

RECONCILING RESILIENCE ACROSS
ECOLOGICAL SYSTEMS, SPECIES AND SUBDISCIPLINES

Essay Review

Unifying the concepts of stability and resilience in ecology

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Abstract

1. Characterizing how ecosystems are responding to rapid environmental change has become a major focus of ecological research. The empirical study of ecological stability, which aims to quantify these ecosystem responses, is therefore more relevant than ever.
2. Based on a historical review and bibliometric mapping of the field of ecological stability, we show that the two main schools relating to the study of stability—one focusing on systems close to their equilibrium and the other on non-equilibrium behaviour—have developed in parallel leading to divergence in both concepts and definitions.
3. We synthesize and expand previous frameworks and capitalize on the latest developments in the field to build towards an integrated framework by elaborating the overarching concept of ecological stability and its properties. Finally, the broad applicability of our work is demonstrated in two empirical cases.
4. *Synthesis.* With rapidly changing environmental conditions, the stability of ecosystems has become a major focus of ecological research. Still, the concept of stability remains a major source of confusion and disagreement among ecologists. The conceptual framework presented here provides a basis to integrate currently diverging views on the study of ecological stability.

KEYWORDS

alternative stable states, equilibrium, latitude, perturbations, recovery, regime shift, resistance, tolerance

GLOSSARY

- **Constancy:** Constancy refers to the invariability of a system in time compared to its reference condition (Oriens, 1974). Constancy can be a consequence of, but is neither necessary nor sufficient for stability (Justus, 2007). Also referred to as 'temporal stability'.
- **Domain of attraction** (Also basin of attraction or stability domain): It is the set of system variable and parameter values under which a system returns to a given reference condition after being perturbed (Carpenter et al., 1999; Grimm & Wissel, 1997).
- **Ecological stability:** Overall ability of a system to remain in the same domain of attraction and to retain its function and structure in the face of perturbations. Stability is a set of system properties that determines the magnitude, duration and irreversibility of change resulting from a perturbation (Noy-Meir, 1974).
- **Latitude:** The maximum amount a system variable can be changed before losing its ability to recover (Walker et al., 2004).

- **Persistence:** The length of time a system maintains a certain reference condition (Grimm & Wissel, 1997; Orians, 1974; Pimm, 1984).
- **Perturbation:** A biotic or abiotic force, agent or process causing a change in system variable(s) and/or parameter(s) (Sutherland, 1981). We distinguish between pulse (instantaneous), press ((quasi-)persistent in time), ramp perturbations (increasing in magnitude over time) and environmental stochasticity, where a system is constantly affected by small, stochastic perturbations (Ives, 1995). Note that these definitions are time scale and study system dependent.
- **Recovery:** The ability to fully return to the reference condition after a perturbation (Domínguez-García et al., 2019; Hillebrand et al., 2018; Westman, 1978).
- **Reference (or reference condition):** The stability of a system is assessed relative to a reference condition, that is, a stable condition of the system's variables and parameters in the absence of perturbations. Reference conditions are not limited to reference states but also include reference dynamics (Justus, 2007).
- **Reference state:** A stable point of a system. As systems are continuously exposed to random perturbations, they often fluctuate around the actual equilibrium point with the centroid of the state distribution located near or in the equilibrium point (Lewontin, 1969). For certain environmental conditions, some systems can have two or more alternative stable states (Scheffer et al., 2001; Van Meerbeek et al., 2019).
- **Reference dynamic:** A dynamic, but stable reference condition. Examples are stable limit cycles or stable trajectories (Holling, 1973).
- **Resilience:** The rate at which a system variable returns to its reference condition following a perturbation (Pimm, 1984). Also referred to as 'engineering resilience'.
- **Resilience sensu Holling:** It is a measure of the ability of the system to absorb changes of state variables and parameters and still remain in the domain of attraction (Holling, 1973). Also referred to as 'ecological resilience'.
- **Resistance:** The ability to resist changes in system variables in response to a perturbation. Resistance is inversely related to the degree of change following a perturbation (Justus, 2007).
- **System parameter:** Factor that influences the system variables, but is, for the most part, uninfluenced by them (e.g. temperature, precipitation; Justus, 2007).
- **System variable:** Represents system parts and describes the structure or functioning of a system (Justus, 2007).
- **Tipping point (or threshold):** Point on the system variable curve where a small perturbation triggers a large, abrupt and sometimes irreversible change of the system variable(s) (Dakos et al., 2019; Lenton, 2013).
- **Tolerance:** The ability of a system to tolerate perturbations, independent from the degree of change and the rate of return after a perturbation (Justus, 2007).

1 | THE BABYLONIAN CONFUSION ABOUT STABILITY

Ecosystem stability is supposed to be one of the 'unifying concepts' in ecology. But this concept, and its relations with other attributes of the systems (e.g. diversity), have caused much controversy, mainly due to confusion as to what is meant by 'stability'. Noy-Meir (1974)

The concept of stability (see the Glossary) appeared on the ecological scene in the 1950s, with pioneering contributions from scientists such as Odum (1953), MacArthur (1955) and Elton (1958).

Soon, the relationship between diversity and stability became a prominent theme in ecological research. In 1974, it was one of the focal points of discussion on the first international congress of ecology in The Hague (The Netherlands; Van Dobben & Lowe-McConnel, 1974). In his contribution to the congress, Noy-Meir (1974) contested the supposedly unifying nature of the stability concept, arguing that it caused much controversy due to confusion about its definition. Two decades later, Grimm and Wissel (1997) identified more than 160 definitions and more than 40 metrics of stability, and called stability '*one of the most nebulous terms in the whole of ecology*'.

Since the early days of the diversity–stability debate (see McCann (2000) for an overview of this debate), a lot of progress

has been made in understanding the relationship between diversity and ecological stability (e.g. Hautier et al., 2015; Isbell et al., 2015; Loreau & de Mazancourt, 2013; Pennekamp et al., 2018). However, it is striking that we are still struggling with many of the same fundamental issues raised almost half a century ago. The concept of stability remains a major source of confusion and disagreement among scientists today (Donohue et al., 2016; Kéfi et al., 2019; Pimm et al., 2019). In addition to the multitude of synonyms and definitions that have been proposed to characterize stability (e.g. Boesch, 1974; Donohue et al., 2016; Orians, 1974), we argue that there is another cause at the root of this confusion that has so far been largely overlooked. Historically, two main schools relating to the study of stability of ecological systems can be distinguished, one focusing on systems close to their equilibrium, and one focusing on non-equilibrium behaviour and different domains of attraction. While the equilibrium literature commonly employs the term 'stability' as overarching property, the non-equilibrium literature revolves around the term 'resilience (*sensu* Holling)'. Here, we bring them together under the umbrella of 'ecological stability'.

The first part of this study aims to develop broader insights in the developments and structure of the extensive field of ecological stability. Systematic reviews or meta-analyses are increasingly common to synthesize scientific evidence, but are impractical to get an overview of broad research fields (Nakagawa et al., 2019). Therefore, we first use a narrative review to provide a historical perspective on the evolution of different views on stability in ecology. A bibliometric mapping exercise is then performed to analyse the impact of the parallel development of the different schools on the ecological literature. In the second part, we build on recent developments and previous frameworks to define the overarching concept of ecological stability, working towards the unification of equilibrium and non-equilibrium stability research. The broad applicability of the framework is then demonstrated in two empirical, quantitative case studies.

2 | TRACING THE ORIGIN OF DIFFERENT VIEWS ON STABILITY

The first steps of the stability research in ecology were taken in the field of theoretical population dynamics (Figure 1). In the 1920s, the Lotka–Volterra equations, used to describe predator–prey interactions (Lotka, 1925; Volterra, 1927), stimulated a new wave of research focusing on the mathematical description of the behaviour of ecological systems close to a stable reference condition, that is, where linear approximations are valid and mathematical models are straightforward to derive. In 1955, MacArthur (1955) was the first to propose a quantitative measure of ecological stability, defined as the persistence of populations over time, based on the number of possible pathways for energy flow in a food web, thereby initiating the diversity–stability debate. After early contributions from empiricists such as Odum (1953) and Elton (1958) in the 1950s on the resistance of communities to environmental perturbations, Pimentel (1961) was the first in the international literature to publish results of a field experiment testing the stability–diversity relationship. The growing interest in diversity–stability relationships resulted in a proliferation of definitions and measures of stability. The 22nd Brookhaven symposium on Biology, in 1969, was dedicated entirely to the diversity–stability debate, with several contributions trying to clear the fog surrounding the concept of stability (Lewontin, 1969; Margalef, 1969). Stability soon evolved to encompass multiple properties, describing the different aspects of the response of a system to perturbations (Boesch, 1974; Orians, 1974). Boesch (1974) was the first to use both the terms resistance and resilience as components of stability to describe the ability of a system to withstand perturbations and to return to a stable state, respectively.

It is during this search for a clear definition of stability that Holling, in 1973, wrote his seminal paper as a critique to the stable equilibrium assumption underlying the mathematical analysis of stability (Holling, 1973). In this work, he developed a new qualitative framework with 'resilience' as its central focus, which

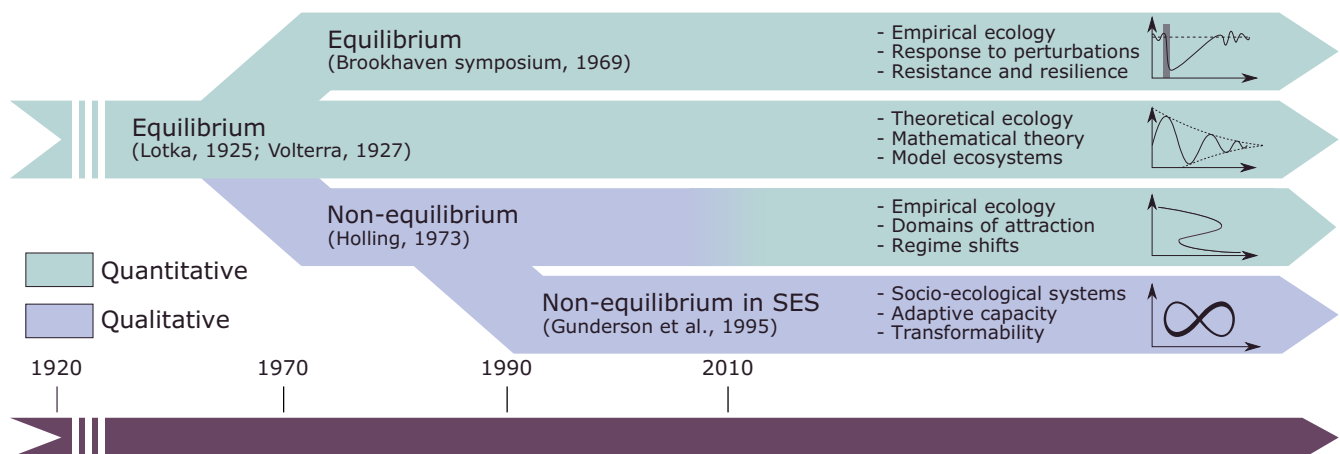


FIGURE 1 Evolution of the equilibrium and non-equilibrium concepts of stability in ecology, divided into a 'quantitative, equilibrium' and 'qualitative, non-equilibrium' view on the behaviour of ecosystems. Central themes (with benchmark publications) are indicated in capital letters. Research foci are added in bullet points. SES, socio-ecological systems

according to Holling (1973) is 'a measure of the persistence of systems and of their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables'. While the equilibrium-centred literature originally defined resilience as a component of stability, Holling used this term to qualitatively describe the behaviour of dynamic systems far from their stable reference condition. The first of Holling's critiques was that ecosystems must be in or near a stable reference state to study their stability and that stable equilibria are very rare or non-existing in nature (Holling, 1973). Another point of criticism was the so-called implicit assumption of a global stable state in equilibrium-centred research, which was therefore considered inappropriate for studying ecosystems with multiple stable states (Nyström et al., 2000). Despite these issues being countered or resolved in the following decades (e.g. DeAngelis & Waterhouse, 1987; Sutherland, 1974), many of Holling's arguments continue to pervade the ecological literature to this day (e.g. Liao, 2012; Sterk et al., 2017). The origin of the development of different concepts of ecological stability is thus due to them being centred on equilibrium or non-equilibrium systems, respectively. Lastly, by drawing a link between social and ecological systems in his early work (Holling, 1969; Holling & Goldberg, 1971; Holling & Orians, 1971), Holling's definition of resilience went on to permeate the field of socioecology (Figure 1).

