ECOLOGY

What makes a terrestrial ecosystem resilient?

A complex set of biotic and abiotic factors determines the resilience of an ecosystem

By **Kathy J. Willis,[1,2] Elizabeth S. Jeffers,[2] Carolina Tovar[1]**

With increasing incidence of extreme climatic events, disease outbreaks, and other environmental perturbations, conservation of terrestrial ecosystems that can retain their structure and function despite environmental shocks has moved rapidly up the international political agenda. International environmental policies and targets such as the Aichi Biodiversity Targets and the Sustainable Development Goals include conserving resilient ecosystems as a key priority.

An ecosystem can display resilience in at least two ways: in the ability to resist an environmental perturbation and not switch to another state, and in how quickly it recovers after the disturbance (*1*). However, research into what makes a terrestrial ecosystem resilient is complex. Many hypotheses have been proposed, suggesting a suite of possible abiotic and biotic attributes responsible for resilience (*1*, *2*). Understanding resilience also requires comparative data sets that span both space and time and that address at least three questions: Where are the most resilient ecosystems, what attributes make them more resilient than others, and how close is an ecosystem to losing its resilience?

The first step toward addressing these questions is to find data sets demonstrating that particular ecosystems display resilience. Some projects fail at this hurdle. It is often difficult to find data sets spanning a long enough time to record the response of an ecosystem to an environmental perturbation, especially in forested ecosystems with trees that have decades-long generation times. Furthermore, the record of a resistant ecosystem will display no change despite a known climatic perturbation and is thus often discarded; a data record that shows no change is harder to publish.

In recent years, new sources of ecological data and algorithms for analyzing resilience have begun to provide answers to the three questions posed above. These studies have been carried out in almost every terrestrial biome (*3*); here, we focus on those undertaken in tropical ecosystems.

WHERE ARE THE MOST RESILIENT TROPICAL ECOSYSTEMS?

Data sets normally used to examine other ecological phenomena have recently been analyzed to determine both forms of resilience. Cole *et al.* (*4*), for example, used data from fossil pollen records to compare tropical forest recovery rates after perturbations between and within regions. In a meta-analysis, they examined 283 forest disturbance and recovery events over the past 20,000 years in Central and South American, African, and Asian rain forest blocks. They found substantial spatial differences in recovery rates; Central American tropical rain forests appeared to recover faster from environmental perturbations than those in South America and Asia.

Species richness, as in this West African tropical rain forest, may not always provide resilience to external perturbations (see the figure).

In another study, Poorter *et al.* (*5*) examined recovery rates of 45 Neotropical forest sites after clearance from 1500 records spanning the past 20 years. Even on this shorter time scale, the authors found strong geographical and climatic variation in recovery rates, with seasonally dry forests appearing to have less resilience than that of humid tropical lowland forests.

Innovative analysis of satellite imagery is starting to provide another important data set for determining spatial patterns of resilience (*6*, *7*). For example, Seddon *et al.* (*6*) used monthly Moderate Resolution Imaging Spectroradiometer (MODIS) satellite data, taken globally at 5-km resolution between 2000 and 2013, to develop a vegetation sensitivity index that captures the relationship between climatic anomalies and relative variance of the vegetation (see the figure, left). This method identifies how sensitive different regions of vegetation have been to climatic variability over the past 14 years. In the tropics, more resilient areas included the woody savannas of the Brazilian Cerrado and the drylands of the Sahel. By contrast, vegetation in parts of the West Africa and the Amazon basins was highly sensitive to climatic perturbations.

WHAT ATTRIBUTES PROVIDE RESILIENCE?

In addition to showing relative patterns of resilience, these spatial and temporal records provide important data sets with which to test the many hypotheses relating to resilience (*1*, *2*) and the complexity of the interacting biotic and abiotic factors that can lead to it (*2*). For example, a key abiotic attribute hypothesized to influence resilience is climate, and there is some evidence emerging to support this. In Neotropical dry forests, the highest rates of above-ground biomass recovery after clearance occurred in regions with higher local rainfall and lower water deficit (the difference between potential evapotranspiration and rainfall) (*5*).

