CellPress

Trends in
Ecology & Evolution

Opinion

Using functional indicators to detect state changes in terrestrial ecosystems

Zhongmin Hu[1,2,*] Vasilis Dakos,[3] and Max Rietkerk[4]

Indicators to predict ecosystem state change are urgently needed to cope with the degradation of ecosystem services caused by global change. With the development of new technologies for measuring ecosystem function with fine spatiotemporal resolution over broad areas, we are in the era of 'big data'. However, it is unclear how large, emerging datasets can be used to anticipate ecosystem state change. We propose the construction of indicators based on functional variables (flows) and state variables (pools) to predict future ecosystem state changes. The indicators identified here may be useful signals for doing so. In addition, functional indicators have explicit ecological meanings that can identify the ecological mechanism that is causing state changes, and can thus be used to improve ecosystem models.

Highlights

Global climate changes and human activities are exerting great pressures on ecosystems, and may cause catastrophic collapse of ecosystem states and services. However, the indicators that can be used to detect ecosystem state change remain a key question.

Although emerging evidence suggests the feasibility of using functional indicators to detect ecosystem state changes, state-based indicators derived from mathematical theory are conventionally used.

The increasingly availability of long-term datasets of ecosystem functions at high spatiotemporal resolution provides us with novel opportunities to detect ecosystem state changes.

Ecosystem models simulate ecosystem biogeochemical cycles. Functional indicators enable us to identify the mechanisms causing state changes, and can be used to diagnose and improve ecosystem models for predicting long-term changes in ecosystem functioning as a consequence of state changes.

The necessity of detecting state change with functional indicators

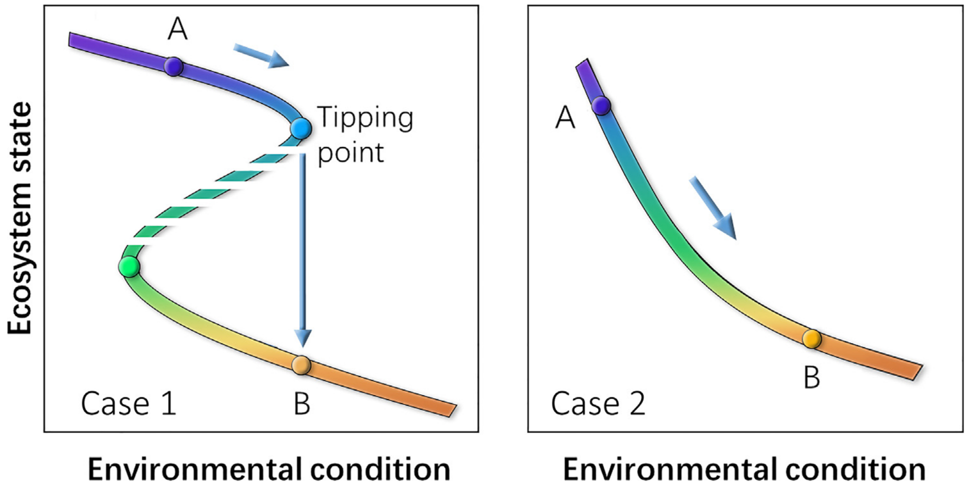
As global change causes ecological disruption across the world, ecosystems are at increasing risk of crossing thresholds, or **tipping points** (see Glossary), and undergoing a rapid shift from existing to new states [1,2]. For example, tropical rain forests may transform into savannah after frequent fire, grasslands become deserts owing to over-grazing or drought stress, and shallow lakes lose transparency because of human-induced eutrophication [3]. These **state changes** are expected to seriously impact on ecosystem services of fundamental importance to human well-being [4]. Predicting whether ecosystems will experience a state change is a key challenge in ecology for those concerned about implementing effective adaptation strategies [5–7].

Ecosystem state changes are mirrored by a change in **ecosystem structure**, which is also referred to as a regime shift, state shift, phase transition, state transition, or structure change. State changes can be categorized as abrupt or smooth. An abrupt ecosystem change may occur when a tipping point is crossed, resulting in the transition to an **alternative state**. In this case, the state change is a **catastrophic transition** (Figure 1, case 1) [3]. Theory suggests that the phenomenon of **critical slowing down (CSD)** will appear when an ecosystem is approaching a tipping point, and some general indicators based on this phenomenon could be used as early-warning signals [3,8]. In contrast to catastrophic transitions, ecosystems can also experience smooth state transitions in which there are no discrete alternative states and changes are continuous [2] (Figure 1, case 2). It is worth noting that smooth transitions cannot be predicted using CSD indicators alone [9].