3 | PARALLEL DEVELOPMENTS OF STABILITY CONCEPTS

To analyse the impact these different views have on the ecological literature, we performed a bibliometric analysis with the R package *BIBLIOMETRIX* (Aria & Cuccurullo, 2017). Bibliometric mapping describes the structure of scientific literature using information on authors, citations or words shared between articles and is used to analyse and visualize the intellectual and conceptual structure of a research field (Börner et al., 2003; Garfield & Sher, 1993; Nakagawa et al., 2019). The intellectual structure shows how certain works influence a scientific research field while the conceptual structure reveals the trends and links between the main themes of the field. To generate a bibliographic collection, we searched for the terms (ecolog* AND stability) or (ecolog* AND resilience) in Clarivate Analytics Web of Science in the period from 1955 to October 2019. We selected the ecological journals, such as *Ecology*, *The American Naturalist*, *Oikos*, *Ecology Letters*, *Journal of Ecology*, *Trends in Ecology & Evolution*, *Frontiers in Ecology and the Environment* and *Journal of Animal Ecology*, complemented with the multidisciplinary journals *Nature*, *Science* and *Proceedings of the National Academy of Sciences of the United States of America* (PNAS) and the socio-ecological journal *Ecology and Society*. In total, we retrieved title, author lists, journal, year of publishing, keywords, text and references of 2,028 unique articles (Figure S1).

The conceptual structure was analysed by a co-occurrence network and a Multiple Correspondence Analysis (MCA). A co-occurrence network shows the links between keywords based on the

co-occurrences in articles with thicker links denoting stronger associations. The MCA analysis is suitable to identify subfields that are revealed by hierarchical cluster analysis (Aria & Cuccurullo, 2017). The closer the keywords are situated in the two-dimensional MCA space, the larger the proportion of articles that treat them together. The intellectual structure was analysed with a bibliographic co-citation analysis of the references of all articles (in total 68,052 references). Two articles are linked in a co-citation network when both are cited in a third article (Small, 1973). The width of the edges between papers is proportional to their association strength. More information on the bibliographic analysis are found in Supplementary methods S1.

The results of the bibliometric analyses visualize a clear conceptual and intellectual schism between the equilibrium and non-equilibrium literature (Figure 2). Their different foci seem to have hampered the exchange of ideas and resulted in separate literatures and research lexica. Equilibrium research has mostly revolved around the behaviour of systems close to their equilibrium in response to small perturbations and characterizes the relationship between stability and biodiversity on quantitative grounds (Figure 2a; McCann, 2000). Stability is measured by the properties resistance, resilience and recovery (Donohue et al., 2016; Hillebrand et al., 2018). Two separate subfields were detected by the MCA (Figure 2b): one relating the mathematical analysis of model systems and the other investigating the empirical relationship between stability and biodiversity. The non-equilibrium literature, on the other hand, has been built on a qualitative interpretation of resilience (*sensu* Holling) and uses stability landscapes to describe, rather than measure, the behaviour of dynamic systems far from their equilibrium (Folke, 2006; Scheffer et al., 2015; Vasilakopoulos & Marshall, 2015).

Apart from some early work on alternative stable states (Holling, 1973; May, 1977), much of the ecological research in the 20th century focused on equilibrium systems (Beisner, 2012). The most important scientific contributions in this field, identified by the co-citation analysis (Figure 2c), span five decades, from MacArthur (1955) until Hooper et al. (2005). The lack of strong differentiation in influence indicates a long-term development and gradual maturing of the concept of ecological stability (Figure 2c). Although originating from Holling's influential paper in 1973, the non-equilibrium movement only gained traction at the end of the 1990s, when scientific evidence about alternative stable states in nature was accumulating (e.g. Knowlton, 1992; Scheffer, 1989). Within the non-equilibrium literature, two closely connected subfields emerged with a large overlap in authors (Figure 2c). The first investigates alternative stable states and regime shifts in ecological systems with Holling (1973) and Scheffer et al. (2001) as main intellectual sources. The second deals with 'resilience (*sensu* Holling), vulnerability and adaptability' of socio-ecological systems. They are relatively young disciplines with a small number of highly influential papers, all published after 2000: Gunderson and Holling (2002), Walker et al. (2004), Folke et al. (2005) and Folke (2006). Together with the thematic map showing the level of development of the themes (Figures S4 and S5), these results

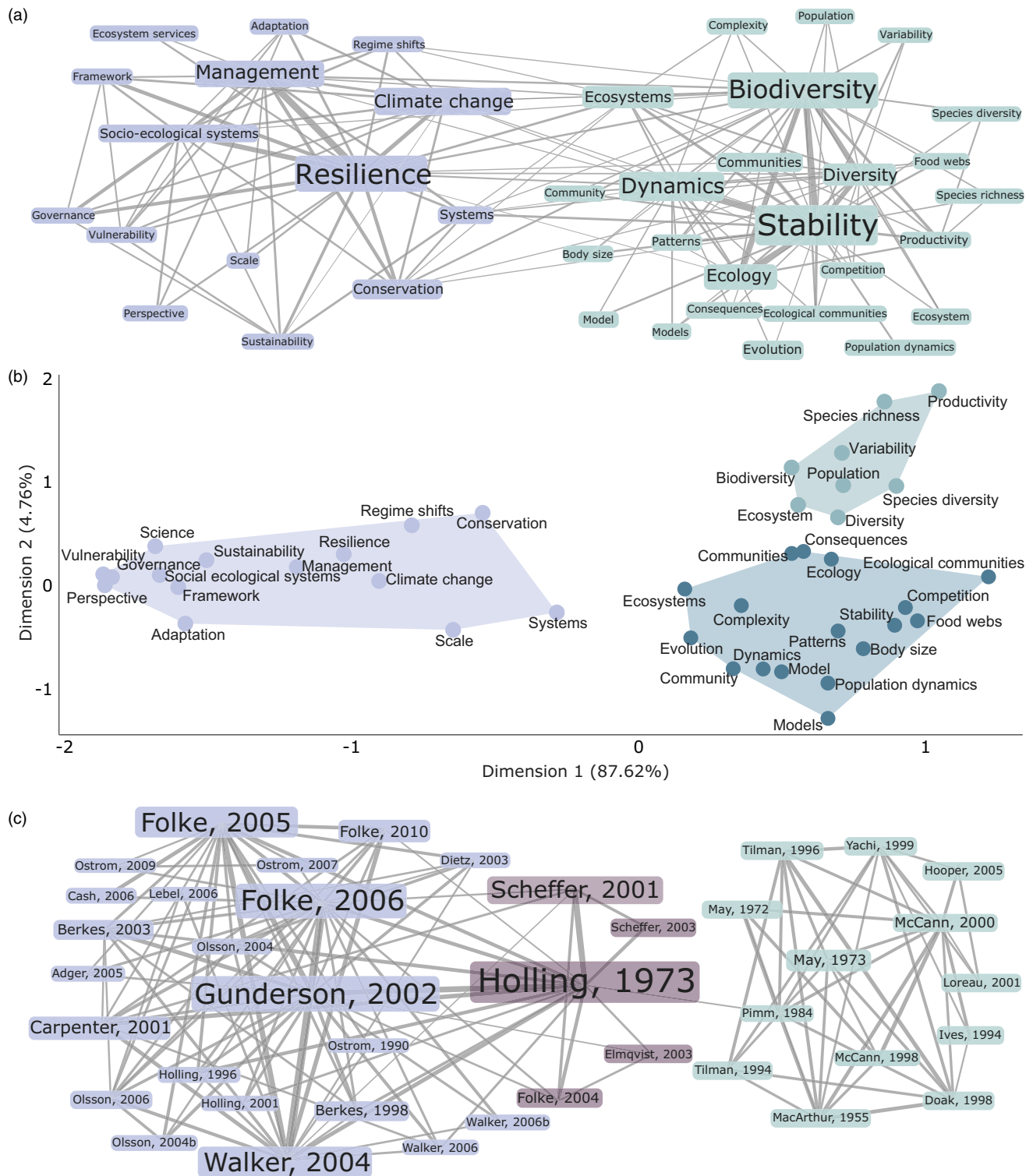


FIGURE 2 Bibliometric analysis of the stability literature in ecology. Different colours denote different clusters, identified by hierarchical cluster analysis: purple colours correspond to non-equilibrium research in (socio-)ecological systems, green colours to equilibrium research. (a) The co-occurrence network reveals two distinct fields in the ecological stability literature. Thickness of the edges between the keywords, not the edge length, is proportional to the association between the keywords. To ensure readability, only strong associations (>15 co-occurrences) between the 40 most frequent keywords are mapped. (b) The conceptual structure map arranges keywords in two-dimensional space according to their association, that is, the proportion of articles that treat them together. The closer the keywords, the larger the association. (c) Co-citation network showing very weak intellectual linkages between the equilibrium and non-equilibrium literature. Thickness of the edges between the articles, not the edge length, is proportional to the association between the two articles and the size of the article name (depicted by first author, year) is proportional to its influence. To ensure readability, only strong associations (>15 co-citations) between the 40 most cited articles are mapped. Extended versions of the co-citation and co-occurrence network are added in Supporting Information (Figures S2 and S3)

suggest that resilience (*sensu* Holling) is an emerging and relatively less-developed theme in ecology (Aria & Cuccurullo, 2017). Despite this, the use of the term resilience (*sensu* Holling) has proliferated in ecology during the last two decades (Figure S6). This has been accompanied by a multitude of definitions and related terms (Donohue et al., 2016), with resilience (*sensu* Holling) often being used as an implicit or vague concept (Myers-Smith et al., 2012; Newton, 2016). Because it is not easily quantified (Pimm et al., 2019; Van Nes & Scheffer, 2007), resilience (*sensu* Holling) has been mainly employed as a theoretical construct, based on the 'ball in a cup' metaphor to visualize properties of systems with different stability domains (Beisner et al., 2003). Despite its conceptual merits, this simple metaphor does not fully grasp the complexity of system responses to perturbations, obstructing efforts to link dimensions of the theoretical stability landscape (e.g. the size and shape of the basin of attraction) to quantitative metrics (Menck et al., 2013; Pimm et al., 2019; Van Nes & Scheffer, 2007). In the last decade, however, major progress has been made to translate the qualitative definition of resilience (*sensu* Holling) to quantitative metrics (Carpenter & Brock, 2006; Dakos et al., 2008; Menck et al., 2013; Van Nes & Scheffer, 2007). Methods for quantifying resilience (*sensu* Holling) in natural systems rely on early warning indicators for critical transitions between alternative stable states (Scheffer et al., 2009) and on distances to the tipping points in system variable \times parameter space (Vasilakopoulos & Marshall, 2015).

Although both equilibrium and non-equilibrium research on stability deal with systems under changing conditions, the two fields have largely progressed in parallel with little intellectual overlap, thereby slowing down scientific progress. Clear evidence of this lack of integration comes from the fact that the equilibrium measures resilience and constancy, in use since the end of the 1960s as properties of stability, have only been adopted as indicators of critical transitions between alternative states in the last two decades (Carpenter & Brock, 2006; Dakos et al., 2008; Van Nes & Scheffer, 2007). In addition, due to its increasing popularity in scientific research and policy contexts (Newton, 2016; Tanner et al., 2015), the lexicon of Holling's resilience framework has recently penetrated the ecological study of systems close to their equilibrium (e.g. Hodgson et al., 2015; Ingrisch & Bahn, 2018; Oliver et al., 2015). Unfortunately, instead of unifying these concepts, the additional terminology creates even more confusion among ecologists. Different terms are used for the same concept (e.g. ecological stability and resilience *sensu* Holling) while the same term is used for different properties (e.g. resilience), because of the lack of proper overarching definitions of stability and all its properties.

4 | DEFINING ECOLOGICAL STABILITY

The divergence in concepts and definitions was identified as an important cause and driver of the schism in the stability literature. In

recent years, several authors have stated the need for a framework integrating equilibrium and non-equilibrium concepts as the way forward. Both Menck et al. (2013) and Mitra et al. (2015) argued, for example, that the two dichotomic views provide complementary insights in the study of multi-stable systems and proposed new measures of stability. However, being based on the contours of the basin of attraction, their applicability is limited to systems exhibiting multi-stability. In addition to the intellectual and conceptual schism, the vagueness and conceptual incoherence surrounding the concept of ecological stability hinders the realization of its full potential in ecological research. To make progress, there is thus first of all a need for a common lexicon based on well-substantiated, integrative definitions of ecological stability and its equilibrium and non-equilibrium properties in ecology. This is fundamental to interpret published results properly, facilitate discussion and allow synthesis. Over the past 60 years, numerous authors have attempted to describe and name the different properties of ecological stability (e.g. Donohue et al., 2016; Grimm & Wissel, 1997; Justus, 2007; Orians, 1974; Pimm, 1984), but besides the work of Justus (2007), these frameworks only covered systems close to their equilibrium. Furthermore, substantial progress has recently been made on the dimensionality of stability in equilibrium systems (Donohue et al., 2016; Hillebrand et al., 2018; Radchuk et al., 2019), and on measuring the dimension of the basin of attraction in non-equilibrium systems (Menck et al., 2013; Vasilakopoulos et al., 2017). Here, we aim to provide an overarching stability framework by building further on the fundamentals of previous frameworks and by capitalizing on recent progress in this field. We first substantiate the concept of ecological stability with its important benchmarks, then provide a set of standard definitions of the different stability properties.

