEON data.

A tipping point research agenda for NEON

The combination of NEON's extensive and site replicated datasets, as well as the strong research community utilizing NEON data, provides an opportunity for progress on a number of challenges that could inform the science of tipping points and nonlinear ecological dynamics more generally. At minimum, there are a variety of specific systems included in the NEON design (e.g., lake plankton communities, woody encroachment in grasslands, and insect pest epidemics) that may potentially display tipping points and capturing these dynamics with established methods would be valuable as additional examples of nonlinear systems (Moore, 2018). A number of these contexts are listed in Figure 2 and the "Approaches for identifying tipping points in different data contexts" section, but these suggestions are not exhaustive as we hope other researchers will identify additional contexts of relevance based on their own experience. In addition, we have identified several specific research areas where tipping point-related conceptual and methodological advances could be achieved using NEON.

1. **Evaluation and processing of high-throughput ecosystem sensor data:** NEON sites include automated sensors for both terrestrial (e.g., carbon flux) and aquatic (e.g., water chemistry and chlorophyll A) ecosystem parameters. Automated processing of data streams and identification of either community shifts or early warning signals of such shifts remains a significant challenge.
2. **Linkages between multiple ecosystem components:** The coordinated measurement of a broad suite

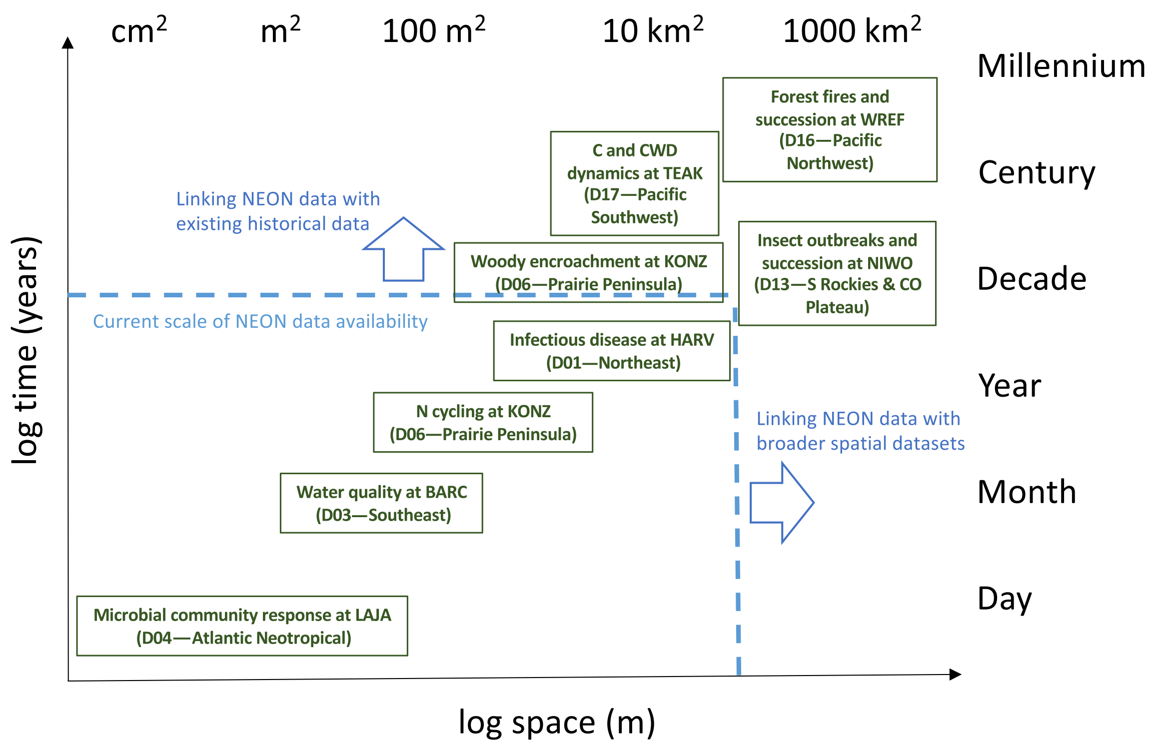

FIGURE 2 Temporal and spatial scales for the natural range of variability (NRV) of key ecological processes that could undergo regime shifts at particular NEON sites. Location of individual boxes represents the timescales likely needed to observe shifts and the spatial extent over which they are likely to occur

of ecosystem parameters (including in some cases colocated aquatic and terrestrial sites) provides ideal circumstances for evaluating if and how nonlinear transitions in certain ecosystem components influence each other and whether tipping point dynamics are propagated or smoothed across components. Additionally, the coordinated measurements allow for the identification of leading and lagging indicators of regime shifts.