Typically, 'state' variables (e.g., biomass and species abundance) [10] are used to calculate CSD indicators. The robustness of CSD state-based indicators varies and even fails in some cases [8], but it is difficult to clarify why. One reason for the difficulty is that such indicators are derived from general theoretical expectations and, as such, lack a link to explicit ecological mechanisms. In real ecosystems, the processes controlling the dynamics of indicators

[1]Key Laboratory of Agro-Forestry Environmental Processes and Ecological Regulation of Hainan Province, Hainan University, Haikou 570228, China
[2]Southern Marine Science and Engineering Guangdong Laboratory (Zhuhai), Guangdong 519082, China
[3]Institut des Sciences de l'Evolution de Montpellier (ISEM), Centre National de la Recherche Scientifique (CNRS), Institut de Recherche pour le Développement (IRD), Université de Montpellier, Ecole Pratique des Hautes Etudes (EPHE), Montpellier, France

 https://doi.org/10.1016/j.tree.2022.07.011



Trends in Ecology & Evolution

Figure 1. Possible trajectories of ecosystem state change. In case 1 (catastrophic transition), the equilibrium curve is folded backwards. The dashed middle section represents an unstable equilibrium and can be interpreted as the division between two alternative stable states on the upper and lower branches. Ecosystems abruptly shift to a new state when environmental conditions pass a threshold (tipping point). The critical slowing down (CSD)-based indicators are developed to detect state changes of this case. In case 2 (smooth transition), only one equilibrium exists for each condition and the ecosystem state can be reversed continuously from state B to A.

[4]Copernicus Institute of Sustainable Development, Utrecht University, 3508 TC Utrecht, The Netherlands

*Correspondence:
huzm@hainanu.edu.cn (Z. Hu).

can vary with ecosystem type [11], thus conflicting with theoretical predictions. Furthermore, CSD state-based indicators are difficult to directly connect to ecosystem processes or **ecosystem functions** that are described by rates (e.g., carbon, water, and nutrient cycles). Therefore, constructing indicators that are closely linked to ecological functions is a promising complementary approach for predicting ecosystem state changes and understanding the underlying mechanisms. Such an approach might also be useful in identifying smooth transitions.

Ecosystem functions comprise the ecosystem processes that cycle materials (e.g., carbon and nitrogen) and transmit energy through the ecosystem [12]. They underpin many aspects of ecosystem services that humans depend upon, such as the provision of food and freshwater, regulation of atmospheric composition, and erosion prevention. Numerous ecological components crucially depend on ecological processes, and monitoring these processes can therefore serve as a proxy for many other ecosystem properties. The development of new technologies (e.g., eddy covariance instrumentation [13] and satellite-based measurements of ecosystem metabolism [14]) has facilitated the expansion of databases containing measurements of real-time ecosystem functions (e.g., flows of carbon, water, and nutrients in terrestrial ecosystems). These datasets may offer an opportunity to quantify ecosystem **resilience** and to detect state changes [15]. Although some studies have attempted to use CSD function-based signals to identify ecosystem state changes [16–18], questions remain about their reliability as indicators for this type of ecological change. We first propose a theoretical basis for using indicators of ecosystem functions to detect state changes for catastrophic and smooth transitions, and compare the reliability of this approach to that of CSD state-based indicators. Second, using vegetated terrestrial ecosystems as an example, we summarize several candidate functional indicators already used by terrestrial ecosystem ecologists. Third, we outline the advantages of using functional indicators to detect ecosystem state changes and discuss future research priorities in this area.

Theoretical test of detecting state change with functional indicators

Because their magnitudes and variabilities are determined by ecosystem structure, terrestrial ecosystem functions (i.e., flows of materials within ecosystems or between ecosystems and the surrounding environment) vary with the composition of vegetation in an area. We hypothesize that metrics relating multiple terrestrial ecosystem functions (e.g., water-use efficiency, transpiration fraction) (Table 1), as well as those that relate ecosystem functions and environmental conditions (e.g., **climatic sensitivity**, precipitation-use efficiency) (Table 1), remain relatively constant if the ecosystem structure is fixed. Conversely, changes in ecosystem structure are mirrored by changes in metrics of function–function and function–environment relationships. Thus, it may be possible to detect ecosystem structural change (i.e., state change) by quantifying the dynamics of function–function relationships and function–environment relationships. Because many functional variables of interest (i) are sensitive to changes in environmental conditions, (ii) vary faster than state variables, and (iii) are often readily observable using new technologies, they offer great promise as signals of ecosystem state change.

To test the feasibility of using functional indicators to detect ecosystem change, the dynamics of several functional indicators (Table 1) were reproduced along an aridity gradient before a critical transition using the water-limitation model developed by Rietkerk *et al.* [19,20] (Box S1 in the supplemental information online). As the results in Box 1 show, CSD function-based indicators are as reliable as CSD state-based indicators in detecting critical transitions before a tipping point. In addition, other functional indicators (e.g., water-use efficiency, transpiration fraction, and precipitation-use efficiency) may be useful signals of upcoming critical and smooth state transitions. More information about the applications and relevance of these indicators in ecosystem ecology can be found in Box 2.

Promising indicators of state change

CSD function-based indicators

Consistent with theory [8,21], variance, **autocorrelation**, and skewness estimated from a state variable (i.e., plant biomass) increase abruptly before the critical transition occurs (see Figure IC in Box 1). Similarly, variance, autocorrelation and skewness calculated using a function variable (i.e., net primary productivity, NPP) exhibit similar temporal trajectories (see Figure IE in Box 1). This suggests that CSD function-based indicators may be of use in detecting catastrophic state changes.

Previous work provides empirical support for the usefulness of these indicators as signals of state change. Hu *et al.* [16] found that indicator values calculated using NPP peaked in the transition zone between a desert and grassland, consistent with theoretical expectation. Liu *et al.* [17] developed a robust early warning system for forest mortality based on temporal autocorrelation of a vegetation index, a proxy for NPP.