First of all, it is important to define two benchmarks to characterize the ecological stability of a system (Grimm & Wissel, 1997; Justus, 2007). The first is the description and delineation of the system under study. In stability analyses, a system is represented by system variables and parameters (Justus, 2007). The system variables (S) represent system parts and describe the structure or functioning of a system (e.g. biomass, vegetation cover). The behaviour of the system under changing conditions is investigated through changes in these variables. In case of multivariate complex systems, dimension-reduction methods (e.g. Principal Component Analysis or Non-metric Multi-Dimensional Scaling) can be employed to reduce complexity to a single (or a few) system variable(s) (Vasilakopoulos et al., 2017). Parameters (P) of a system are factors that influence the system variables, but are, for the most part, uninfluenced by them (e.g. temperature, precipitation). Second, the stability of a system is determined by comparison with a reference condition of the system's descriptors (variables and parameters; Connell & Sousa, 1983; Grimm & Wissel, 1997; Justus, 2007). These are often stable reference states, but can also be a reference dynamic like a stable limit cycle or a stable trajectory (see case study 1), corresponding to Orians' cyclical and trajectory stability (Orians, 1974). Reference states and dynamics are also referred to as point and non-point attractors respectively (Ives & Carpenter, 2007). Both the choice of

the system descriptors and the reference condition can alter our perception of stability and therefore must be selected with care.

Stability is assessed with respect to a perturbation (Connell & Sousa, 1983; Justus, 2007). The terms perturbation and disturbance have been inconsistently used in ecology to indicate the cause and/or effect of external forces on ecosystems (Rykiel, 1985). The latter term has also been used in Grime's CSR framework to describe forces that lead to the destruction of biomass, in contrast to stress, which constrains biomass production (Grime, 1974). While resolving these inconsistencies is beyond the scope of this work (but see Battisti et al., 2016; Dornelas, 2010; Rykiel, 1985), to capture all facets of contemporary and future global change we broadly define perturbations as forces, agents or processes that cause changes in the above-mentioned system variable(s) and/or parameter(s). Many real-world perturbations affect both variables and parameters (Justus, 2007). Deforestation, for example, will directly influence the biomass dynamics and affect environmental conditions (e.g. by increasing soil erosion and decomposition of soil carbon). Up until this point, most empirical and theoretical research has focused on pulse (or discrete) perturbations that are limited in time, such as fire, floods and extreme droughts (Donohue et al., 2016; Figure 3). However, to better reflect the reality of ecological systems, there is a need to expand this research to include other types of perturbations as well (Donohue et al., 2016). This includes press perturbations that are persistent in time (e.g. habitat loss) and ramp perturbations, which increase progressively in time (e.g. climate warming; Bender et al., 1984; Donohue et al., 2016). Environmental stochasticity, where a system is constantly affected by small, stochastic perturbations (Ives, 1995), is sometimes considered as a fourth type of perturbation (Arnoldi

et al., 2019; Domínguez-García et al., 2019). Note that the definitions of the perturbation types are time scale and study system dependent. A drought, for example, is commonly defined as a pulse perturbation, but can last several months or longer and is experienced differently by a perennial tree than by an annual insect.

A system is considered stable if it retains its reference condition (state or dynamic) and thus its function, structure and identity under changing conditions. When this is only true for small perturbations the system is defined as locally stable, while if it holds for all possible perturbations then the system is said to be globally stable (Lewontin, 1969; Pimm, 1984). More specifically, the ecological stability of a system determines its ability to continue to function in the face of perturbations (Orwin & Wardle, 2004). It can be measured by a set of properties that determine the magnitude, duration and irreversibility of system variable changes relative to a reference condition after a perturbation (Donohue et al., 2013; Justus, 2007, 2012; Noy-Meir, 1974). The five properties that jointly define stability are (without introducing new terminology): (a) resistance is the ability to withstand change following a perturbation, (b) resilience is the rate at which a system returns to the reference after change, (c) recovery is the ability to fully return to the reference, (d) latitude is the maximum amount a system variable can be changed before losing its ability to recover, and (e) tolerance is the ability of a system to tolerate perturbations. The first three properties are defined with respect to the reference condition, the latter two with respect to the boundaries of the basin of attraction. Resilience has been used in ecology to denote a variety of concepts (e.g. ecological vs. engineering resilience). To avoid further confusion, we advocate restricting this term to the return rate as this corresponds to

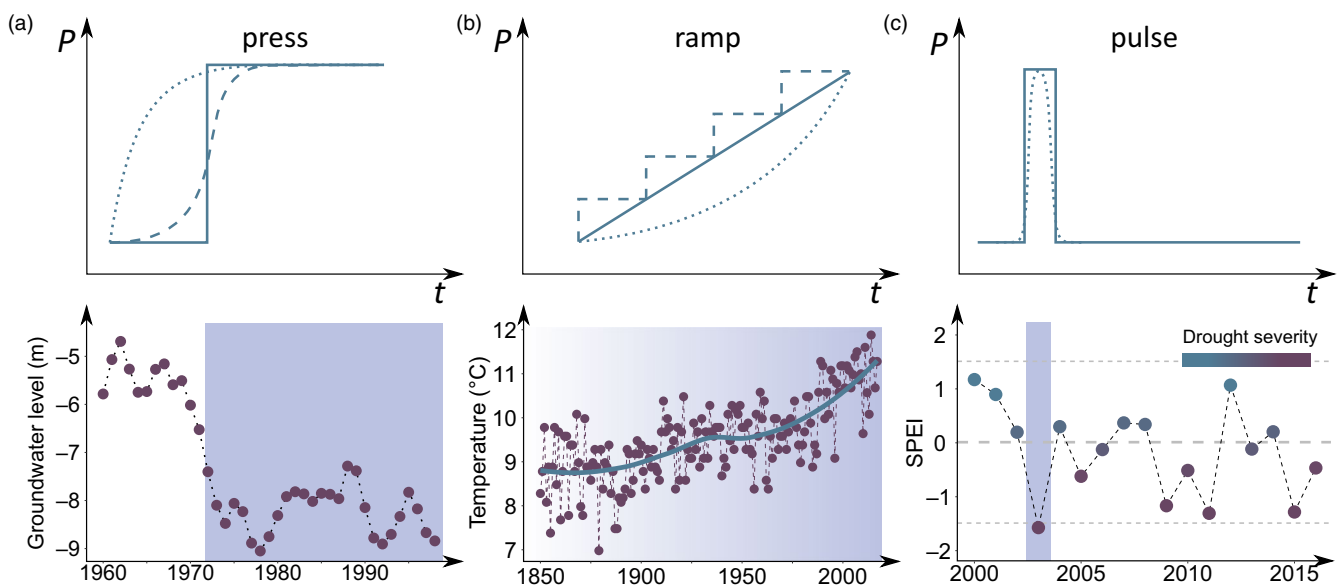


FIGURE 3 Different types of perturbations that change system parameters (P) over time (t), that is, press, ramp and pulse perturbations (top row), with real-world examples from Belgium (bottom row): Permanent lowering of the groundwater table near the nature reserve 'Kalmthoutse heide' due to groundwater extraction (Becker et al., 2004; TNO GDN, 2018); increasing mean annual temperature between 1,850–2,017 in Uccle (KMI, 2018) and the SPEI (Standardized Precipitation-Evapotranspiration) drought index during the growing season (7-month lag in April–October) from 2000 to 2017 (Delvaux et al., 2015). In 2003, an extreme drought was recorded (SPEI < −1.5). Perturbations are in the bottom row denoted by purple bars. Shade of purple corresponds to the magnitude of the perturbation

its meaning in the English language (Pimm et al., 2019). It is also the original definition in ecology (e.g. Stiven, 1971) and in many other fields, such as mathematics, physics, material engineering and psychology (Gunderson, 2000). Latitude is sometimes suggested to be the width of the basin of attraction (Walker et al., 2004), but as a system is not necessarily equally vulnerable to displacements in all directions, this definition is not a good property of stability (Mitra et al., 2015). Perturbations larger than the tolerance threshold will move the system beyond the boundaries of the domain of attraction, resulting in a shift to another reference condition. Tolerance should be used to refer to the perturbation itself (e.g. the tolerance of arid shrublands to grazing or tolerance of forests to drought) and latitude for displacements of the system variable (e.g. how much can the shrub cover be reduced before desertification takes place (Kéfi et al., 2007)). Tolerance is also sometimes used in the literature to describe the response of species or organisms along a gradient of environmental conditions, which can be measured as the breadth of the corresponding species response (or performance) curve. For example, in addition to warming tolerance, Deutsch et al. (2018) define a species' thermal tolerance as the range between the minimum and maximum critical temperature it can withstand. Note that the definitions of the individual properties imply greater stability as the property increases, which simplifies interpretation.

While our proposed framework draws heavily on previous work in the field of ecological stability, it also differs from previous attempts to unify stability concepts in a number of important ways. First, we include both equilibrium and non-equilibrium properties of stability (in contrast to Donohue et al., 2016; Hillebrand et al., 2018; Pimm, 1984; Walker et al., 2004). Second, we do not only describe a system through system variables but also by its parameters, to be able to describe every facet of a changing system (in contrast to Domínguez-García et al., 2019; Grimm & Wissel, 1997; Menck et al., 2013; Orians, 1974; Westman, 1978). Third, we make a distinction between latitude and tolerance and expand beyond pulse perturbations to be able to study the complexity of real-world perturbations (in contrast to Justus, 2007). Table 1 shows how the properties of previous frameworks fit in our framework.

All five components of stability—resistance, resilience, recovery, latitude and tolerance—are separately necessary, but not sufficient measures for assessing stability. Moreover, they are conceptually independent properties of a system (Justus, 2007). For instance, a system can be highly resistant to change but once changed, its resilience or recovery can be very low. In the same way, even a system that has low resilience and is severely displaced by a large perturbation may still return to its reference condition, and thus show full recovery, have a large latitude and exhibit high tolerance. Nevertheless, the individual properties can be correlated, thereby reducing the dimensionality of ecological stability (Domínguez-García et al., 2019; Donohue et al., 2013). Furthermore, these relationships can be altered by different types of perturbations (Radchuk et al., 2019), stressing the need for multi-dimensional assessments of stability. Attempts to develop a single metric to measure ecological stability (e.g. Mitra et al., 2015; Vasilakopoulos & Marshall, 2015) ignore the

complexity and multidimensionality of this concept (Domínguez-García et al., 2019; Kéfi et al., 2019). Compared to resilience, resistance and recovery, much less effort has gone into quantifying latitude and tolerance in empirical ecology, as quantitative research has mostly focused on systems close to their equilibrium. And yet, Holling's definition of resilience—how much perturbation a system can absorb before it shifts states (Holling & Clark, 1975)—actually refers to the tolerance component of stability (Connell & Sousa, 1983). In agricultural sciences, tolerance of crops to abiotic perturbations (e.g. drought, frost, salt) is an important field of study, as it is directly related to yield stability (Mickelbart et al., 2015). These concepts are also critical to understand how natural ecosystems are responding to global change. Importantly, interactions between multiple global change drivers could decrease the latitude and the tolerance to the individual drivers. For example, warmer temperatures increase drought-induced tree mortality for a given level of drought (Allen et al., 2010; Williams et al., 2013).

Orians (1974), Connell and Sousa (1983), Pimm (1984) and Grimm and Wissel (1997) also included the concepts of constancy and persistence into their definition of stability. The first refers to the (in) variability of a system over time—something which Lehman and Tilman (2000) would later refer to as temporal stability. Persistence is the length of time a system maintains a certain reference condition and is often, but not exclusively, used in studies on populations of species (Orians, 1974; Pimm, 1984). These concepts could be measured independent of perturbations. Hence, constancy or persistence do not, by themselves, contribute to ecological stability, as they may simply reflect the absence or limited levels of perturbation (Figure S7). A community that has been constant in time may still be severely impacted by medium or large perturbations (Justus, 2007). MacArthur (1955) had already noted in 1955 that constancy is one possible consequence of stability, not a defining property of it. Furthermore, a system that is on a certain trajectory can be stable according to the definition but is not constant over time. This also sheds light on Holling's conclusion that managing for constancy (or according to his definition, for stability) can be detrimental to the ability of a system to cope with future perturbations. A much-used example in this context is that of fire control in US national parks. Human control measures were successful in suppressing frequent small fires in the otherwise fire-prone forests of the western US. An unintended consequence of this, however, was the accumulation of fuel loads and changes in forest structure that primed the system for a series of huge fires causing widespread tree mortality (Holling, 1987; Keifer et al., 2006; Ryan et al., 2013). The forest management aimed for constancy but eroded the ecological stability of the forest ecosystems to fire, thereby paving the way for a regime shift to a new stability domain. Additionally, both decreasing (i.e. slowing down) and increasing (i.e. flickering) constancy have been identified as early warning signals for critical transitions and thus the loss of stability (Carpenter & Brock, 2006; Scheffer et al., 2009). Nevertheless, constancy or persistence is useful metric when studying stability in the face of stochastic perturbation regimes or recurring perturbations.