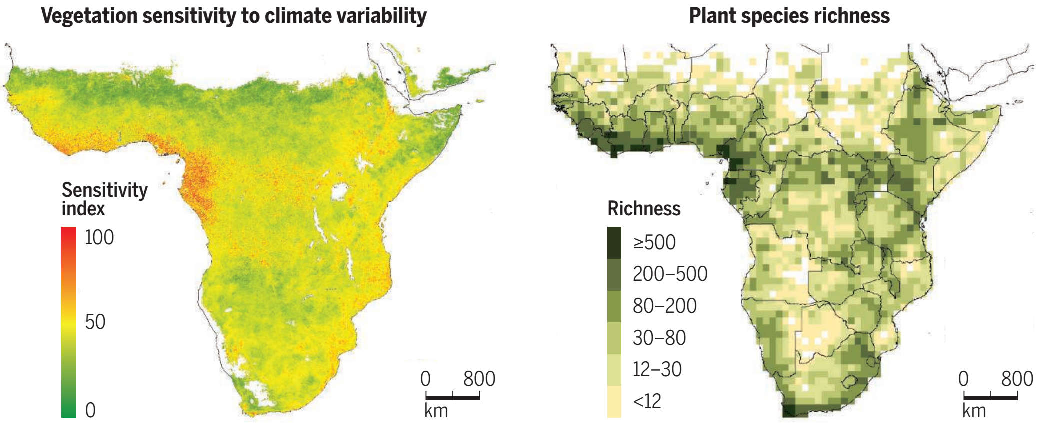
Other studies have hypothesized that the number of times an ecosystem is disturbed, the less resilient it becomes, as indicated by a slowing down in recovery rates after each subsequent disturbance. However, this relationship does not always hold true, especially over longer time intervals. Cole *et al.* (*4*), for example, found the opposite effect in the fossil tropical forest data sets; the more times a system was disturbed, the faster it recovered, presumably because the vegetation became dominated by forest species that could tolerate and respond quickly to disturbance. The type of

[1]Royal Botanic Gardens, Kew, Richmond TW9 3AB, UK. [2]Oxford Long-term Ecology Laboratory, Department of Zoology, University of Oxford, Oxford OX1 3PS, UK. Email: k.willis@kew.org

Published by AAAS

No insurance policy, necessarily

Recent data suggest that at a continental scale, those regions in Africa rich in tropical plant species (*13*) are also the most sensitive to climate variability (*6*), implying that higher species richness does not necessarily lead to greater resilience.



GRAPHIC: J. YOU/*SCIENCE*

disturbance apparently can also influence the resilience of an ecosystem, and this varies according to vegetation type. For example, in tropical grasslands such as those in West Africa, disturbance by fires buffers ecosystems from forest encroachment and thus promotes grassland resilience (*8*). By contrast, frequent disturbance by fires in tropical forest-savanna transition zones can lead to loss of resilience in forest communities (*9*).

Another abiotic attribute hypothesized to account for ecosystem resilience is soil type. Again, there is some evidence to support this. In Poorter *et al.*'s study, high soil fertility had a positive influence on biomass recovery in Neotropical secondary forest plots (*5*). Similarly, a modeling study that incorporated remote sensing and field data predicts that rain forest situated on soils with low clay content will be least affected by an increase in the length of the dry season and will thus have higher resilience (*10*). Belowground biotic attributes may also be important in determining the resilience of an ecosystem; in particular, plants that have root systems associated with mycorrhizal fungi may have greater resilience to water stress in tropical dry forests (*11*).

There is also a suite of biotic factors to consider. Possibly the most widely cited is the insurance hypothesis. This suggests that more biodiverse ecosystems will be more resilient to environmental perturbations because they contain a greater number of species available to replace functions carried out by lost species. This certainly appears to be the case at the community level in some ecosystems (*12*) but does not necessarily hold at the continental scale. For example, regions with the highest tropical plant species richness in Africa (see the figure, right) (*13*) appear to be most sensitive to climate perturbations (see the figure, left) (*6*)—the opposite finding to the insurance hypothesis.

According to another biotic hypothesis, it is the characteristics of the component species (such as wood density, rooting depth, and leaf-area index) that make ecosystems more resilient (*1*). Here, some clear trends are starting to emerge. For example, Greenwood *et al.* (*14*) found that across forested biomes, mortality rates after drought were lower for species with greater wood density and lower specific leaf area. A global meta-analysis also identified these two characteristics as important for withstanding drought in tropical rain forests, whereas in tropical grasslands, plants with deeper roots were more resilient to drought (*3*).