Indicators of ecosystem function–environment relations

Climatic sensitivity

Studies have found that NPP is more sensitive to inter-annual variations in precipitation in drier ecosystems than in wetter ecosystems, both at regional and continental scales [22,23]. That is, the precipitation sensitivity of NPP increases steadily with climate aridity. These findings suggest that precipitation sensitivity may signal smooth state changes driven by directional precipitation change. After changing the maximum growth rate parameter (Box 1 for explanation), the Rietkerk model reproduced the correlation between precipitation sensitivity and climate, producing a signal that identified smooth state transitions along the aridity gradient (Figure S1 in the supplemental information online).

Glossary

Alternative state: more than one ecosystem stable state can exist under the same environmental conditions.
Autocorrelation: the degree of similarity between the values of the same variables over successive time intervals.
Catastrophic transition: also known as a critical transition, an abrupt, irreversible state change when an ecosystem passes a critical threshold.
Climatic sensitivity: the degree to which an ecosystem function responds to variations in climatic factors.
Critical slowing down (CSD): a phenomenon that is expected to occur when a system approaches a tipping point. CSD takes place when the dominant eigenvalue, characterizing the return rate to equilibrium upon small perturbations, approaches zero at 0.2pt?>tipping points. At an intuitive level, CSD can be understood from a ball-in-a-basin diagram. The slope of the basin represents the rate of change and, close to the tipping point where the basin of attraction becomes shallower, return to equilibrium following small perturbations will become slower.
Ecosystem function: a general term that includes stocks of materials (e.g., carbon, water, mineral nutrients) and rates of processes involving fluxes of energy and matter between trophic levels and the environment. Important ecosystem functions include primary production, evapotranspiration, decomposition of dead matter, and nutrient recycling.
Ecosystem structure: the biophysical architecture of an ecosystem, which is implicitly determined by the plant species composition in terrestrial ecosystems.
Resilience: the ability of an ecosystem can tolerate disturbances without shifting to a qualitatively different state. CSD occurs when resilience declines and the ecosystem approaches a critical transition.
State change: changes in ecosystem physical components and quality which are mirrored by changes in ecosystem structure. This is also referred to as regime shift, state shift, phase transition, state transition, or structure change.
Tipping point: marks the abrupt shift between contrasting ecosystem states (broadly termed regime shifts) when environmental conditions cross a specific threshold.

Table 1. Functional indicators used for detecting state changes in terrestrial ecosystems[a]

Category	Indicator	Definition	Usage	Caveat	Case study
CSD function-based indicators	Variance, autocorrelation, skewness, recovery rate, etc.	Instead of state variables, functional variables (e.g., NPP or GPP) are used to construct CSD indictors for predicting catastrophic state change	Increase in variance, autocorrelation skewness, and recovery rate etc. when approaching the tipping point	Context information such as driver characteristic, soil, climate, and temporal scale may affect robustness [18]	[16–18,38]
Function–environment relationship (the indicators are constructed from the relationships between environmental factors, e.g., precipitation, and ecosystem functions)	Climate sensitivity (here precipitation sensitivity is used as an example)	Slope of the environment–function relationship or the relative response of ecosystem function to an environmental change [22]	Increase in precipitation sensitivity when ecosystem shifts from forest to grassland, and to desert	Interactions of other environmental factors may strengthen or weaken the sensitivity	[16,22,30,39]
	Precipitation-use efficiency (PUE)	Ratio of vegetation productivity to annual precipitation [23]	Lower PUE in degraded ecosystems or lower-complexity ecosystems	Intraspecies physiological flexibility may cause temporal variations in PUE without state change	[24,40,41]
Function–function relationship (the indicators are constructed from the relationships between ecosystem functions)	Ecosystem-level water-use efficiency (WUE)	The ratio of vegetation productivity to ecosystem evapotranspiration [42]	Lower WUE in degraded or lower-complexity ecosystems	High intraspecies variations in plant water-use strategy may make ecosystem WUE variable within the same ecosystem type [43]	[42,44]
	Transpiration fraction (*T*/ET)	The ratio of plant transpiration to whole ecosystem evapotranspiration [27]	Lower *T*/ET in degraded or lower-complexity ecosystems	Intraspecies physiological flexibility may cause temporal variation in *T*/ET without state change	[26]

[a]According to the availability of the case studies, the examples given are mostly terrestrial ecosystems in arid regions where water limitation is the key stress. Therefore, the functional indicators addressed are mostly centered around water or precipitation.

Precipitation-use efficiency

Because vegetation productivity in arid ecosystems is tightly coupled to precipitation, precipitation-use efficiency (PUE) – the ratio of productivity to precipitation – remains relatively constant over time [23]. However, changes in the composition of an ecosystem plant community induce changes to the precipitation–NPP relationship, resulting in variations in PUE. Therefore, PUE may be useful for identifying both smooth and critical ecosystem state changes. The Rietkerk model produced a gradual decrease in PUE with aridity (see Figure IG,H in Box 1), which is consistent with the field observations described in Box 2.

Alternatively, increasing precipitation is associated with enhanced PUE. Ecosystems experiencing higher rates of precipitation support more extensive vegetation, which reduces runoff and promotes infiltration and retention of water in the soil. Soil moisture retention increases the portion of precipitation available to support plant growth, thereby increasing PUE. This mechanism is also supported by field observations which show a positive correlation between PUE and vegetation cover driven by the biomass–retention feedback loop [24].