3. **Analysis of aerial images to identify sharp transitions:** NEON collects extensive high-resolution aerial imagery of all sites, and strong spatial patterning with discrete boundaries can be a characteristic indicator of systems with nonlinear dynamics. However, algorithmic or automated image analysis in ecological contexts is a difficult process that requires continued research effort.
4. **Analysis of remotely sensed data to identify individuals, species, and environmental conditions:** NEON collects extensive remote sensing data on sites, with the added ability to conduct substantial groundtruthing efforts. These data can potentially be interpreted to provide a range of derived datasets (species identity, tree abundance, water availability, etc.) that can be used to monitor spatial or temporal tipping points.
5. **Multisite comparisons:** The network of NEON sites allows comparison of systems that experience similar, but slightly varying, weather or climate events creating opportunities to evaluate tipping points with stressors of different durations or magnitudes (Ratajczak et al., 2017). Alternatively, if different sites experience similar conditions, the identification of tipping points across systems can provide robustness to analyses and predictions.
6. **Large-scale environmental gradients:** The range of NEON sites spans large gradients of environmental conditions. This provides the potential to identify discontinuities in the frequency distribution or the presence of community states across different environmental conditions (Figure 5). Differences in tipping points in response to changing environmental conditions (e.g., climate change and nutrient enrichment) can also be evaluated across the range of conditions to understand how they are influenced by the broader environment.

Assessing tipping points using NEON

Tipping points can be identified in empirical systems in a number of ways and utilizing different types of data. Here, we present a set of approaches for identifying tipping points that can be applied to data being collected by NEON. Because of the nature of the NEON monitoring scheme, we focus on approaches that utilize only observational data as opposed to experimental methods (e.g., Petraitis et al., 1999). In observational data, tipping points manifest as a set of characteristic patterns, and here, we describe the expected patterns in different types of data that would indicate a regime shift or a more linear response to changing environmental conditions. We will focus on the general scenario of regime shifts with environmental (abiotic) drivers that produce shifts in the biotic community that can be measured as the abundance of particular community members as this is a common scenario and likely relevant to many NEON users. However, conceptually, tipping points could occur in other response variables, such as ecosystem functions, and be evaluated in an analogous manner with metrics other than population abundance. We focus on three data contexts in particular: time series, spatial patterns, and frequency distributions of community states across environmental conditions.

The most common approach for identifying tipping points is monitoring of state parameters (e.g., community composition and abundances of individual species) and/or observing a dramatic shift in the state of the system (Andersen et al., 2009; Lees et al., 2006; Schröder et al., 2005). However, this is conceptually insufficient to identify a regime shift because it ignores the role of exogenous drivers. Substantial changes in a community following a disturbance, such as a major storm or disease outbreak, do not necessarily indicate a tipping point, even if such a notable discontinuity would be identifiable in a time series. The change could simply be a predictable and linear response to a strong driver, which is well within the dynamics expected for a system, and community recovery would be expected if the driver returned to baseline conditions. A lack of recovery or continued shift toward an alternate attractor after the disturbance would be stronger evidence for the presence of a tipping point. A major, nonlinear change in the state of a system (e.g., abundance of a dominant species) generally needs to be coupled with either a trivial or linear change in an external driver in order to show that the state change was not simply a response to a major environmental shift. However, access to coordinated community and environmental data is rare, and thus, the approaches we present can be limited in their application. But NEON, with the establishment of large-scale and consistent monitoring efforts, presents a unique opportunity to utilize colocated time series data on multiple community and environmental parameters and drastically expand approaches to evaluating tipping points in natural systems.