TABLE 1 The different stability properties with their synonyms and related terms (~) as used in the ecological literature

Property	Short definition	Synonyms and related terms	Source
Resistance	The ability to withstand changes	Inertia	Orians (1974)
		Reactivity	Neubert and Caswell (1997)
		~Robustness	Dunne et al. (2002)
		~Sensitivity	Nakajima (1992)
Resilience	Rate of return after a displacement	Elasticity	Orians (1974)
		Resiliency	Boesch (1974)
		Stability	Holling (1973)
		~Adjustment stability	Connell and Sousa (1983), Margalef (1969)
		Engineering resilience	Holling (1996)
		Recovery	Côté and Darling (2010), Lloret et al. (2011)
		Asymptotic stability	Donohue et al. (2016)
Recovery	Ability to fully recover	Malleability	Westman (1978)
		Resilience	Lloret et al. (2011)
Latitude	Distance to threshold on the system variable axis	Amplitude	Hurd et al. (1971), Orians (1974), Westman (1978)
		Domain of attraction stability	Grimm and Wissel (1997)
		~Adjustment stability	Connell and Sousa (1983)
		Precariousness	Hodgson et al. (2015), Walker et al. (2004)
		~Basin stability	Menck et al. (2013)
		~Horizontal component of resilience	Vasilakopoulos and Marshall (2015)
		Attractor	Domínguez-García et al. (2019)
Tolerance	Ability to tolerate perturbations	Resilience	Holling (1973)
		Ecological resilience	Holling (1996)
		Domain of attraction stability	Justus (2007)
		~Basin stability	Menck et al. (2013)
		~Vertical component of resilience	Vasilakopoulos and Marshall (2015)
		Precariousness	Mitra et al. (2015)
		Stability threshold	Klinshov et al. (2015)
		Attractor	Domínguez-García et al. (2019)

Ecological stability is deliberately defined in terms of function and structure. Some authors propose stability metrics based on community composition like compositional turnover (Donohue et al., 2013) or robustness (Donohue et al., 2016). We argue that these are not adequate to study stability. Ecological systems could reorganize and undergo compositional changes in the face of changing condition while retaining their function and structure. In his first definition of resilience, Holling (1973) already highlighted the importance of adaptive capacity as an essential feature of stable ecosystems. Managing for constancy in species composition is therefore not necessarily the best strategy for preserving ecosystems on the long run.

5 | MEASURING ECOLOGICAL STABILITY

Diversity and stability are commonly used in ecology to express aspects of ‘organization’ of ecosystems. They must be measurable. Diversity, related to the

distribution of the present biomass, to its complexity at a given time, may have achieved this desirable status, but much ambiguity remains concerning definition and measurement of stability (Margalef, 1969).

In addition to the myriad definitions of ecological stability and its components, an equally large number of measures for quantifying the response of a system to perturbations have been proposed in the literature. This is not only a source of confusion but can also impact the interpretation of results and slow down the progress towards synthesis—as different metrics can yield different (and in some cases even conflicting) estimates of a system’s stability (Ingrisch & Bahn, 2018). Previous studies have provided a comprehensive overview of the different types of metrics used to quantify stability (see e.g. Ingrisch & Bahn, 2018; Orwin & Wardle, 2004; Todman et al., 2016), which we will not repeat here. Below, we demonstrate the broad applicability and unifying nature of the proposed framework in two quantitative case studies. But first, we present the metrics that we will use and elaborate on their properties. Although we think there is a need for

standardized and easy-to-use metrics of the stability components to allow for comparisons across studies and the summary of ecological evidence through meta-analyses, it is not our goal to provide these here. Instead, we aim to highlight the properties these metrics should aspire to have and provide examples that meet these criteria.

Appropriate measures of the stability properties that are measured in system variable \times time ($S \times T$) space (i.e. resistance, resilience, recovery and latitude) should meet the following criteria (Isbell et al., 2015; Orwin & Wardle, 2004): (a) it should be dimensionless and standardized so that it can be compared across studies; (b) it should be symmetric, capturing both increases and decreases in the system variable (i.e. positive and negative perturbations); (c) it should be a monotonic function of the stability property; (d) it should be bounded for all possible values and not tend to infinity and (e) it should be applicable to all types of ecosystems and system variables. The metrics below meet these criteria. For measuring resistance and resilience, we adapt the indices proposed by Orwin and Wardle (2004) to be applicable across systems, perturbations and fields of research. Resistance is standardized against a reference condition of the system variable and is the dimensionless (relative) ratio of a system variable measured before and after a perturbation. To meet the above-mentioned criteria (bounded and symmetric), resistance is measured as follows:

$$\text{Resistance} = 1 - \frac{2 \times |S_R - S_X|}{S_R + |S_R - S_X|}, \quad (1)$$

where S_R is the reference value of the system variable and S_X is the value of the system variable at a standardized period of time x (t_{p+x}) after t_p the time at which the perturbation occurred (Figure 4a–d). Equation 1 is bounded between -1 and 1 . Resistance = 1 corresponds to no change (maximal resistance), while Resistance = 0 is equivalent to a relative change of -100% or $+100\%$ (Orwin & Wardle, 2004). Negative values occur when S_X is higher than $2 \times S_R$. To avoid over- or underestimating of resistance, S_R should ideally be estimated using data from a period of time during which the system was ‘undisturbed’ (i.e. the average of the values in the undisturbed period under similar environmental conditions). To take into account the stochasticity of the study system, this period should be as long as possible, given the data availability and the time frame of the study. It should further be adapted to the temporal dynamics of the system (e.g. life cycle, phenology). In studies of vegetation in seasonal climates, for example, the time period to calculate the reference condition should ideally span several years to capture the phenological changes and variation between years. For experimental research, the value of the control (or average of multiple controls) at t_{p+x} should be used as S_R , as this would explicitly account for the effects of any unmeasured or unknown perturbations. For pulse perturbations, the value of the system variable at maximum deviation from the reference (S_0 attained at time t_0) should be taken as S_X (hence $t_{p+x} = t_0$) so that S_X measures the maximal deviation from the reference S_R after the perturbation. ‘ $S_0 = S_X$ ’ is a frequently made assumption in ecological research, but is rarely verified. In many studies, S_X has been measured during or immediately after the

pulse perturbation, but this does not account for possible system inertia, which would manifest as a lagged response. Until now, most metrics of ecological stability have been developed exclusively for pulse perturbations (e.g. Isbell et al., 2015) and cannot be generalized to more complex system responses and other types of perturbations. In the case of press or ramp perturbations (Figure 3a,b), a system could be set on a trajectory of change and t_0 might fall beyond the timeframe of the study (Margalef, 1969; Oliver et al., 2015). In these cases, Equation (1) is still valid, but the timing t_{p+x} at which S_X is measured should be standardized. For plants in seasonal climates, this could be 1 year after the perturbation started. In other systems, different standardized timings should be explored and agreed upon.

Resilience indices that are measured at long time scales (e.g. the long-term rate of return or time to full resilience) are mostly used in theoretical research (Arnoldi et al., 2018). These indices require the system to return to its reference condition (state or dynamic) within the time frame of the study, which limits the applicability of these indices in empirical research for several reasons. First, return time can take longer than the time frame of the experimental or observational study. Second, additional perturbations may inhibit the system from completely returning (Yeung & Richardson, 2016). Although the short-term response of a system can strongly differ from the long-term (or asymptotic) response (see Arnoldi et al. (2018) and Neubert and Caswell (1997) for a discussion), short-term resilience of the system after a specified amount of time provides a more practical measure for empirical studies. Standardizing resilience by the amount of change caused by the perturbation and taking into account the above-mentioned requirements, resilience can be measured as:

$$\text{Resilience} = \frac{2 \times |S_R - S_0|}{|S_R - S_0| + |S_R - S_Y|} - 1, \quad (2)$$

where S_R is as above, S_0 is the value of the system variable at maximum deviation from the reference, t_0 is the time at which the maximum deviation is observed and S_Y is the value of the system variable after a standardised period of time y (t_{0+y}) following t_0 (Figure 4a). Equation 2 is standardised by the maximum observed change ($|S_R - S_0|$) and bounded between -1 and 1 . A value of 1 indicates full resilience at the time of measurement (t_{0+y}). The index takes a value of 0 when the observed change at t_y ($|S_R - S_Y|$) equals the maximum observed change ($|S_R - S_0|$). This occurs either when the system is not recovered at all, or when the system is $|S_R - S_0|$ units away from the reference in the opposite direction. If $|S_R - S_Y| > |S_R - S_0|$, the index will be negative. For vegetation studies in seasonal climates, y is often equal to 1 year. If a system is fully recovered after 1 year, resilience equals 1 , as is the case if resilience had been measured based on return time (Donohue et al., 2016). However, this metric can also be applied to other fields of ecology where other standardised time periods (y) may be more appropriate. In microbial ecology, for example, resilience is measured on the scale of days, but there seems to be less consensus on the appropriate time window (e.g. see Guillot et al., 2019; Orwin et al., 2006; Rivest et al., 2015). Standardised time windows to measure resistance and resilience are

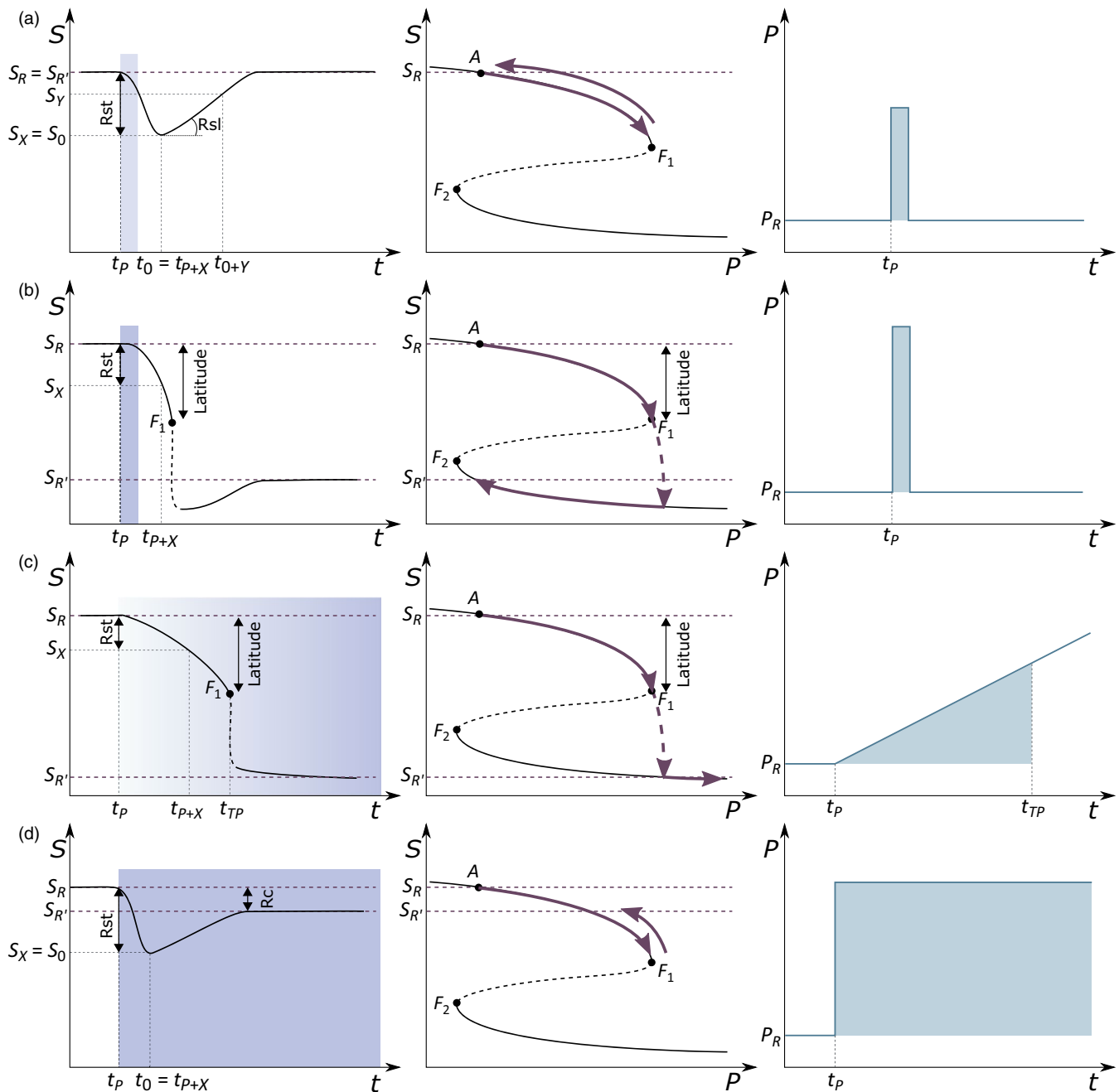


FIGURE 4 The behaviour of a system in response to different perturbation types. The left column shows the changes of the system variable (S) over time (t) with a stable reference condition S_R (dashed line) with the shade of purple denoting the magnitude of the perturbation, the middle column shows the $S \times P$ space (with F_1 and F_2 being tipping points) and the right column shows parameter (P) changes over time with the green shaded area corresponding to the duration and intensity of the parameter perturbation. (a) The system undergoes a pulse perturbation affecting the parameter P , smaller than its tolerance. The maximum deviation from the reference (S_0) is determined by the resistance (R_{st}). Over time the system recovers fully ($S_{R'}$ equals S_R). The rate of return is a measure of resilience (R_{sl}). Note that the measurement of tolerance is complex and cannot be shown on the graphs. (b) Following the pulse perturbation larger than the tolerance, the system does not return to its previous reference condition and undergoes a regime shift to $S_{R'}$. (c) Gradual response of a system to a ramp perturbation allows for the measurement of latitude. Resistance is measured by the deviation of the system at a fixed time (t_{p+X}) following the perturbation (at t_p). (d) System recovers partially in response to a press perturbation. The difference between $S_{R'}$ and S_R is determined by the recovery capacity

important to allow for comparison among studies and thus to facilitate synthesis. Further research is needed to reach a consensus on standardised periods in different fields of ecology. Importantly, the proposed metrics allow for flexibility because study-specific time frames

could provide interesting insights on top of those generated by the standardised values.