Indicators of ecosystem function–function relationships

Ratio of plant transpiration to evapotranspiration

The ratio of plant transpiration to evapotranspiration (*T*/ET) describes the fate of precipitation entering an ecosystem (i.e., water loss due to uptake by vegetation vs loss due to runoff or evaporation from the soil). In natural ecosystems, *T*/ET varies with ecosystem type, and differences in *T*/ET between forests, grasslands, and arid shrublands suggest that this ratio declines with increasing aridity (Figure S2A in the supplemental information online). Further supporting this relationship, Wang *et al.* [25] found a sharp decline of *T*/ET from grassland (0.8) to desert (0.3) in drylands in Northwest China. Moreover, it is widely observed that *T*/ET correlates positively with plant aboveground biomass [26], demonstrating the importance of positive feedback between plant biomass and soil water retention. The Rietkerk model predicted a gradual decrease of *T*/ET with aridity based on this positive feedback (see Figure IG,H in Box 1), which is consistent with the field observations described above. Together, these findings support that change in *T*/ET is driven by positive feedback, and that this indicator is useful as a signal of state change.

Box 1. A case study on the use of ecosystem functional indicators

To test our hypothesis that ecosystem functional indicators can signal ecosystem state changes, we adopted the theoretical model of Rietkerk *et al.* [19,20] to simulate the temporal trajectories of the indicators in the cases of both catastrophic and smooth state changes. This model simulates how plant biomass and productivity change with increasing aridity in water-limited ecosystems. The model captures the positive feedback between plant biomass and water infiltration as the mechanism that causes a catastrophic transition with increasing aridity, in other words less plant biomass → less water infiltrates into soil for plant growth → less plant biomass. The model has successfully reproduced the abrupt ecosystem state change observed in arid regions [20]. We calculated critical slowing down (CSD) indicators, namely variability, lag-one autocorrelation, and skewness, with both simulated plant biomass (CSD state-based) and vegetation productivity (CSD function-based). We treat the CSD indicators calculated using vegetation productivity as functional indicators because they are metrics derived from ecosystem functions. In addition, we also calculated other functional indicators: precipitation sensitivity of vegetation productivity, precipitation-use efficiency, plant transpiration fraction, and ecosystem water-use efficiency (WUE) (see Table 1 in main text). We set model experiments by reducing precipitation along a decreasing precipitation gradient, and variations in the indicators before the ecosystem collapse were regarded as signals of smooth change (Figure I). We considered abrupt changes in the indicators when approaching the tipping point to be signals of catastrophic change.

Plant biomass declined linearly with a decrease in mean annual precipitation until precipitation was lower to 50 mm/year. At this point, plant biomass abruptly decreased to zero (Figure IA). The CSD state-based indicators derived from biomass warned of the approaching ecosystem collapse (i.e., abrupt increases in the indicators occurred immediately before the tipping point) (Figure IC). For example, the variability of biomass varies in a narrow range of 0.33–0.46 (mean 0.37, dimensionless) before the catastrophic change, but abruptly jumped to 0.52, 0.57, 0.69, 0.8 when approaching the tipping point. CSD function-based indicators based on net primary productivity (NPP) gave a similar warning as the CSD state-based signals (Figure IE). The other functional indicators – precipitation-use efficiency (PUE), productivity sensitivity to inter-annual variations in precipitation, the ratio of transpiration to evapotranspiration (*T*/ET), and ecosystem WUE – also dropped abruptly when the tipping point approached (Figure IG). In addition, most of these functional indicators exhibited directional and accelerating decreases along the aridity gradient; however, precipitation sensitivity was relatively constant before abruptly decreasing (Figure IG).

We also compared the performance of the indicators in the case of smooth state changes (right panels in Figure I, $W_0 = 0.8$ in Equation 5 of Box S1 in the supplemental information online). The results suggest that plant biomass linearly declines with decreases in mean annual precipitation and was close to 0 when approaching the extinction point (Figure IB). Except for autocorrelation, the CSD state-based indicators exhibited abrupt increases before the extinction point, in contrast to their relative stability before the extinction point (Figure ID). Similarly, all the CSD function-based indicators also exhibited relative stability preceding abrupt increases that signaled a trajectory toward the extinction point (Figure IF). For the other functional indicators, except sensitivity, all exhibit directional decrease across the entire aridity gradient (Figure IH), suggesting their usefulness as indicators of smooth change before the extinction point. These results suggest that the CSD function-based indicators are as useful as CSD state-based indicators for predicting abrupt state change before the tipping or extinction point. The non-CSD functional indicators can also track the smooth change before the tipping point and extinction point.

Note that the model predicts relatively constant precipitation sensitivity along the rainfall gradient before the extinction of plant biomass (Figure IG,H), which is inconsistent with the behavior of other indicators. We speculated the reason might be that the model considers plant maximum growth rate ($g_{\max}$ in Equation 3 in Box S1 in the supplemental information online) as a constant without integrating changes in this physiological parameter associated with climate conditions. In nature, community-level growth rate is driven by plant community composition, which varies along a climate gradient and favors species with appropriate water-use strategies. To test this speculation, we used linearly increasing $g_{\max}$ with precipitation instead of the original constant value in the model, yielding a steady increase of sensitivity with precipitation decline, consistent with observations our speculation (Figure S1 in the supplemental information online).