Approaches for identifying tipping points in different data contexts

Time series

Time series, or temporal data, are the most straightforward data that can be used to identify tipping points. Tipping points in time series appear as a rapid shift in community composition (or any relevant response metric) that then persists at the new level, rather than returning to the original baseline (Scheffer & Carpenter, 2003). In addition, the community response should be out of proportion with changes in environmental drivers, particularly at the point of transition (Figure 3). At larger temporal scales, there may be a general correlation between community and driver such that the separate regimes are aligned with different levels of the driver, but at the transition point, the community response will be out of proportion to the environmental change. Additionally, the temporal signature and alignment of community state and environmental drivers can be useful in discriminating between different types of transitions; for example, later recovery (due to hysteresis) will distinguish phase shifts (Figure 3b) from alternate stable states (Figure 3c). Time series are also the type of data most likely to be well suited for the evaluation of a variety of early warning signal metrics such as increased autocorrelation or critical slowing down (Dakos et al., 2012).

Detecting regime shifts in an ecosystem over time necessarily requires extensive time series, ideally with high temporal resolution, both to detect the shift and subsequent stability. Most plot-based or sensor-based NEON data products from individual sites lend themselves to time series analyses. Data collection began at most NEON sites within the last 5 years; while 5 years is longer than many ecological studies, in many cases it is still limited for the detection of change in an ecosystem state over time. Thus, communities or ecosystem states with rapid turnover times would be best suited for the detection of tipping points over time within the data currently available from NEON. Many aquatic communities (particularly planktonic) often display such rapid changes, and these communities are more likely to be monitored via in situ sensors, which can monitor the community with high temporal resolution, alongside automated monitoring of environmental conditions. Thus, the datasets with the potential to observe tipping point on the shortest timescales are NEON's measurements in streams, lakes, and rivers that include collection of macroinvertebrates, micro- and macroalgae, aquatic plants, and microbes. On longer timescales, but well within the expected lifetime of NEON, measures of