The third property, recovery, can be measured as the similarity between the new equilibrium condition, established after a perturbation,

and the original reference (Figure 4d; Orians, 1974; Westman, 1978). To measure recovery, we propose the following metric:

$$\text{Recovery} = 1 - \frac{2 \times |S_R - S_{R'}|}{S_R + |S_R - S_{R'}|}, \quad (3)$$

where S_R is as above and $S_{R'}$ is the value of the system variable at the reference condition after perturbation. For measuring $S_{R'}$, the same considerations apply as for S_R . Recovery is bounded between -1 and 1 and takes the maximum value if the system is completely recovered. Recovery = 0 when $S_{R'}$ is -100% or +100% of S_R . Negative values occur when $S_{R'}$ is larger than $2 \times S_R$.

The quantification of latitude as the distance to the tipping point in $S \times T$ space requires measured time series of both the system variable and parameters in a system experiencing a shift to a new equilibrium. Furthermore, the exact threshold or tipping point, which indicates the equilibrium shift, should be located but is not always easy to identify. Nonlinear modelling techniques like threshold generalised additive models (TGAMs) are suggested solutions (Vasilakopoulos et al., 2017). Alternatively, a large dataset with observations along the system variable and parameter axes could provide the necessary information to quantify these properties (e.g. Hirota et al., 2011). As both kinds of information are difficult to obtain, research on early warning indicators to detect shifts ahead in time is extremely important. If the necessary data are available, latitude can be calculated at any point in time. At a certain point in time A, the latitude is standardised against the value of the system variable at A (S_A) and is measured as:

$$\text{Latitude} = \frac{2 \times |S_A - S_{TP}|}{S_A + |S_A - S_{TP}|}, \quad (4)$$

where S_{TP} is the value of the system variable at the tipping point (Figure 4b,c). Equation 4 is bounded between 0 and 2. Latitude = 1 corresponds to a threshold at a relative change of -100% or +100%, while Latitude = 0 corresponds to situations where infinitesimally small departures from the reference condition result in an equilibrium shift. Values larger than 1 occur when S_{TP} is higher than $2 \times S_A$.

The fifth property of stability, tolerance, can be quantified as the largest perturbation that a system can sustain over a certain length of time, without shifting states. It, therefore, stands apart from the other stability properties as it is not measured in $S \times T$ space, but involves changes of the system parameter(s). As with latitude, tolerance requires observing a regime shift. Existing tolerance metrics measured as the maximum pulse perturbation a system can tolerate or as the horizontal distance to the tipping point in system variable \times parameter ($S \times P$) space (e.g. Craine et al., 2013; Vasilakopoulos & Marshall, 2015) ignore the complex nature of perturbations. It is important to take both the intensity and duration of a perturbation into account when quantifying the perturbation (e.g. Granier et al., 1999). The intensity of the perturbation should be defined relative to 'average' conditions. For example, a drop in precipitation from 100 to 0 mm per year is not the same as from 2,000 to 1,900 mm.

Vicente-Serrano et al. (2010), for example, standardised the water deficit (or surplus) based on a log-logistic distribution to calculate the Standardised Precipitation Evapotranspiration Index (SPEI) of droughts. Importantly, it is the magnitude of the perturbation experienced by the system that is of actual interest and is what should be compared across systems and studies (Vicca et al., 2012). In drought experiments, for example, it is not the change in the amount of precipitation that matters, but rather the change in plant-available water (Vicca et al., 2012). The latter does not only depend on the amount of precipitation but also on the land cover, soil physical-chemical properties, other climatic conditions and the ecophysiological state of the plant among other factors. In contrast to the Standardised Precipitation Index (SPI), the SPEI includes both precipitation and the atmospheric evaporative demand and thus provides a more reliable measure of drought intensity than only considering precipitation (Beguería et al., 2014; Vicente-Serrano et al., 2010), although it does not take the duration of the drought into account. Note that SPEI is not without criticism (Zang et al., 2020). Besides droughts, the standardization of perturbation metrics has received much less attention. More research is needed to develop standardised metrics for different perturbations and perturbation types (pulse, press and ramp) and find ways to take into account both the intensity and duration of the perturbation. Given the research gap on standardised measurements of perturbations, we do not provide a general formula to measure the tolerance property here.

6 | CASE STUDY 1: MEASURING STABILITY BEYOND STABLE STATES

Early theoretical work on stability assumed that ecosystems or species assemblages were close to their stable reference state. Deviations from these stable states in response to perturbations allowed for quantitative measurements of ecological stability. However, it was soon acknowledged that stability is not limited to systems with stable reference states (Sutherland, 1981), but should also include ones following stable reference dynamics. Here, we demonstrate the evaluation of stability with respect to a reference dynamic. We analyse the growth of individual trees in response to drought based on tree ring data (Figure 5a,b), and explore whether species mixing influences drought responses. Growing trees are not in or close to a stable state but instead follow a stable trajectory, that is, when the reference condition changes according to a trajectory (Holling & Goldberg, 1971). The association of anomalies in the long-term growth trend with drought events is used to obtain measures of stability. This technique, known as detrending, has been frequently applied to study vegetation dynamics based on remote-sensing time series (De Keersmaecker et al., 2017; Verbesselt et al., 2010).

Our analysis is based on data from the FunDiveEUROPE exploratory research platform (Baeten et al., 2013), which was designed to study how tree species diversity affects ecosystem functioning in European forests. Specifically, we used tree ring data collected in the Alto Tajo Natural Park of central Spain to quantify the resilience

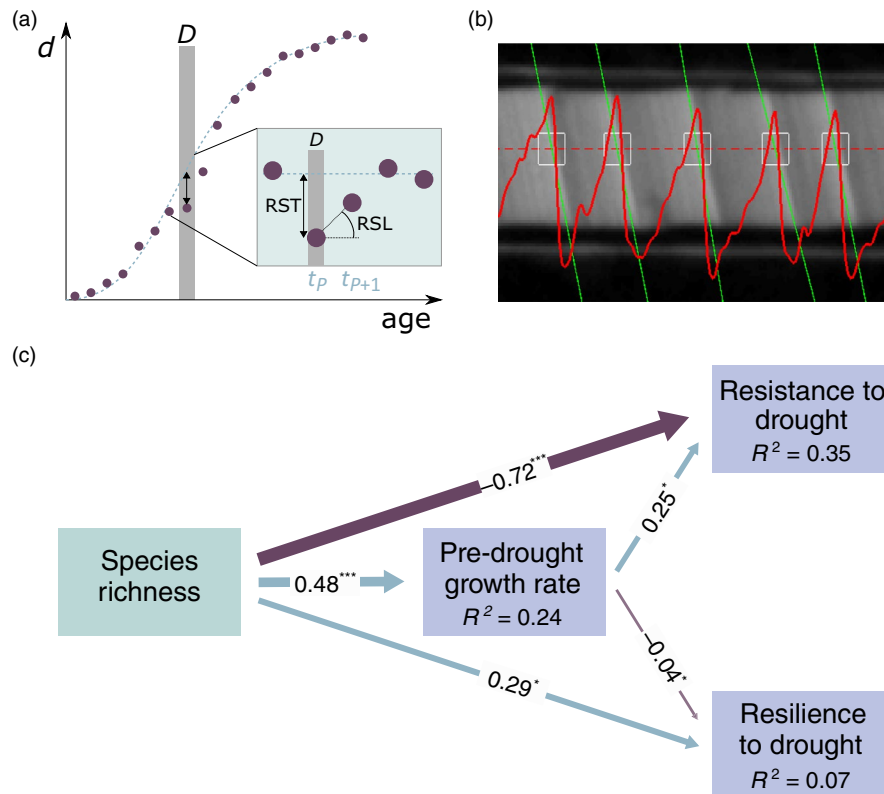


FIGURE 5 (a) Age–diameter relationship of an individual tree (dashed line, reference dynamic) derived from wood core measurements (purple circles). Inset: Measuring ecological stability to a drought perturbation (grey bar) based on deviations from the modelled overall age–diameter relationship. t_p = time of perturbation, RST: resistance, RSL: resilience. (b) Measuring tree ring width based on X-ray computed tomography images. Ring boundaries (green lines) are detected by the analysis of wood density profiles in red (Picture: Astrid Vannoppen). (c) Piecewise structural equation model capturing the direct and indirect effects of tree species richness on the resistance and resilience to drought of *Pinus sylvestris* trees in central Spain. Green arrows represent positive effects, whereas purple arrows correspond to negative ones. Arrow width is proportional to the size of the standardized model coefficients (shown on the arrows). * $p < 0.05$, *** $p < 0.001$ and lightly shaded lines represent non-significant effects. R^2 values are reported for each endogenous variable in the model. The model was fit using the `PIECEWISESEM` package in R (Lefcheck, 2016)

and resistance of two pine species (*Pinus sylvestris* and *P. nigra*) to the severe drought of 2005, which had a profound effect on tree growth in this region. Growth data from a total of 219 trees (90 *P. sylvestris* and 129 *P. nigra*) distributed across a diversity gradient (1 to 4 species) were analysed. First, the long-term growth trajectory of each tree was modelled by applying a 30-year moving spline function to each tree ring series. This function explicitly ignores high-frequency, year-to-year variation in growth driven by climate variation, focusing instead on capturing the ontogenetic growth trajectory of each tree. The predicted values of growth obtained from this function in the 3 years pre-drought were then used as the reference value S_R and compared to the observed values of growth during (S_0) and 1 year after the drought ($=S_1$) to quantify the resistance and resilience of each tree using Equations (1) and (2).

Using these data we then explored how a tree's resistance and resilience to drought were influenced by (a) the diversity of its neighbourhood and (b) its mean growth rate in the 3 years pre-drought (to test whether fast-growing trees were more or less susceptible to drought). Piecewise structural equation modelling was used to account for the direct effects of species richness on resistance and resilience, as well as the indirect effects mediated by changes in mean

growth rates along the diversity gradient. The results (*P. sylvestris*: Figure 5c, *P. nigra*: Figure S8) mirror those of previous work that had focused on the constancy (or temporal stability) of plot-level productivity in these forests (Jucker et al., 2014). For both species, trees in mixed-species plots grew faster than those in monoculture. However, trees in mixed stands were generally less resistant to drought, possibly as a result of stronger competition for water with oaks during drought (Jucker et al., 2014). This negative effect of diversity on resistance was partially compensated for by the fact that fast-growing trees tended to be more resistant to drought than slow-growing ones (i.e. by enhancing tree growth, diversity had an indirect positive effect on resistance to drought). Moreover, tree growth of *P. sylvestris* in mixed stands recovered more quickly from drought.

7 | CASE STUDY 2: REGIME SHIFT IN LAKES FROM A STABILITY VIEWPOINT

Abrupt shifts between alternative stable states, or regime shifts, have been observed in many ecosystems like coral reefs (Nyström et al., 2000), woodlands (Hirota et al., 2011) and grasslands (Noy-Meir, 1975).

However, maybe the most well-known and well-studied example is the shift between clear-water and turbid stable states in phosphorous-limited shallow lake systems (Scheffer, 1989; Scheffer et al., 1993). Although first studied from a quantitative equilibrium point of view (Scheffer, 1989), shallow lakes later became the textbook example of regime shifts from a non-equilibrium perspective (Scheffer & Carpenter, 2003). In the clear-water state of Lake Veluwe (Figure 6a), phytoplankton production was limited by low levels of phosphorous, allowing for a well-developed submerged aquatic vegetation (charophyte cover, Figure 6b). Increasing nutrient loads at the beginning of the 1960s induced a regime shift to a turbid state in 1964, characterised by phytoplankton dominance and the loss of submerged vegetation (Figure 6b,c). Once a threshold is exceeded and the sudden regime shift has taken place, feedback mechanisms that control key system processes maintain the new ecosystem state even if nutrient deposition subsequently declines (Carpenter et al., 1999). In clear-water lakes, anoxic phosphorus recycling from sediments is inhibited, which, in turn, limits phytoplankton growth. In a turbid state, algal blooms create anoxic conditions, thereby boosting anoxic phosphate recycling and inducing further algal growth (Carpenter et al., 1999). The restoration of lake Veluwe to a clear-water state in the 1990s (Figure 6c), after reducing the nutrient load and biomanipulation, showed hysteresis (Figure 6b).