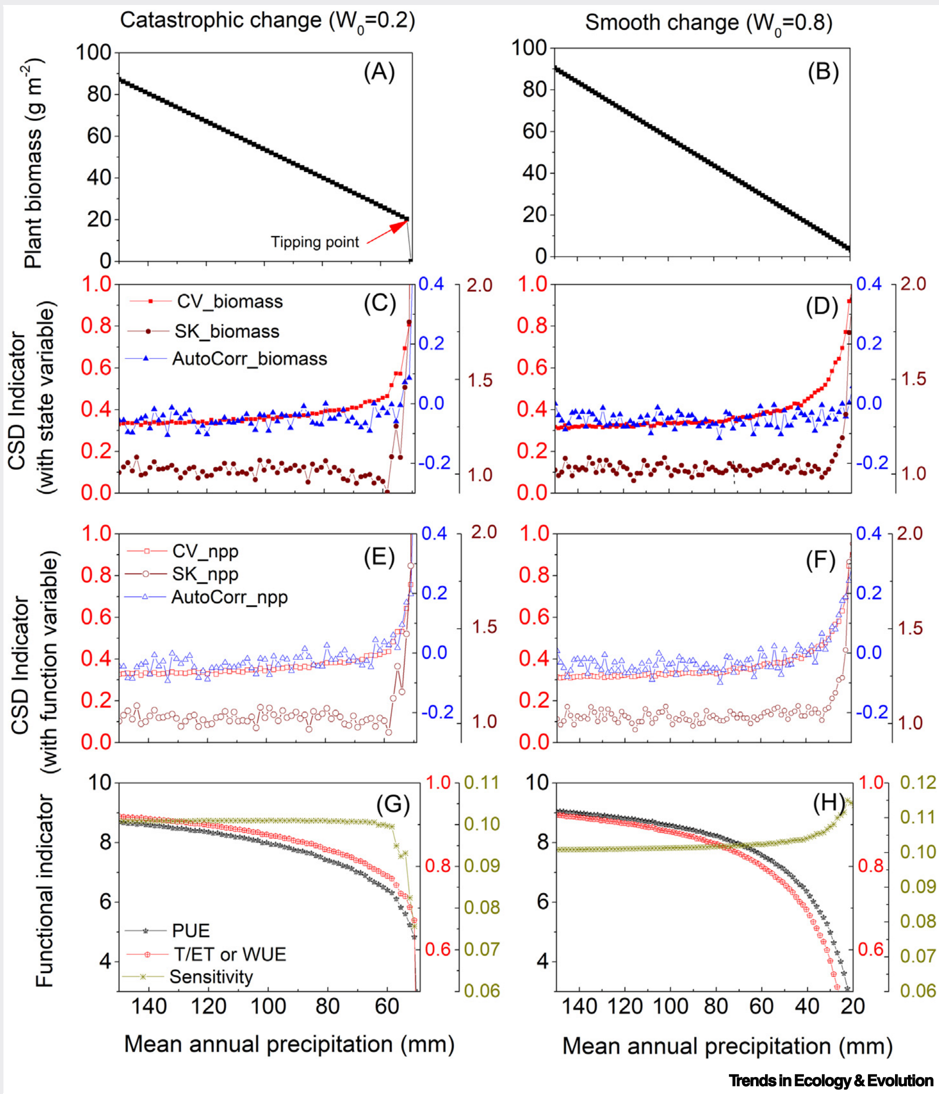


Figure I. Trajectories of plant biomass (A,B), CSD state-based indicators calculated with plant biomass (C,D), and CSD function-based indicators calculated with net primary productivity (NPP) (E,F) and other functional indicators (G,H) with aridity. The left panels illustrate the dynamics of the indicators in the case of a critical transition, and the right panels illustrate the dynamics in the case of a smooth transition. Detailed explanations for the model producing the trajectories and the indicators are given in Box S1 in the supplemental information online. *T*/ET and ecosystem WUE illustrate the same trajectory (G,H) because *T* and NPP were calculated with the same algorithm of soil water in the theory model (Equations 3 and 4 in Box S1 in the supplemental information online). All the CSD indicators are dimensionless and the unit is g.mm^{-1} for PUE, WUE, and sensitivity.

Ecosystem water-use efficiency

For a specific ecosystem, plant productivity and ecosystem water consumption (i.e., evapotranspiration) should be well balanced as a consequence of natural selection. This implies that ecosystem water-use efficiency (WUE) for an ecosystem type should be relatively constant (Figure S2B in the supplemental information online and Box 2). Studies have demonstrated that ecosystem

Box 2. Meaning and application of functional indicators in global change ecology

CSD function-based indicators

The three indicators (i.e., variability, autocorrelation, and skewness of NPP) are widely investigated as the indicators of ecosystem stability [45,46], resilience [40], and asymmetry of climatic responses [31,45], respectively, in the field of global change ecology. For example, asymmetry of NPP is widely adopted to clarify how NPP responds to climate anomalies [45]. The explicit meanings of these indicators make it easy to clarify the ecological mechanism underlying the dynamics of the indicators, as well as to link them to ecosystem models [16,47,48].