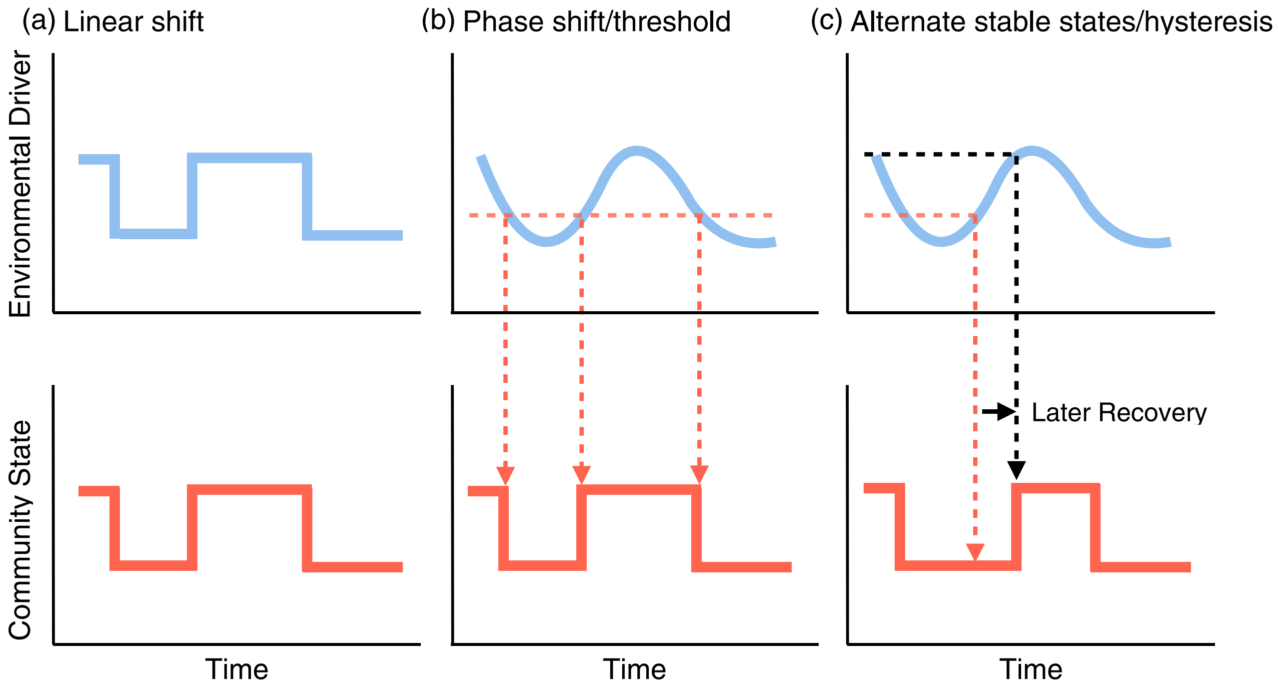

FIGURE 3 Examples of time series data displaying major community shifts under linear (a), phase shift (b), and alternate stable states (c) dynamics. In all three scenarios, communities undergo rapid shifts; however, in the linear case (a) the environmental driver itself must undergo rapid changes, as might be expected from a major disturbance. In contrast, both phase shift (b) and alternate stable states (c), dynamics display tipping points that cause rapid community shifts with a smoothly varying environmental driver. While forward and recovery transitions occur at the same tipping point for a phase shift (b), there are separate tipping points in alternate stable states (c), which leads to a later recovery, only when the system returns past the second tipping point

biomass and diversity of terrestrial plant communities, invertebrates, and small mammals may also be useful datasets to identify tipping points.

Microbial communities in particular present an opportunity for exploring tipping points on a shorter timescale, but also present their own challenges. Change and turnover are extremely rapid, creating the possibility of major changes in communities over very short time periods, but the same characteristics may create noisier data, making it more difficult to identify relevant patterns. NEON monitors microbial communities in terrestrial soils as well as aquatic systems; looking for regime shifts over time in these communities could be fruitful, particularly at the functional level, or higher taxonomic levels, where noise could be reduced.

Spatial patterns

Identifying tipping points via spatial patterns is largely analogous to the approach for time series except that changes in, and correlations between, environmental drivers and community response variables are observed along spatial gradients. Rather than shifts occurring at a point in time with a fast transition to a new state, the change happens over a narrow spatial extent. This generally appears as a sharp boundary between community states rather than a transition zone with community types grading into each other. The most characteristic pattern for a tipping point observed in a spatial context is a system with a smoothly varying environmental driver, and an overlying community undergoing a sharp transition. This is seen, for example, in the sharp zonation of salt marsh plant communities as a result of both salinity tolerance and competition (Pennings & Callaway, 1992). Alternatively, systems with tipping points can display a highly patchy pattern of community composition with sharp boundaries and repeated transitions between states, while underlying environmental conditions remain largely homogeneous (Rietkerk et al., 2004, black arrows in Figure 4). This pattern is expected when transitions are largely driven by positive feedbacks between the community and the local environment rather than a larger underlying environmental gradient.

When evaluating tipping points via spatial patterns, sharp community shifts by themselves are insufficient evidence. Just as with a time series, changes in community should be uncorrelated with any environmental drivers at the point of transition. This can be evaluated most readily in remotely sensed data of NEON sites that