Merging the equilibrium-centred view with the analysis of dynamical systems allows the quantitative analysis of the different

components of stability of the lake system with charophyte cover as system variable and phosphorous concentration as the parameter (Figure 6b,c). With time series of charophyte cover, the latitude can be quantified (see formula 4). For the onset of the phosphorous increases (year 1959), the latitude is 0.4 (with $S_A = 80\%$ and $S_{TP} = 60\%$), meaning that a relative change less than $\sim 100\%$ in charophyte cover over 6 years was necessary to provoke a regime shift. Such regime shifts perfectly fit in the quantitative framework of ecological stability (Figure 6b). The resistance to the phosphorous input equals 0 (macrophytes almost disappeared completely, with $t_0 = 1,973$ in formula 1), and as the system did not recover at all during the first year after t_0 , the initial resilience was 0 as well (formula 2). In response to the restoration, the resilience of the system was 0.08 (with $t_V = 1,990$, the first year of restoration of charophyte cover, formula 2). The new equilibrium state after restoration was not attained during the period covered by the dataset. Hence, recovery could not be calculated.

8 | CONCLUDING REMARKS AND FUTURE DIRECTIONS

Recent rapid changes in natural perturbation regimes have been documented in many ecosystems across the world, boosting scientific research on ecological stability. Albeit being a relatively intuitive concept, stability remains a major source of confusion and

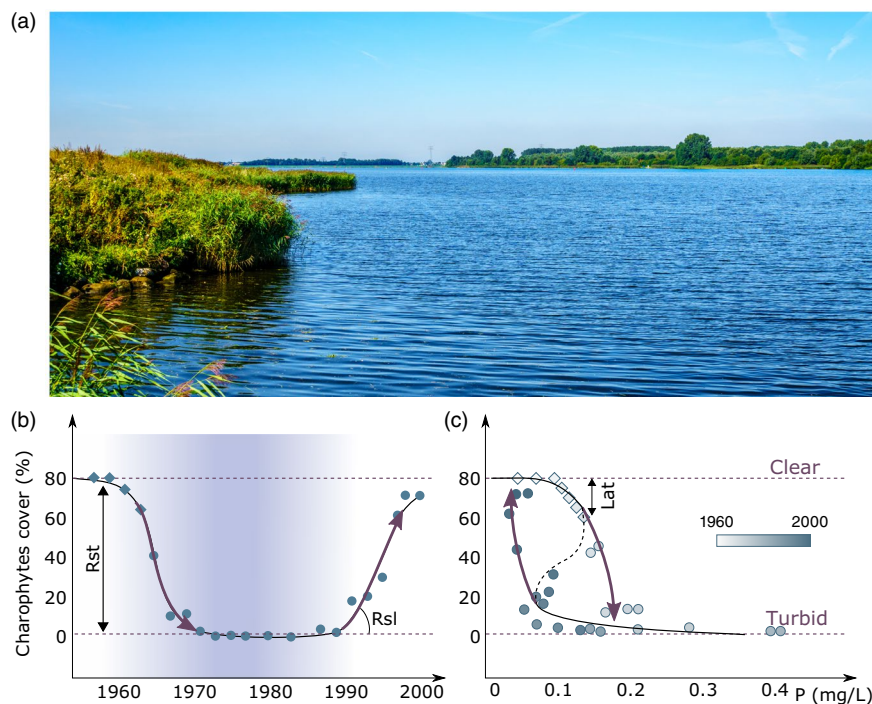


FIGURE 6 (a) The Veluwe lake in the Netherlands, created in 1957 as a result of land reclamation (Picture: Harry Beugelink). (b) A regime shift occurred in the Veluwe lake (The Netherlands) in the 1960s from a clear state with extensive cover of charophytes to a turbid state in response to increasing nutrient loads (purple background; Ibelings et al., 2007). Recovery occurred in the 1990s after reducing nutrient input and biomanipulation. Shade of purple corresponds to the magnitude of the perturbation. Rst: Resistance, Rsl: Resilience. (c) The state of the lake shows a sudden dramatic shift to an alternative state in response to the increased nutrient load. The resilience of the lake system showed hysteresis. Lat: Latitude. Circles are measured values of charophyte cover and phosphorous concentration, with time-dependent colour gradient in panel c (Ibelings et al., 2007). Diamonds are inferred values, based on the description in Ibelings et al. (2007)

disagreement in ecological research. Given the immediacy of the challenge posed by global change and the recent upsurge of conceptual papers, there is an urgent need to resolve this ambiguity. The conceptual framework presented here provides a basis to integrate currently existing views on the study of system responses to changing conditions. We first substantiate the concept of ecological stability and define the different properties that jointly constitute stability (resistance, resilience, recovery, tolerance and latitude). We then discuss the properties that metrics of the stability components should have and demonstrate the broad applicability of our framework in two case studies. A next step could be to work towards a set of standardised, operational and easy-to-use metrics of the stability components, to allow for comparisons across studies and the summary of ecological evidence through meta-analyses. Finally, we highlight some important knowledge gaps to guide future research efforts. Standardised time windows to measure resistance and resilience in different fields of ecology are important to allow for comparison among studies and require further attention. More research is also needed to develop standardised metrics to measure the magnitude of different perturbations and perturbation types (pulse, press and ramp), taking into account both the intensity and duration of the perturbation. The focus here is on individual perturbations. Evidently, perturbations do not occur in isolation. Natural ecosystems often face recurring perturbations (Sousa-Silva et al., 2018) or multi-directional change imposed by a combination of different stressors (De Laender, 2018). Except for full-factorial experimental designs, where data from the control and the individual perturbation treatments allow for a full analysis of variance, disentangling the response of ecosystems to multiple perturbations is still a big challenge (Yue et al., 2017). Disequilibrium dynamics due to lags in the ecosystem response (Svenning & Sandel, 2013), different types of perturbations (Radchuk et al., 2019) and perturbations with opposing effects on the system variable (Yue et al., 2017) further complicate the study of ecological stability. Expanding the framework to multi-directional change with appropriate metrics and baselines is another big hurdle to take. Here, we provided the necessary integrating framework to tackle these challenges and move research on ecological stability forward. Understanding how and to what extent different global change drivers affect the functioning of ecosystems is central to mitigate the impact of global change and develop efficient management efforts.

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AUTHORS' CONTRIBUTIONS

K.V.M. and J.-C.S. conceived the idea of the study; K.V.M. performed the review and bibliometric analysis; T.J. analysed the tree ring data; K.V.M. wrote the manuscript. All authors contributed substantially to the revisions.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Bibliography (bibliometric analysis): see <https://doi.org/10.6084/m9.figshare.14224505.v1> (Van Meerbeek, 2021). Individual tree growth data (case study 1): FunDivEUROPE online data portal (<https://data.botanik.uni-halle.de/fundiveurope/>). Charophyte cover and phosphorous concentration (case study 2): Ibelings et al. (2007).

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REFERENCES

- Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D. D., Hogg, E. H. T., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S. W., Semerci, A., & Cobb, N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, 259(4), 660–684. <https://doi.org/10.1016/j.foreco.2009.09.001>
- Aria, M., & Cuccurullo, C. (2017). bibliometrix: An R-tool for comprehensive science mapping analysis. *Journal of Informetrics*, 11(4), 959–975. <https://doi.org/10.1016/j.joi.2017.08.007>
- Arnoldi, J.-F., Bideault, A., Loreau, M., & Haegeman, B. (2018). How ecosystems recover from pulse perturbations: A theory of short-to long-term responses. *Journal of Theoretical Biology*, 436, 79–92. <https://doi.org/10.1016/j.jtbi.2017.10.003>
- Arnoldi, J.-F., Loreau, M., & Haegeman, B. (2019). The inherent multidimensionality of temporal variability: How common and rare species shape stability patterns. *Ecology Letters*, 22(10), 1557–1567. <https://doi.org/10.1111/ele.13345>
- Baeten, L., Verheyen, K., Wirth, C., Brulheide, H., Bussotti, F., Finér, L., Jaroszewicz, B., Selvi, F., Valladares, F., Allan, E., Ampoorter, E., Auge, H., Avăcăriei, D., Barbaro, L., Bărnoaiea, I., Bastias, C. C., Bauhus, J., Beinhoff, C., Benavides, R., ... Scherer-Lorenzen, M. (2013). A novel comparative research platform designed to determine the functional significance of tree species diversity in European forests. *Perspectives in Plant Ecology Evolution and Systematics*, 15(5), 281–291. <https://doi.org/10.1016/j.ppees.2013.07.002>
- Battisti, C., Poeta, G., & Fanelli, G. (2016). The concept of disturbance. In C. Battisti, G. Poeta, & G. Fanelli (Eds.), *An introduction to disturbance ecology* (pp. 7–12). Springer.
- Beguieria, S., Vicente-Serrano, S. M., Reig, F., & Latorre, B. (2014). Standardised precipitation evapotranspiration index (SPEI) revisited: Parameter fitting, evapotranspiration models, tools, datasets and drought monitoring. *International Journal of Climatology*, 34(10), 3001–3023.