Climatic sensitivity

Climatic sensitivity quantifies how an ecosystem function responds to variations in climatic factors (here, precipitation). To quantify climatic sensitivity, widely used approaches include regressing climatic factors with an ecosystem function (e.g., NPP), using a linear function, or calculating the relative function response in comparison to environmental change [49]. A steeper slope or larger response indicates a higher sensitivity [30,49]. For example, spatial variations in the precipitation sensitivity of vegetation productivity have been investigated to predict how changes in precipitation may affect the stability of vegetation productivity [22,23].

Precipitation-use efficiency (PUE)

PUE, or rainfall-use efficiency, is conventionally quantified as the ratio of NPP to annual precipitation [23]. Higher PUE suggests that the ecosystem can take advantage of precipitation for plant growth more efficiently. Several studies suggest that the variations in PUE are the consequences of changes to plant community composition. For example, Hu *et al.* [24] found a continuous increase in PUE along a spatial precipitation gradient in temperate grasslands of Inner Mongolia, and this spatial variation could be largely explained by changes in plant community structure. Similarly, long time-series of satellite photographs (1990–2011) in the same region showed an overall increase in PUE in the degraded grasslands [41]. This trend mainly reflects reestablishment of plant communities resulting from the implementation of national ecological restoration projects. Similarly, Bernardino *et al.* [50] identified the tipping points of ecosystem state transitions in global drylands with long-term time-series PUE datasets.

Ecosystem water-use efficiency (WUE)

Ecosystem WUE is the ratio of primary productivity to evapotranspiration. Measurements taken by global flux towers illustrate distinct magnitudes of ecosystem WUE among ecosystem types (Figure S2 in the supplemental information online). A study in the arid region of northern China illustrated an abrupt decline of WUE from 2.8 kg H_2O $g^{-1}C$ (forest) to 1.5 kg H_2O $g^{-1}C$ (grassland) within the 400–500 mm precipitation climatic isocline boundary situated between semi-humid and arid zones [44].

primary productivity and evapotranspiration are closely coupled in most terrestrial ecosystems, supporting the idea of a conservative WUE [27]. The mechanism underlying this coupling includes processes occurring within the leaf stomata, and all are driven by external environmental factors in the same direction. The Rietkerk model produced gradual changes in WUE during both a smooth and catastrophic state change to a non-vegetation state (see Figure IG,H in Box 1). This suggests that ecosystem WUE is promising for signaling smooth and catastrophic transitions.

Advantages of functional indicators

Data availability

The development of new technologies has resulted in the proliferation of large datasets that aggregate measurements taken over extended periods of time. Instruments such as eddy covariance towers make long-term *in situ* observations that are compiled into large global databases (https://fluxnet.org/data); extensive measurements of ecosystem function (e.g., vegetation productivity, water and energy fluxes) have also been collected via remote sensors or satellites (https://modis.gsfc.nasa.gov/data) and aggregated into databases. The abundance of easily accessible information can be used to construct functional indicators, thereby enabling quantification of ecosystem function resilience [14,15,28].

Explicit ecological meaning

Most of the functional indicators discussed here have explicit ecological meanings (Box 2) that are defined by the ecosystem processes that modulate their behavior. Thus, ecologists can use these meanings to construct a framework for predicting the robustness and behavior of various indicators under changing environmental conditions. Ecosystem biogeochemical models simulate ecosystem functions on daily to decadal timescales. Through the application of these functional indicators, it might be feasible to test and improve the ability of models to detect the long-term dynamics of ecosystem functions that accompany state change.

It is important to note that these indicators have been intensively investigated in the field of ecosystem ecology, especially against the background of global climate change [16,22,23,29–31]. Note that some environmental and biotic factors may interfere with the robustness of the indicators (Table 1 for caveats). Measures should be taken to exclude the interfering effects before using the indicators to detect state changes.

Future research priorities

Applications in other ecosystem types

The ecosystems addressed in this paper are mostly water-limited grassland ecosystems, and the state changes occurring within them are primarily driven by variations in water availability. However, other ecosystem types experience state changes driven by a diversity of limiting factors, and applying functional indicator analysis to these ecosystem types will require the identification of these factors and the construction of corresponding functional indicators. For example, nutrient availability/uptake is the key factor of ecosystem transition in eutrophication-induced phytoplankton blooms and in some types of desertification. In these cases, nutrient-related functional indicators (e.g., nutrient-use efficiency, nutrient sensitivity) could be used to detect ecosystem state changes. Expanding the use of functional indicators to predict state changes in other ecosystem types should be a research priority.

Linkage with ecosystem models

Ecosystem models (e.g., CLM [32], OCHIDEE [33], CABLE [34]) simulate ecosystem biogeochemical cycles, the hydrological cycle, and energy flows, and can be coupled to climate models to predict the effects of global change on ecosystem functioning. Although not uncommon in aquatic systems [35,36], simulations that integrate climate change-induced state change into terrestrial ecosystem models are limited. For models to predict long-term changes in ecosystem function, the mechanisms that cause state changes need to be well-reproduced in ecosystem models. Models can be evaluated based on how well they capture the dynamics of the functional indicators. To achieve this, it may be necessary to investigate the parameters and modules that control the dynamics of the functional indicators. In addition, positive feedback loops are key factors that drive abrupt ecosystem state change. Although most positive feedback loops are integrated into ecosystem models, whether they accurately reflect the intensity of real-world feedback that drives state change is unclear. Therefore, comparing the strength of the positive feedback in model predictions to empirical observations via functional indicators may be a useful assessment of how well these processes are integrated into the model. For example, models may underestimate water–nitrogen–productivity feedback and thus underestimate the precipitation-sensitivity of vegetation productivity [37]. Indirect factors induced by climate change may also affect the strength of the key types of positive feedback that govern state change and should also be considered.