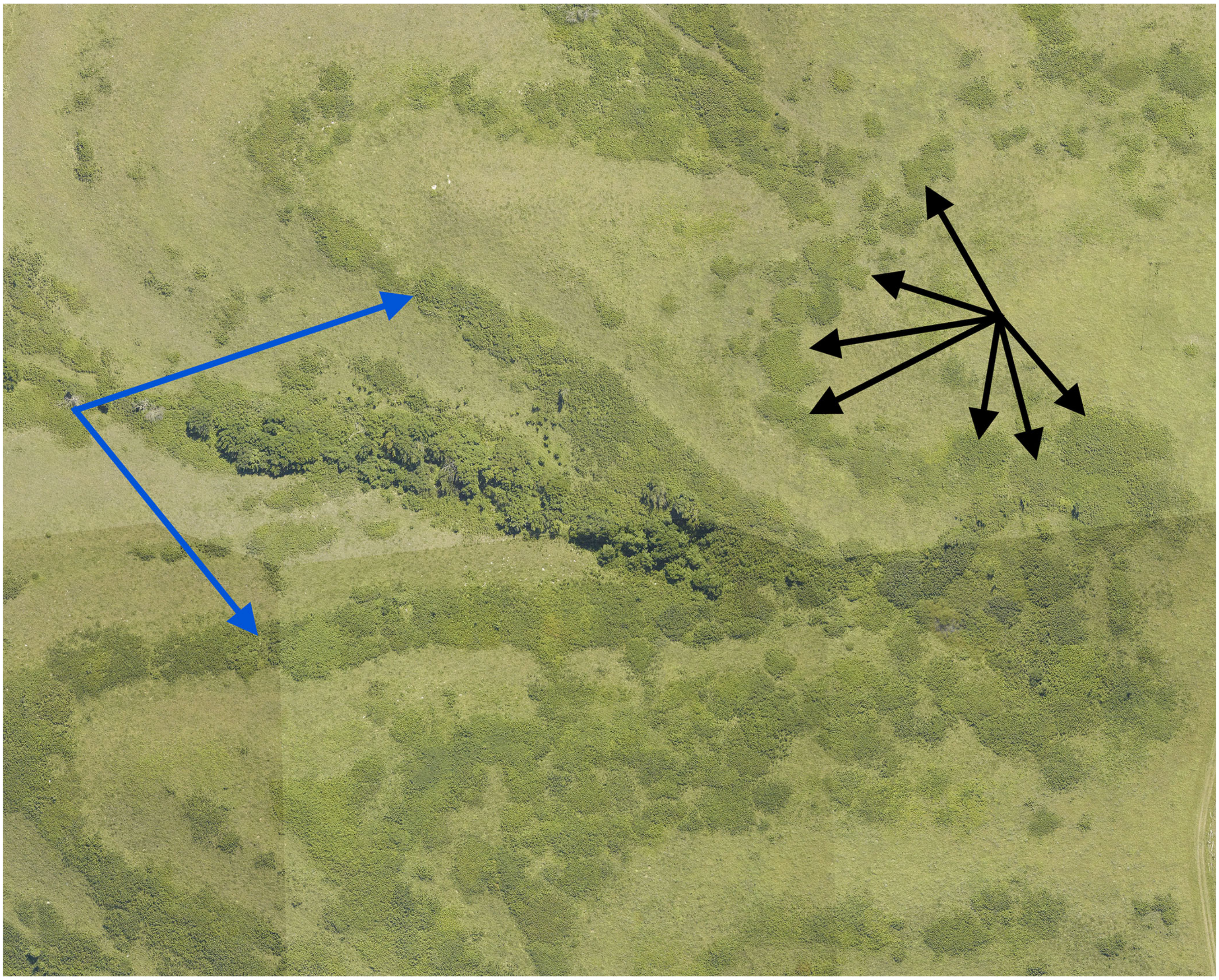

FIGURE 4 High-resolution aerial imagery of sites (here from the Konza Prairie site in eastern Kansas) can be used to observe spatial patterns in community composition. In the image, we identify spatial features that reflect two different types of community shifts. The blue arrows indicate larger bands of vegetation that follow contour lines on the hilly landscape and are associated with different soil layers that can support woody vegetation. Black arrows indicate patchy distribution of shrubs within a band that arises from random establishment followed by local expansion of individuals facilitated by their access to deeper water resources and ability to reduce fire potential (following Ratajczak et al., 2011)

allow overlay of data layers for both community and environmental variables. To identify a tipping point, there should be significant changes in the community, but environmental drivers should display more gradual changes or potentially even be homogeneous. If the environment itself presents sharp transitions, equivalent community shifts should not be taken as an indication of a tipping point (the blue arrows in Figure 4 point to different bands of plant assemblages that are a result of separate soil layers exposed at different elevations along a hill slope). This is a critical consideration, as the presence of discontinuous drivers is also potentially more likely in the spatial context than in a time series, as numerous environmental factors may naturally have sharp breaks or steep gradients (e.g., slope or altitude at a cliff face and soil moisture in riparian zones).

NEON remote sensing data are particularly well suited to detecting tipping points across space within a site. At 1-m resolution and 10×10-km flight boxes, NEON hyperspectral and lidar data products cover multiple habitat types at most sites, at a resolution that is often fine enough to capture individual plants. NEON RGB camera imagery provides even higher resolution data, up to 10 cm, and can supplement lidar and hyperspectral data by detecting particular features on the landscape. A number of projects are ongoing to process raw NEON remote sensing data and provide derived products, such as tree crown delineation (e.g., Weinstein et al., 2020), tree cover identified to species (e.g., Fricker et al., 2019; Scholl et al., 2020), water availability (e.g., Chadwick et al., 2020), and maps of soil conditions and plant foliar chemistry (e.g., Chadwick & Asner, 2018). These efforts will aid detection of step changes in state variables across the landscape and will facilitate tipping points analysis by providing more straightforward data on community composition and relevant environmental parameters than raw remote sensing data.