HOW CLOSE IS A SYSTEM TO LOSING RESILIENCE?

Determining which biotic and abiotic factors contribute to resilient ecosystems is important for maintaining and enhancing them. However, when determining conservation strategies, it is also critically important to be able to identify when an ecosystem is about to lose its resilience and cross a threshold from a desirable to an undesirable stable state. Several methods have been proposed to do this. For example, at the continental scale, Hirota *et al.* (*15*) have shown that tropical and subtropical ecosystems in Africa, Australia, and South America switch to a savanna state when forest cover is less than 60%. This has direct implications for the management of tropical forests, where deforestation is a huge issue.

Another proposed method is to examine recovery rates from disturbances on the basis of the hypothesis that the closer a system is to a threshold, the slower the recovery rate will be (*1*). This approach appears to work in models but only seems to hold true for some terrestrial ecosystems. For example, Verbesselt *et al.* (*7*) found that recovery rates from perturbations slowed down sharply once mean annual precipitation fell below 1500 mm in evergreen tropical forests in South America, Africa, and Southeast Asia, possibly indicating a tipping point about to be crossed. By contrast, another study in the Amazon rain forests found only evidence of gradual change to several transitional forest states in response to a lengthening of the dry season (*10*), rather than an abrupt change from forest to another state.

There is also the fundamental question of whether switching between alternative states is always necessarily a bad thing. Recent studies indicate that tropical grasslands persist in a permanent transitional state and that the ability to switch between forest and savanna in response to perturbations underpins their resilience (*9*).

The recent studies discussed above are starting to test the many hypotheses that exist to explain resilience in terrestrial ecosystems. They reaffirm the complexity of resilience but also provide clear pointers for future research and conservation. In tropical ecosystems, soil type, belowground processes, and rooting depth are potentially important areas of future research with direct management applications. The factors responsible for resilience of tropical grasslands are another knowledge gap needing more research. Given the importance of terrestrial ecosystem resilience to natural resource security and supply across the globe, research into the attributes underpinning it should be high on any international agenda. ■

REFERENCES

1. D. Hodgson, J. L. McDonald, D. J. Hosken, *Trends Ecol. Evol.* **30**, 503 (2015).
2. B. L. Timpane-Padgham, T. Beechie, T. Klinger, *PLOS ONE* **12**, e0173812 (2017).
3. K. J. Willis *et al.*, in *State of the World's Plants, 2017 Report*, K. J. Willis, Ed. (Royal Botanic Gardens, Kew, 2017), pp. 42–49.
4. L. E. S. Cole, S. A. Bhagwat, K. J. Willis, *Nat. Commun.* **5**, 3906 (2014).
5. L. Poorter *et al.*, *Nature* **530**, 211 (2016).
6. A. W. R. Seddon, M. Macias-Fauria, P. R. Long, D. Benz, K. J. Willis, *Nature* **531**, 229 (2016).
7. J. Verbesselt *et al.*, *Nat. Clim. Change* **6**, 1028 (2016).
8. P. Laris, S. Dadashi, A. Jo, S. Wechsler, *Plant Ecol.* **217**, 583 (2016).
9. I. Oliveras, Y. Malhi, *Philos. Trans. R. Soc. B Biol. Sci.* **371**, 20150308 (2016).
10. N. M. Levine *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **113**, 793 (2016).
11. K. Allen *et al.*, *Environ. Res. Lett.* **12**, 023001 (2017).
12. M. Hisano, E. B. Searle, H. Y. H. Chen, *Biol. Rev.* **93**, 439 (2018).
13. H. P. Linder, *Front. Ecol. Evol.* 10.3389/fevo.2014.00038 (2014).
14. S. Greenwood *et al.*, *Ecol. Lett.* **20**, 539 (2017).
15. M. Hirota, M. Holmgren, E. H. Van Nes, M. Scheffer, *Science* **334**, 232 (2011).

10.1126/science.aar5439

Science

What makes a terrestrial ecosystem resilient?

Kathy J. Willis, Elizabeth S. Jeffers and Carolina Tovar

Science **359** (6379), 988-989.
DOI: 10.1126/science.aar5439