Concluding remarks

New technologies are now delivering large real-time datasets of ecosystem functions. To take advantage of this wealth of data, we propose the construction of indicators based on functional variables in addition to state variables, as well as the use of their dynamics to detect state changes in terrestrial ecosystems. Because functional-based indicators have explicit ecological meanings

Outstanding questions

What functional indicators can be used to predict state changes in ecosystems that are constrained by factors other than water shortage (e.g., tundra, tropic rainforests, and aquatic ecosystems)?

Can functional indicators be used to understand or predict positive feedback mechanisms and their role in state changes?

Which are the important functional indicators that are, and are not, successfully represented by ecosystem models?

How can modeled functional indicators be improved such that forecasting of ecosystem state changes also improves?

and are connected to ecological processes, they are more readily interpretable for assessing the risk of state change than are state-based indicators. Future research priorities (see Outstanding questions) include the development of functional-based indicators for different ecosystem types, as well as the use of ecosystem models to test and describe the long-term changes that precede critical or smooth state changes.

Acknowledgments

This research was jointly supported by the National Natural Science Foundation of China (grant no. 31922053), National Key R&D Program of China (grant no. 2017YFA0604801), Second Tibetan Plateau Scientific Expedition and Research Program (grant no. 2019QZKK0405), Key R&D Program of Hainan (grant no. ZDYF2022SHFZ042), and the start-up fund of Hainan University [no. KYQD(ZR)21096]. The authors appreciate Dr Andrea Stephens and three anonymous reviewers for their constructive comments on earlier versions of this manuscript.

Declaration of interests

The authors declare no conflicts of interest.

Supplemental information

Supplemental information associated with this article can be found, in the online version, at https://doi.org/10.1016/j.tree.2022.07.011

References

1. Masson-Delmotte, V. *et al. Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press (in press)
2. Lenton, T. (2011) Early warning of climate tipping points. *Nat. Clim. Chang.* 1, 201–209
3. Scheffer, M. *et al.* (2001) Catastrophic shifts in ecosystems. *Nature* 413, 591–596
4. Costanza, R. *et al.* (1996) The value of the world's ecosystem services and natural capital. *Nature* 387, 253–260
5. Scheffer, M. *et al.* (2012) Anticipating critical transitions. *Science* 338, 344–348
6. Rietkerk, M. *et al.* (2021) Evasion of tipping in complex systems through spatial pattern formation. *Science* 374, abj0359
7. Arani, B.M.S. *et al.* (2021) Exit time as a measure of ecological resilience. *Science* 372, eaay4895
8. Dakos, V. *et al.* (2014) Resilience indicators: prospects and limitations of early warnings of regime shifts. *Phil. Trans. R. Soc. B* 370, 20130263
9. Kéfi, S. *et al.* (2013) Early warning signals also precede non-catastrophic transitions. *Oikos* 122, 641–648
10. Guttal, V. and Jayaprakash, C. (2008) Changing skewness: an early warning signal of regime shifts in ecosystems. *Ecol. Lett.* 11, 450–460
11. Smith, A.B. *et al.* (2019) Alternatives to genetic affinity as a context for within-species response to climate. *Nat. Clim. Chang.* 9, 787–794
12. Chapin, F.S. *et al.* (2011) *Principles of Terrestrial Ecosystem Ecology* ((2nd edn)), Springer Science+Business Media
13. Baldocchi, D. *et al.* (2001) FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. *Bull. Am. Meteorol. Soc.* 82, 2415–2434
14. Schimel, D. and Schneider, F.D. (2019) Flux towers in the sky: global ecology from space. *New Phytol.* 224, 570–584
15. Yu, R. *et al.* (2019) Anticipating global terrestrial ecosystem state change using FLUXNET. *Glob. Change Biol.* 25, 2352–2367
16. Hu, Z. *et al.* (2018) Shifts in the dynamics of productivity signal ecosystem state transitions at the biome-scale. *Ecol. Lett.* 21, 1457–1466
17. Liu, Y. *et al.* (2019) Reduced resilience as an early warning signal of forest mortality. *Nat. Clim. Chang.* 9, 880–885
18. Bestelmeyer, B.T. *et al.* (2011) Analysis of abrupt transitions in ecological systems. *Ecosphere* 2, 1–26
19. Rietkerk, M. *et al.* (1997) Site-specific properties and irreversible vegetation changes in semi-arid grazing systems. *Oikos* 80, 241–252
20. Rietkerk, M. *et al.* (2004) Self-organized patchiness and catastrophic shifts in ecosystems. *Science* 305, 1926–1929
21. Scheffer, M. *et al.* (2009) Early-warning signals for critical transitions. *Nature* 461, 53–59
22. Maurer, G.E. *et al.* (2020) Sensitivity of primary production to precipitation across the United States. *Ecol. Lett.* 23, 527–536
23. Huxman, T.E. *et al.* (2004) Convergence across biomes to a common rain-use efficiency. *Nature.* 429, 651–654
24. Hu, Z. *et al.* (2010) Precipitation-use efficiency along a 4500-km grassland transect: rain-use efficiency in Chinese grasslands. *Glob. Ecol. Biogeogr.* 19, 842–851
25. Wang, H. *et al.* (2021) Evapotranspiration components and water use efficiency from desert to alpine ecosystems in drylands. *Agric. Forest Meteorol.* 298-299, 108283
26. Hu, Z. *et al.* (2009) Partitioning of evapotranspiration and its controls in four grassland ecosystems: application of a two-source model. *Agric. Forest Meteorol.* 149, 1410–1420
27. Law, B. *et al.* (2002) Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation. *Agric. Forest Meteorol.* 113, 97–120
28. Rocha, J. (2022) Ecosystems are showing symptoms of resilience loss. *Environ. Res. Lett.* 17, 065013
29. Oliver, T.H. *et al.* (2015) Biodiversity and resilience of ecosystem functions. *Trends Ecol. Evol.* 30, 673–684
30. Seddon, A.W.R. *et al.* (2016) Sensitivity of global terrestrial ecosystems to climate variability. *Nature.* 531, 229–232
31. Al-Yaari, A. *et al.* (2020) Asymmetric responses of ecosystem productivity to rainfall anomalies vary inversely with mean annual rainfall over the conterminous United States. *Glob. Change Biol.* 26, 6959–6973
32. Oleson, K. *et al.* (2010) *Technical Description of version 4.0 of the Community Land Model (CLM), NCAR Technical Note NCAR/TN-478+STR*, University Corporation for Atmospheric Research
33. Krinner, G. *et al.* (2005) A dynamic global vegetation model for studies of the coupled atmosphere-biosphere system. *Glob. Biogeochem. Cycles* 19, GB1015
34. Wang, Y.P. *et al.* (2011) Diagnosing errors in a land surface model (CABLE) in the time and frequency domains. *J. Geophys. Res.* 116, G01034
35. Kuhlmann Andersen, T. *et al.* (2020) Predicting ecosystem state changes in shallow lakes using an aquatic ecosystem model: Lake Hinge, Denmark, an example. *Ecol. Appl.* 30, eo2160