Distribution of community states across environmental conditions

Evaluating the distribution of communities in relation to environmental drivers provides a third approach to evaluating tipping points or regime shifts. This approach is conceptually related to the spatial pattern approach described above but does not focus on a spatial gradient of environmental conditions in a specific location. Rather it utilizes data from a much larger set of locations and looks for discontinuities in the frequency distribution or the presence of community states across different environmental conditions (Figure 5). In a system with phase shift or threshold dynamics, there will be a sharp transition in the relationship between environmental conditions and community metrics rather than a linear relationship or a well-mixed distribution (Figure 5b). However, a system with alternate stable states has multiple basins of attraction, which produce bimodal or multimodal distributions of community states in relation to an environmental driver (Figure 5c). In these systems, internal feedbacks between the community and environment push systems at intermediate community states toward one of the attractors even when the driver sits at an intermediate level, creating regions of increased density or frequency.

The pattern of community change across different environmental conditions needs to be evaluated across a broad range of conditions, which may not be available at a single site. Thus, this approach is most amenable to analysis across NEON, either at the site level or by including data from multiple plots at a range of sites. In contrast to detecting tipping points temporally, detecting tipping points across varying environmental conditions can take advantage of the broad distribution of NEON sampling even in the early stages of data collection. NEON data cover an extensive climate space (Schimel et al., 2007), enabling detection of nonlinearity in response variables over large gradients in temperature and rainfall. Other environmental parameters, such as soil chemistry, regional land use patterns, water quality, or spatial structure, can also be assessed across the network and may provide additional drivers that could produce regime shifts (Villarreal et al., 2018). However, with this approach there is a risk of an uneven distribution of driver values across sites. Such a pattern could itself produce a multimodal distribution of community states. Thus, care needs to be taken so that sites provide an even, or at least well-distributed, set of environmental conditions.

SYNTHESIS

The establishment of NEON presents a unique opportunity for the study of tipping points in ecological systems.

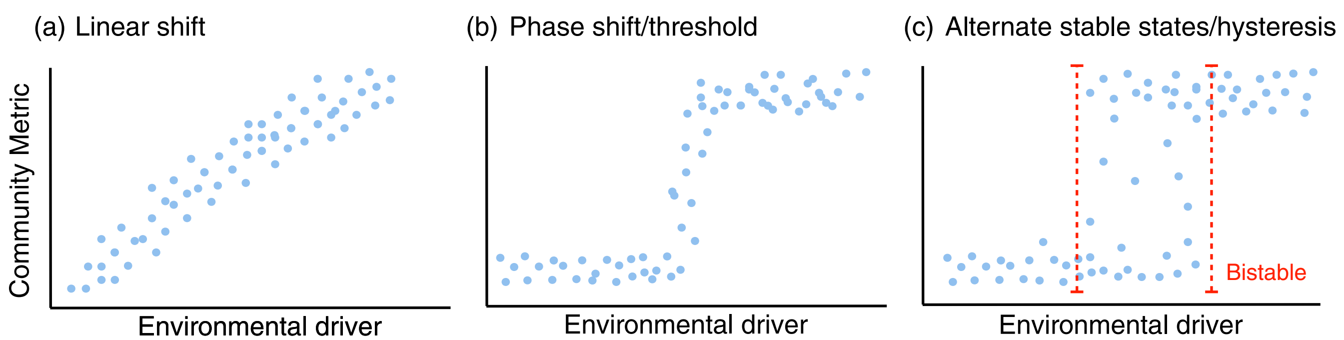

FIGURE 5 Potential relationships between environmental conditions and community types that could be observed across NEON sites. Environmental drivers can be a broad range of climatic (temperature and precipitation), geographic (latitude and altitude), biogeochemical (soil or water chemistry), or anthropogenic (distance to roads or cities, nearby land use patterns) parameters. Community metrics are any variable that could reflect an aspect of community composition, particularly the prevalence of key community members (e.g., total biomass or percent tree cover). Separate panels indicate different types of transitions and with no tipping point (a), a phase shift with a single tipping point (b), or two tipping points and a bimodal distribution indicative of alternate stable states (c)