- Beisner, B. E. (2012). The shifting states of resilience: Easier to define than to measure. *Ideas in Ecology and Evolution*, 5. <https://doi.org/10.4033/iee.2012.5.13.c>
- Beisner, B. E., Haydon, D. T., & Cuddington, K. (2003). Alternative stable states in ecology. *Frontiers in Ecology and the Environment*, 1(7), 376–382.
- Bender, E. A., Case, T. J., & Gilpin, M. E. (1984). Perturbation experiments in community ecology: Theory and practice. *Ecology*, 65(1), 1–13. <https://doi.org/10.2307/1939452>
- Boesch, D. F. (1974). Diversity, stability and response to human disturbance in estuarine ecosystems. In W. H. van Dobben & R. H. Lowe-McConnell (Eds.), *Unifying concepts in ecology: Report of the plenary sessions of the First international congress of ecology, The Hague, the Netherlands* (pp. 109–114). Springer, Netherlands, Dordrecht.
- Börner, K., Chen, C., & Boyack, K. W. (2003). Visualizing knowledge domains. *Annual Review of Information Science and Technology*, 37(1), 179–255. <https://doi.org/10.1002/aris.1440370106>
- Carpenter, S. R., & Brock, W. A. (2006). Rising variance: A leading indicator of ecological transition. *Ecology Letters*, 9(3), 311–318. <https://doi.org/10.1111/j.1461-0248.2005.00877.x>
- Carpenter, S. R., Ludwig, D., & Brock, W. A. (1999). Management of eutrophication for lakes subject to potentially irreversible change. *Ecological Applications*, 9(3), 751–771.
- Connell, J. H., & Sousa, W. P. (1983). On the evidence needed to judge ecological stability or persistence. *The American Naturalist*, 121(6), 789–824. <https://doi.org/10.1086/284105>
- Côté, I. M., & Darling, E. S. (2010). Rethinking ecosystem resilience in the face of climate change. *PLoS Biology*, 8(7), e1000438. <https://doi.org/10.1371/journal.pbio.1000438>
- Craine, J. M., Ocheltree, T. W., Nippert, J. B., Towne, E. G., Skibbe, A. M., Kembel, S. W., & Fargione, J. E. (2013). Global diversity of drought tolerance and grassland climate-change resilience. *Nature Climate Change*, 3(1), 63–67. <https://doi.org/10.1038/nclimate1634>
- Dakos, V., Matthews, B., Hendry, A. P., Levine, J., Loeuille, N., Norberg, J., Nosil, P., Scheffer, M., & De Meester, L. (2019). Ecosystem tipping points in an evolving world. *Nature Ecology & Evolution*, 3(3), 355–362. <https://doi.org/10.1038/s41559-019-0797-2>
- Dakos, V., Scheffer, M., van Nes, E. H., Brovkin, V., Petoukhov, V., & Held, H. (2008). Slowing down as an early warning signal for abrupt climate change. *Proceedings of the National Academy of Sciences of the United States of America*, 105(38), 14308–14312. <https://doi.org/10.1073/pnas.0802430105>
- De Becker, P., Van Daele, T., & Huybrechts, W. (2004). *Grondwaterpeilmetingen in Vlaamse Natuurgebieden*. Instituut voor Natuurbehoud.
- De Keersmaecker, W., Lhermitte, S., Hill, M., Tits, L., Coppin, P., & Somers, B. (2017). Assessment of regional vegetation response to climate anomalies: A case study for Australia using GIMMS NDVI time series between 1982 and 2006. *Remote Sensing*, 9(1), 34. <https://doi.org/10.3390/rs9010034>
- De Laender, F. (2018). Community- and ecosystem-level effects of multiple environmental change drivers: Beyond null model testing. *Global Change Biology*, 24(11), 5021–5030. <https://doi.org/10.1111/gcb.14382>
- DeAngelis, D. L., & Waterhouse, J. C. (1987). Equilibrium and nonequilibrium concepts in ecological models. *Ecological Monographs*, 57(1), 1–21. <https://doi.org/10.2307/1942636>
- Delvaux, C., Journée, M., & Bertrand, C. (2015). The FORBIO Climate data set for climate analyses. *Advances in Science and Research*, 12(1), 103–109. <https://doi.org/10.5194/asr-12-103-2015>
- Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences*, 105(18), 6668–6672.
- Domínguez-García, V., Dakos, V., & Kéfi, S. (2019). Unveiling dimensions of stability in complex ecological networks. *Proceedings of the National Academy of Sciences of the United States of America*, 116(51), 25714–25720. <https://doi.org/10.1073/pnas.1904470116>
- Donohue, I., Hillebrand, H., Montoya, J. M., Petchey, O. L., Pimm, S. L., Fowler, M. S., Healy, K., Jackson, A. L., Lurgi, M., McClean, D., O'Connor, N. E., O'Gorman, E. J., & Yang, Q. (2016). Navigating the complexity of ecological stability. *Ecology Letters*, 19(9), 1172–1185. <https://doi.org/10.1111/ele.12648>
- Donohue, I., Petchey, O. L., Montoya, J. M., Jackson, A. L., McNally, L., Viana, M., Healy, K., Lurgi, M., O'Connor, N. E., & Emmerson, M. C. (2013). On the dimensionality of ecological stability. *Ecology Letters*, 16(4), 421–429. <https://doi.org/10.1111/ele.12086>
- Dornelas, M. (2010). Disturbance and change in biodiversity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1558), 3719–3727. <https://doi.org/10.1098/rstb.2010.0295>
- Dunne, J. A., Williams, R. J., & Martinez, N. D. (2002). Network structure and biodiversity loss in food webs: Robustness increases with connectance. *Ecology Letters*, 5(4), 558–567. <https://doi.org/10.1046/j.1461-0248.2002.00354.x>
- Elton, C. S. (1958). *The ecology of invasions by animals and plants*. Methuen.
- Folke, C. (2006). Resilience: The emergence of a perspective for social-ecological systems analyses. *Global Environmental Change*, 16(3), 253–267. <https://doi.org/10.1016/j.gloenvcha.2006.04.002>
- Folke, C., Hahn, T., Olsson, P., & Norberg, J. (2005). Adaptive governance of social-ecological systems. *Annual Review of Environment and Resources*, 30, 441–473. <https://doi.org/10.1146/annurev.energy.30.050504.144511>
- Garfield, E., & Sher, I. H. (1993). Key words plus [TM]-algorithmic derivative indexing. *Journal-American Society for Information Science*, 44, 298.
- Granier, A., Bréda, N., Biron, P., & Villette, S. (1999). A lumped water balance model to evaluate duration and intensity of drought constraints in forest stands. *Ecological Modelling*, 116(2–3), 269–283. [https://doi.org/10.1016/S0304-3800\(98\)00205-1](https://doi.org/10.1016/S0304-3800(98)00205-1)
- Grime, J. P. (1974). Vegetation classification by reference to strategies. *Nature*, 250(5461), 26–31.
- Grimm, V., & Wissel, C. (1997). Babel, or the ecological stability discussions: An inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia*, 109(3), 323–334. <https://doi.org/10.1007/s004420050090>
- Guillot, E., Hinsinger, P., Dufour, L., Roy, J., & Bertrand, I. (2019). With or without trees: Resistance and resilience of soil microbial communities to drought and heat stress in a Mediterranean agroforestry system. *Soil Biology and Biochemistry*, 129, 122–135. <https://doi.org/10.1016/j.soilbio.2018.11.011>
- Gunderson, L. H. (2000). Ecological resilience—In theory and application. *Annual Review of Ecology and Systematics*, 31(1), 425–439. <https://doi.org/10.1146/annurev.ecolsys.31.1.425>
- Gunderson, L. H., & Holling, C. S. (2002). *Panarchy: Understanding transformations in human and natural systems*. Island Press.
- Hautier, Y., Tilman, D., Isbell, F., Seabloom, E. W., Borer, E. T., & Reich, P. B. (2015). Anthropogenic environmental changes affect ecosystem stability via biodiversity. *Science*, 348(6232), 336–340. <https://doi.org/10.1126/science.aaa1788>
- Hillebrand, H., Langenheder, S., Lebrecht, K., Lindström, E., Östman, Ö., & Striebel, M. (2018). Decomposing multiple dimensions of stability in global change experiments. *Ecology Letters*, 21(1), 21–30. <https://doi.org/10.1111/ele.12867>
- Hirota, M., Holmgren, M., Van Nes, E. H., & Scheffer, M. (2011). Global resilience of tropical forest and savanna to critical transitions. *Science*, 334(6053), 232–235.
- Hodgson, D., McDonald, J. L., & Hosken, D. J. (2015). What do you mean, 'resilient'? *Trends in Ecology & Evolution*, 30(9), 503–506. <https://doi.org/10.1016/j.tree.2015.06.010>
- Holling, C. S. (1969). Stability in ecological and social systems. *Brookhaven Symposia in Biology*, 22, 128.

- Holling, C. S. (1973). Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, 4(1), 1–23. <https://doi.org/10.1146/annurev.es.04.110173.000245>
- Holling, C. S. (1987). Simplifying the complex: The paradigms of ecological function and structure. *European Journal of Operational Research*, 30(2), 139–146. [https://doi.org/10.1016/0377-2217\(87\)90091-9](https://doi.org/10.1016/0377-2217(87)90091-9)
- Holling, C. S. (1996). Engineering resilience versus ecological resilience. *Engineering within Ecological Constraints*, 31(1996), 32.
- Holling, C. S., & Clark, W. C. (1975). Notes towards a science of ecological management. In *Unifying concepts in ecology* (pp. 247–251). Springer.
- Holling, C. S., & Goldberg, M. A. (1971). Ecology and planning. *Journal of the American Institute of Planners*, 37(4), 221–230. <https://doi.org/10.1080/01944367108977962>
- Holling, C. S., & Orians, G. (1971). Toward an urban ecology. *Bulletin of the Ecological Society of America*, 52(2), 2–6.
- Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A. J., Vandermeer, J., & Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, 75(1), 3–35. <https://doi.org/10.1890/04-0922>
- Hurd, L. E., Mellinger, M. V., Wolf, L. L., & McNaughton, S. J. (1971). Stability and diversity at three trophic levels in terrestrial successional ecosystems. *Science*, 173(4002), 1134–1136.
- Ibelings, B. W., Portielje, R., Lammens, E. H. R. R., Noordhuis, R., van den Berg, M. S., Joosse, W., & Meijer, M. L. (2007). Resilience of alternative stable states during the recovery of shallow lakes from eutrophication: Lake Veluwe as a case study. *Ecosystems*, 10(1), 4–16. <https://doi.org/10.1007/s10021-006-9009-4>
- Ingrisch, J., & Bahn, M. (2018). Towards a comparable quantification of resilience. *Trends in Ecology & Evolution*. <https://doi.org/10.1016/j.tree.2018.01.013>
- Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., Bezemer, T. M., Bonin, C., Bruelheide, H., de Luca, E., Ebeling, A., Griffin, J. N., Guo, Q., Hautier, Y., Hector, A., Jentsch, A., Kreyling, J., Lanta, V., Manning, P., ... Eisenhauer, N. (2015). Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature*, 526(7574), 574–577. <https://doi.org/10.1038/nature15374>
- Ives, A. R. (1995). Measuring resilience in stochastic systems. *Ecological Monographs*, 65(2), 217–233. <https://doi.org/10.2307/2937138>
- Ives, A. R., & Carpenter, S. R. (2007). Stability and diversity of ecosystems. *Science*, 317(5834), 58–62.
- Jucker, T., Bouriaud, O., Avacaritei, D., Dănilă, I., Duduman, G., Valladares, F., & Coomes, D. A. (2014). Competition for light and water play contrasting roles in driving diversity–productivity relationships in Iberian forests. *Journal of Ecology*, 102(5), 1202–1213. <https://doi.org/10.1111/1365-2745.12276>
- Justus, J. (2007). Complexity, diversity, and stability. *A Companion to the Philosophy of Biology*, 321–350.
- Justus, J. (2012). Carnap on concept determination: Methodology for philosophy of science. *European Journal for Philosophy of Science*, 2(2), 161–179. <https://doi.org/10.1007/s13194-011-0027-5>
- Kéfi, S., Domínguez-García, V., Donohue, I., Fontaine, C., Thébault, E., & Dakos, V. (2019). Advancing our understanding of ecological stability. *Ecology Letters*. <https://doi.org/10.1111/ele.13340>
- Kéfi, S., Rietkerk, M., Alados, C. L., Pueyo, Y., Papanastasis, V. P., ElAich, A., & De Ruiter, P. C. (2007). Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. *Nature*, 449(7159), 213–217.
- Keifer, M., van Wagtenonk, J. W., & Buhler, M. (2006). Long-term surface fuel accumulation in burned and unburned mixed-conifer forests of the central and southern Sierra Nevada, CA (USA). *Fire Ecology*, 2(1), 53–72.
- Klinshov, V. V., Nekorkin, V. I., & Kurths, J. (2015). Stability threshold approach for complex dynamical systems. *New Journal of Physics*, 18(1), 13004.
- KMI. (2018). Average annual mean temperature. Retrieved from <https://www.meteo.be/nl/klimaat/klimatologisch-overzicht/2018/jaar>
- Knowlton, N. (1992). Thresholds and multiple stable states in coral reef community dynamics. *American Zoologist*, 32(6), 674–682.
- Lefcheck, J. S. (2016). PIECEWISESEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, 7(5), 573–579. <https://doi.org/10.1111/2041-210X.12512>
- Lehman, C. L., & Tilman, D. (2000). Biodiversity, stability, and productivity in competitive communities. *The American Naturalist*, 156(5), 534–552.
- Lenton, T. M. (2013). Environmental tipping points. *Annual Review of Environment and Resources*, 38, 1–29.
- Lewontin, R. C. (1969). The meaning of stability. *Brookhaven Symposia in Biology*, 22, 13–24.
- Liao, K.-H. (2012). A theory on urban resilience to floods – A basis for alternative planning practices. *Ecology and Society*, 17(4). <https://doi.org/10.5751/ES-05231-170448>
- Lloret, F., Keeling, E. G., & Sala, A. (2011). Components of tree resilience: Effects of successive low-growth episodes in old ponderosa pine forests. *Oikos*, 120(12), 1909–1920. <https://doi.org/10.1111/j.1600-0706.2011.19372.x>
- Loreau, M., & de Mazancourt, C. (2013). Biodiversity and ecosystem stability: A synthesis of underlying mechanisms. *Ecology Letters*, 16, 106–115. <https://doi.org/10.1111/ele.12073>
- Lotka, A. J. (1925). *Elements of physical biology*. Williams and Wilkins.
- MacArthur, R. (1955). Fluctuations of animal populations and a measure of community stability. *Ecology*, 36(3), 533–536. <https://doi.org/10.2307/1929601>
- Margalef, R. (1969). *Diversity and stability: A practical proposal and a model of interdependence*. Clearinghouse for Federal Scientific and Technical Information.
- May, R. M. (1977). Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature*, 269(5628), 471. <https://doi.org/10.1038/269471a0>
- McCann, K. S. (2000). The diversity–stability debate. *Nature*, 405(6783), 228. <https://doi.org/10.1038/35012234>
- Menck, P. J., Heitzig, J., Marwan, N., & Kurths, J. (2013). How basin stability complements the linear-stability paradigm. *Nature Physics*, 9(2), 89. <https://doi.org/10.1038/nphys2516>
- Mickelbart, M. V., Hasegawa, P. M., & Bailey-Serres, J. (2015). Genetic mechanisms of abiotic stress tolerance that translate to crop yield stability. *Nature Reviews Genetics*, 16(4), 237–251. <https://doi.org/10.1038/nrg3901>
- Mitra, C., Kurths, J., & Donner, R. V. (2015). An integrative quantifier of multistability in complex systems based on ecological resilience. *Scientific Reports*, 5, 16196. <https://doi.org/10.1038/srep16196>
- Myers-Smith, I. H., Trefry, S. A., & Swarbrick, V. J. (2012). Resilience: Easy to use but hard to define. *Ideas in Ecology and Evolution*, 5. <https://doi.org/10.4033/iee.2012.5.11.c>
- Nakagawa, S., Samarasinghe, G., Haddaway, N. R., Westgate, M. J., O'Dea, R. E., Noble, D. W. A., & Lagisz, M. (2019). Research weaving: Visualizing the future of research synthesis. *Trends in Ecology & Evolution*, 34(3), 224–238. <https://doi.org/10.1016/j.tree.2018.11.007>
- Nakajima, H. (1992). Sensitivity and stability of flow networks. *Ecological Modelling*, 62(1–3), 123–133. [https://doi.org/10.1016/0304-3800\(92\)90085-S](https://doi.org/10.1016/0304-3800(92)90085-S)
- Neubert, M. G., & Caswell, H. (1997). Alternatives to resilience for measuring the responses of ecological systems to perturbations. *Ecology*, 78(3), 653–665.