36. Mooij, W. *et al.* (2007) Predicting the effect of climate change on temperate shallow lakes with the ecosystem model PCLake. *Hydrobiologia* 584, 443–454
37. Cheng, K. *et al.* (2021) Improvement of predicting ecosystem productivity by modifying carbon–water–nitrogen coupling processes in a temperate grassland. *J. Plant Ecol.* 14, 10–21
38. Chen, N. *et al.* (2017) Rising variability, not slowing down, as a leading indicator of a stochastically driven abrupt transition in a dryland ecosystem. *Am. Nat.* 191, E1–E14
39. Guo, Q. *et al.* (2012) Spatial variations in aboveground net primary productivity along a climate gradient in Eurasian temperate grassland: effects of mean annual precipitation and its seasonal distribution. *Glob. Change Biol.* 18, 3624–3631
40. Eby, S. *et al.* (2017) Alternative stable states and spatial indicators of critical slowing down along a spatial gradient in a savanna ecosystem. *Glob. Ecol. Biogeogr.* 26, 638–649
41. Hu, Z.M. *et al.* (2012) Assessment of changes in the state of the rangelands of Inner Mongolia, China between 1998 and 2007 using remotely sensed data. *Rangel. J.* 34, 103–109
42. Hu, Z. *et al.* (2008) Effects of vegetation control on ecosystem water use efficiency within and among four grassland ecosystems in China. *Glob. Change Biol.* 14, 1609–1619
43. Tang, X. *et al.* (2014) How is water-use efficiency of terrestrial ecosystems distributed and changing on Earth? *Sci. Rep.* 4, 7483
44. Gao, Y. *et al.* (2014) Water use efficiency threshold for terrestrial ecosystem carbon sequestration in China under afforestation. *Agric. Forest Meteorol.* 195, 32–37
45. Knapp, A.K. and Smith, M.D. (2001) Variation among biomes in temporal dynamics of aboveground primary production. *Science* 291, 481–484
46. Gherardi, L. and Sala, O. (2015) Enhanced interannual precipitation variability increases plant functional diversity that in turn ameliorates negative impact on productivity. *Ecol. Lett.* 18, 1293–1300
47. Piao, S. *et al.* (2020) Interannual variation of terrestrial carbon cycle: Issues and perspectives. *Glob. Change Biol.* 26, 300–318
48. Wu, D. *et al.* (2018) Asymmetric responses of primary productivity to altered precipitation simulated by ecosystem models across three long-term grassland sites. *Biogeosciences* 15, 3421–3437
49. Piao, S. *et al.* (2013) Evaluation of terrestrial carbon cycle models for their response to climate variability and to CO_2 trends. *Glob. Change Biol.* 19, 2117–2132
50. Bernardino, P.N. *et al.* (2020) Global-scale characterization of turning points in arid and semi-arid ecosystem functioning. *Glob. Ecol. Biogeogr.* 29, 1230–1245