The regular data collection of so many ecosystem properties across such a large range of locations is generally unprecedented (Kao et al., 2012). This creates an opportunity to assess tipping points in a variety of ecosystems and components of those ecosystems. While in many cases NEON will not be able to act as a sentinel monitoring system, providing a warning of when other systems or locations are about to undergo a major community shift, the strength of NEON lies in the amount of data being collected which provides context for any particular system or metric where a shift is observed. Some studies have questioned the potential for research on tipping points to provide predictions specific enough to make useful management recommendations (Hillebrand et al., 2020). But the unprecedented scale and nature of NEON provides an opportunity for some of the most complete evaluations of ecological dynamics available to researchers. As a result, tipping point identification can be more nuanced and robust because of the number of potential drivers that can be monitored in coordination, including both on-the-ground measurements and remotely sensed data. This can help exclude alternative explanations relating to potential external drivers that may undergo major shifts themselves. Even in research programs explicitly studying tipping points, the number of environmental drivers or covariates that can be feasibly monitored is limited, but the broader mission of NEON allows for extensive effort even if it is not clearly relevant to tipping points. The ability to continue monitoring over a long time period (minimally 30 years) will provide exceptional baselines to recognize natural variability and extended opportunities to observe tipping points. This richness of data around a tipping point may also allow researchers to study tipping point dynamics in real systems to refine and test theory that can be applicable to other systems. Similarly, the coordination of remote sensing and ground-based data can be used to develop remote sensing proxies for community measures that in turn can be used at broader scales and provide more effective sentinel monitoring opportunities.

Linking NEON with other datasets

Because tipping points and regime shifts in natural systems can occur across a broad range of scales, there may be limitations in some cases to evaluating them only with NEON data (see Figure 2). Continued collection of data by NEON will extend the length of time series and partially mitigate these limitations and the spatial extent of data can be expanded by linking NEON data to broader datasets being collected at or near NEON core sites, such as from NSF-LTER sites that are colocated with NEON sites. These additional datasets can be used to create envelopes of the historical natural range of variation, or at least a longer ecological record, for many key parameters needed to address tipping points. For example, data on tree populations and growth parameters exist for several of the forested NEON terrestrial sites (e.g., Harvard Forest in the Northeast Domain and Niwot Ridge in the Southern Rockies and Colorado Plateau domain), with some extending back in time to the 1940s (e.g., the Wind River Experimental Forest in the Pacific Northwest domain). Other monitoring networks, such as the AmeriFlux network (for flux tower sites), the PhenoCam network (a set of digital cameras used to track plant phenological patterns), and the USFS Forest Inventory and Analysis program can be combined with NEON efforts to expand the spatial scale of available data for some metrics and a number of efforts are underway to connect these data streams (Hufkens et al., 2018; Novick et al., 2018; Richardson et al., 2018). Similarly, high-resolution aerial or satellite imagery can be acquired from a variety of sources and analyzed using approaches developed around NEON data to extend analyses based on spatial patterning.

Linking site-level NEON instrumental data streams to broader landscape patterns can also extend spatial inferences about tipping points. For example, plot data within the footprint of NEON forested domains could be placed in a broader landscape context in a spatially explicit manner to better understand spatial dynamics of ecological drivers and responses and explore landscape indicators of tipping points (e.g., patch size or shape of disturbed area). In addition, NEON data can be linked across sites in ways that may provide unique insights. In particular, the near or actual colocation of terrestrial and aquatic sites (where possible) provides an opportunity to test linkages across ecosystems in the realm of tipping points (Creed et al., 2018). Colocation may allow for new ways of testing how changes in terrestrial processes (e.g., nutrient cycling) can lead to tipping points in connected aquatic streams, rivers, and lakes. Because of the complexity and interdisciplinary nature of such studies, NEON may provide a rare opportunity to study the effects and responses of cross-system drivers at significant scales.