- Newton, A. C. (2016). Biodiversity risks of adopting resilience as a policy goal. *Conservation Letters*, 9(5), 369–376. <https://doi.org/10.1111/conl.12227>
- Noy-Meir, I. (1974). Stability in arid ecosystems and the effects of man on it. Structure, functioning and management of ecosystems. *Proceedings of the First International Congress of Ecology*, Pudoc, Wageningen, 220–225.
- Noy-Meir, I. (1975). Stability of grazing systems: An application of predator-prey graphs. *The Journal of Ecology*, 63(2), 459–481. <https://doi.org/10.2307/2258730>
- Nyström, M., Folke, C., & Moberg, F. (2000). Coral reef disturbance and resilience in a human-dominated environment. *Trends in Ecology & Evolution*, 15(10), 413–417. [https://doi.org/10.1016/S0169-5347\(00\)01948-0](https://doi.org/10.1016/S0169-5347(00)01948-0)
- Odum, E. P. (1953). *Fundamentals of ecology*. W.B. Saunders Company.
- Oliver, T. H., Heard, M. S., Isaac, N. J. B., Roy, D. B., Procter, D., Eigenbrod, F., Freckleton, R., Hector, A., Orme, C. D. L., Petchey, O. L., Proença, V., Raffaelli, D., Suttle, K. B., Mace, G. M., Martín-López, B., Woodcock, B. A., & Bullock, J. M. (2015). Biodiversity and resilience of ecosystem functions. *Trends in Ecology & Evolution*, 30(11), 673–684. <https://doi.org/10.1016/j.tree.2015.08.009>
- Orians, G. H. (1974). Diversity, stability and maturity in natural ecosystems. In W. H. van Dobben & R. H. Lowe-McConnell (Eds.), *Unifying Concepts in Ecology: Report of the plenary sessions of the First international congress of ecology, The Hague, the Netherlands* (pp. 139–150). Springer, Netherlands, Dordrecht.
- Orwin, K. H., & Wardle, D. A. (2004). New indices for quantifying the resistance and resilience of soil biota to exogenous disturbances. *Soil Biology and Biochemistry*, 36(11), 1907–1912. <https://doi.org/10.1016/j.soilbio.2004.04.036>
- Orwin, K. H., Wardle, D. A., & Greenfield, L. G. (2006). Context-dependent changes in the resistance and resilience of soil microbes to an experimental disturbance for three primary plant chronosequences. *Oikos*, 112(1), 196–208. <https://doi.org/10.1111/j.0030-1299.2006.13813.x>
- Park Williams, A., Allen, C. D., Macalady, A. K., Griffin, D., Woodhouse, C. A., Meko, D. M., Swetnam, T. W., Rauscher, S. A., Seager, R., Grissino-Mayer, H. D., Dean, J. S., Cook, E. R., Gangadagamage, C., Cai, M., & McDowell, N. G. (2013). Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change*, 3(3), 292. <https://doi.org/10.1038/nclimate1693>
- Pennekamp, F., Pontarp, M., Tabi, A., Altermatt, F., Alther, R., Choffat, Y., & Griffiths, J. I. (2018). Biodiversity increases and decreases ecosystem stability. *Nature*, 563(7729), 109–112.
- Pimentel, D. (1961). Species diversity and insect population outbreaks. *Annals of the Entomological Society of America*, 54(1), 76–86. <https://doi.org/10.1093/aesa/54.1.76>
- Pimm, S. L. (1984). The complexity and stability of ecosystems. *Nature*, 307(5949), 321. <https://doi.org/10.1038/307321a0>
- Pimm, S. L., Donohue, I., Montoya, J. M., & Loreau, M. (2019). Measuring resilience is essential to understand it. *Nature Sustainability*, 2(10), 895–897. <https://doi.org/10.1038/s41893-019-0399-7>
- Radchuk, V., Laender, F. D., Cabral, J. S., Boulangeat, I., Crawford, M., Bohn, F., Raedt, J. D., Scherer, C., Svenning, J.-C., Thonicke, K., Schurr, F. M., Grimm, V., & Kramer-Schadt, S. (2019). The dimensionality of stability depends on disturbance type. *Ecology Letters*, 22(4), 674–684. <https://doi.org/10.1111/ele.13226>
- Rivest, D., Paquette, A., Shipley, B., Reich, P. B., & Messier, C. (2015). Tree communities rapidly alter soil microbial resistance and resilience to drought. *Functional Ecology*, 29(4), 570–578. <https://doi.org/10.1111/1365-2435.12364>
- Ryan, K. C., Knapp, E. E., & Varner, J. M. (2013). Prescribed fire in North American forests and woodlands: History, current practice, and challenges. *Frontiers in Ecology and the Environment*, 11(s1), e15–e24. <https://doi.org/10.1890/120329>
- Rykiel, E. J. (1985). Towards a definition of ecological disturbance. *Australian Journal of Ecology*, 10(3), 361–365. <https://doi.org/10.1111/j.1442-9993.1985.tb00897.x>
- Scheffer, M. (1989). Alternative stable states in eutrophic, shallow freshwater systems: A minimal model. *Hydrobiological Bulletin*, 23(1), 73–83. <https://doi.org/10.1007/BF02286429>
- Scheffer, M., Bascompte, J., Brock, W. A., Brovkin, V., Carpenter, S. R., Dakos, V., Held, H., van Nes, E. H., Rietkerk, M., & Sugihara, G. (2009). Early-warning signals for critical transitions. *Nature*, 461(7260), 53. <https://doi.org/10.1038/nature08227>
- Scheffer, M., & Carpenter, S. R. (2003). Catastrophic regime shifts in ecosystems: Linking theory to observation. *Trends in Ecology & Evolution*, 18(12), 648–656. <https://doi.org/10.1016/j.tree.2003.09.002>
- Scheffer, M., Carpenter, S. R., Dakos, V., & van Nes, E. H. (2015). Generic indicators of ecological resilience: Inferring the chance of a critical transition. *Annual Review of Ecology, Evolution, and Systematics*, 46, 145–167. <https://doi.org/10.1146/annurev-ecolsys-112414-054242>
- Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., & Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, 413(6856), 591–596.
- Scheffer, M., Hosper, S. H., Meijer, M. L., Moss, B., & Jeppesen, E. (1993). Alternative equilibria in shallow lakes. *Trends in Ecology & Evolution*, 8(8), 275–279. [https://doi.org/10.1016/0169-5347\(93\)90254-M](https://doi.org/10.1016/0169-5347(93)90254-M)
- Small, H. (1973). Co-citation in the scientific literature: A new measure of the relationship between two documents. *Journal of the American Society for Information Science*, 24(4), 265–269. <https://doi.org/10.1002/asi.4630240406>
- Sousa-Silva, R., Verheyen, K., Ponette, Q., Bay, E., Sioen, G., Titeux, H., Van de Peer, T., Van Meerbeek, K., & Muys, B. (2018). Tree diversity mitigates defoliation after a drought-induced tipping point. *Global Change Biology*, 24(9), 4304–4315. <https://doi.org/10.1111/gcb.14326>
- Sterk, M., van de Leemput, I. A., & Peeters, E. T. H. M. (2017). How to conceptualize and operationalize resilience in socio-ecological systems? *Current Opinion in Environmental Sustainability*, 28, 108–113. <https://doi.org/10.1016/j.cosust.2017.09.003>
- Stiven, A. E. (1971). The spread of *Hydramoeba* infections in mixed hydra species systems. *Oecologia*, 6(2), 118–132. <https://doi.org/10.1007/BF00345714>
- Sutherland, J. P. (1974). Multiple stable points in natural communities. *The American Naturalist*, 108(964), 859–873. <https://doi.org/10.1086/282961>
- Sutherland, J. P. (1981). The fouling community at Beaufort, North Carolina: A study in stability. *The American Naturalist*, 118(4), 499–519. <https://doi.org/10.1086/283844>
- Svenning, J.-C., & Sandel, B. (2013). Disequilibrium vegetation dynamics under future climate change. *American Journal of Botany*, 100(7), 1266–1286. <https://doi.org/10.3732/ajb.1200469>
- Tanner, T., Lewis, D., Wrathall, D., Bronen, R., Cradock-Henry, N., Huq, S., Lawless, C., Nawrotzki, R., Prasad, V., Rahman, M. A., Alaniz, R., King, K., McNamara, K., Nadiruzzaman, M. D., Henly-Shepard, S., & Thomalla, F. (2015). Livelihood resilience in the face of climate change. *Nature Climate Change*, 5(1), 23. <https://doi.org/10.1038/nclimate2431>
- TNO GDN. (2018). *DINOloket*. Retrieved from <https://www.dinoloket.nl/en/subsurface-models>
- Todman, L. C., Fraser, F. C., Corstanje, R., Deeks, L. K., Harris, J. A., Pawlett, M., Ritz, K., & Whitmore, A. P. (2016). Defining and quantifying the resilience of responses to disturbance: A conceptual and modelling approach from soil science. *Scientific Reports*, 6, 28426. <https://doi.org/10.1038/srep28426>
- Van Dobben, W. H., & Lowe-McConnell, R. H. (1974). *Unifying concepts in Ecology - Report of the plenary sessions of the First International congress of Ecology*. Dr. W. Junk B.V. Publishers & Centre for Agricultural Publishing and Documentation.

- Van Meerbeek, K. (2021). Data from: Bibliography ecological stability [Dataset]. *figshare*, <https://doi.org/10.6084/m9.figshare.14224505.v1>
- Van Meerbeek, K., Muys, B., Schowaneck, S. D., & Svenning, J.-C. (2019). Reconciling conflicting paradigms of biodiversity conservation: Human intervention and rewilding. *BioScience*, 69(12), 997–1007. <https://doi.org/10.1093/biosci/biz106>
- Van Nes, E. H., & Scheffer, M. (2007). Slow recovery from perturbations as a generic indicator of a nearby catastrophic shift. *The American Naturalist*, 169(6), 738–747. <https://doi.org/10.1086/516845>
- Vasilakopoulos, P., & Marshall, C. T. (2015). Resilience and tipping points of an exploited fish population over six decades. *Global Change Biology*, 21(5), 1834–1847. <https://doi.org/10.1111/gcb.12845>
- Vasilakopoulos, P., Raitsos, D. E., Tzanatos, E., & Maravelias, C. D. (2017). Resilience and regime shifts in a marine biodiversity hotspot. *Scientific Reports*, 7(1), 13647. <https://doi.org/10.1038/s41598-017-13852-9>
- Verbesselt, J., Hyndman, R., Newnham, G., & Culvenor, D. (2010). Detecting trend and seasonal changes in satellite image time series. *Remote Sensing of Environment*, 114(1), 106–115. <https://doi.org/10.1016/j.rse.2009.08.014>
- Vicca, S., Gilgen, A. K., Camino Serrano, M., Dreesen, F. E., Dukes, J. S., Estiarte, M., Gray, S. B., Guidolotti, G., Hoepfner, S. S., Leakey, A. D. B., Ogaya, R., Ort, D. R., Ostrogovic, M. Z., Rambal, S., Sardans, J., Schmitt, M., Siebers, M., van der Linden, L., van Straaten, O., & Granier, A. (2012). Urgent need for a common metric to make precipitation manipulation experiments comparable. *New Phytologist*, 195(3), 518–522. <https://doi.org/10.1111/j.1469-8137.2012.04224.x>
- Vicente-Serrano, S. M., Beguería, S., & López-Moreno, J. I. (2010). A multiscalar drought index sensitive to global warming: The standardised precipitation evapotranspiration index. *Journal of Climate*, 23(7), 1696–1718.
- Volterra, V. (1927). *Variazioni e fluttuazioni del numero d'individui in specie animali conviventi*. C. Ferrari.
- Walker, B., Holling, C. S., Carpenter, S., & Kinzig, A. (2004). Resilience, adaptability and transformability in social–ecological systems. *Ecology and Society*, 9(2). <https://doi.org/10.5751/ES-00650-090205>
- Westman, W. E. (1978). Measuring the inertia and resilience of ecosystems. *BioScience*, 28(11), 705–710. <https://doi.org/10.2307/1307321>
- Yeung, A. C. Y., & Richardson, J. S. (2016). Some conceptual and operational considerations when measuring 'resilience': A response to Hodgson et al *Trends in Ecology & Evolution*, 31(1), 2–3. <https://doi.org/10.1016/j.tree.2015.10.005>
- Yue, K., Fornara, D. A., Yang, W., Peng, Y., Li, Z., Wu, F., & Peng, C. (2017). Effects of three global change drivers on terrestrial C: N: P stoichiometry: A global synthesis. *Global Change Biology*, 23(6), 2450–2463. <https://doi.org/10.1111/gcb.13569>
- Yue, K., Fornara, D. A., Yang, W., Peng, Y., Peng, C., Liu, Z., & Wu, F. (2017). Influence of multiple global change drivers on terrestrial carbon storage: Additive effects are common. *Ecology Letters*, 20(5), 663–672. <https://doi.org/10.1111/ele.12767>
- Zang, C. S., Buras, A., Esquivel-Muelbert, A., Jump, A. S., Rigling, A., & Rammig, A. (2020). Standardised drought indices in ecological research: Why one size does not fit all. *Global Change Biology*, 26(2), 322–324.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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