Ecosystem models and early warning systems to identify tipping points

In this review, we focus on identification of tipping points retrospectively and suggest methods for recognizing regime shifts that have already happened in datasets. However, a critical challenge that remains is the need to identify when systems are approaching a tipping point, particularly if that can facilitate preemptive actions (Hughes et al., 2013). Ecosystem models are crucial tools for predicting future ecological changes, but lack of robust ecological input data can limit their predictive ability. Predicting abrupt or long-term ecological change is challenging; future conditions are unrealized and directional climate change complicates projections of future ecological functioning, which may impede model-informed conservation or land management policies (Beckage et al., 2011; Bonan & Doney, 2018). Process-based models can mechanistically represent ecosystem functioning over millennia (Kelly et al., 2016), and the use of millennial-scale records within a mechanistic model has elucidated long-lasting biogeochemical legacies (Bartowitz et al., 2019; Hudiburg et al., 2017). Similarly, increased ecological data availability may help decrease parameter uncertainty in ecosystem models, leading to more accurate simulations (Fisher & Koven, 2020). Field data-model fusion is an essential tool to improve understanding of ecological functioning (Peng et al., 2011) and is a backbone to frameworks for early warning systems or signals (EWS). Current EWS frameworks for biodiversity loss use on-the-ground data with models to better understand and quickly show areas that are vulnerable to or are in the initial stages of biodiversity loss (Barnard et al., 2017). An EWS framework could be expanded using NEON data to inform predictive ecological models and could be an important tool to predict abrupt tipping points across space and time. Additionally, the extent of data collected by NEON may serve as a useful basis for developing theory around tipping points and EWS that can further refine their efficacy. The large spatial and (continuingly increasing) temporal range of NEON data makes it well suited to use for predictions of ecological tipping points that could influence conservation and landscape management decisions and policy.

Tipping points and ecological forecasting

The value of NEON's repeated, standardized sampling for near-term ecological forecasting is well recognized (Dietze et al., 2018), and enabling forecasting was an explicit goal in the design of the NEON project (Schimel et al., 2007). The coordinated nature of sampling numerous ecosystem components is particularly valuable for forecasting models because they can consider potential linkages and their consequences. Nonlinearity in response variables presents a major challenge for forecasting, but is therefore one of the most valuable components to capture in ecosystem models (Dippner & Kröncke, 2015; Oliver & Roy, 2015). In developing models for iterative forecasting, specifically targeting ecosystem components that are likely to exhibit nonlinear responses can be a useful approach to identifying and quantifying the most sensitive variables, resulting in the most significant improvements to models and frameworks. There is evidence that efforts toward those ends are scaling up across the NEON user community (e.g., with the NEON Ecological Forecasting Challenge).

Social importance of tipping points in conservation and management

Identifying tipping points in ecological systems, particularly when the systems provide valuable ecosystem services or are under management, is an important step in building support for management or conservation efforts. Minimally, this is true because systems with tipping points are the strongest candidates for preventative, rather than reactive, efforts as recovery after the system has passed a critical threshold is substantially more challenging (Kelly et al., 2014; Selkoe et al., 2015). Beyond that, management of systems with tipping points is likely to be more effective in a social context when managers and stakeholders understand the implications of regime shifts and nonlinear dynamics (Kerner & Thomas, 2014). Without an understanding of an approaching tipping point, resource users may be unwilling to take appropriate precautionary actions based on the observation of past actions that had little impact on the system. Based on those experiences, it would be a reasonable inference that if past disturbances had little or no impact on the system, then future ones should not either. But such an extrapolation would be fundamentally flawed in systems with a tipping point. In systems that have already passed a tipping point, the particular dynamics and shape (i.e., linear vs. hysteretic) of recovery pathways are also important to communicate clearly; community trust may be eroded if little response is observed to even significant management interventions, while they remain subthreshold. Managing expectations can help prevent pressure to abandon efforts before they have had the opportunity to be successful. While NEON itself is not designed to include or monitor the effects of management efforts, the scale of monitoring enabled by NEON data may provide substantial opportunity to develop general theory, inform expectations, and enable broader communication with stakeholders. That work can in turn be applied to other social–ecological systems where management efforts are more critical and/or contentious.

CONCLUSIONS

The importance of tipping points and regime shifts in ecological systems is becoming more apparent as anthropogenic influences continue to impact individual ecosystems and the planet as a whole (Biggs et al., 2018). The potential for planetary and climate tipping points makes this case strongest of all (Barnosky et al., 2012; Lenton et al., 2019). NEON provides an opportunity to study tipping points in both systems where they can be easily studied to understand basic dynamics and in specific systems where potential changes are of practical or conservation importance (Figure 2). This allows NEON-based work to inform and test the basic theory needed to address large-scale issues or be transferable to a variety of other systems and to have practical impacts on systems in need of specific insights for conservation or management. While important challenges exist, the unprecedented scale and coordinated nature of NEON research may lead to theoretical insights and methodological advances related to tipping points through an integrated assessment of regime shifts across temporal, spatial, and environmental correlation domains.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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