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Unifying the concepts of stability and resilience in ecology

Essay review

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Abstract

1. Characterising 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 behavior - 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 integrating framework by elaborating the 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, perturbations, latitude, recovery, resilience, regime shift, resistance, temporal stability, tolerance

Glossary

- **Constancy:** Constancy refers to the invariability of a system in time compared to its reference condition (Orians, 1974). Constancy can be a consequence of, but is neither necessary nor sufficient for stability (Justus, 2007).
- **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 disturbed (Carpenter, Ludwig, & Brock, 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, Holling, Carpenter, & Kinzig, 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 dependent.
- **Recovery:** The ability to fully return to the reference condition after a perturbation (Domínguez-García, Dakos, & Kéfi, 2019; Hillebrand et al., 2018; Westman, 1978).

- **Reference** (or reference condition): The stability of a system is assessed relative to a reference condition, i.e. 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, Carpenter, Foley, Folke, & Walker, 2001).
- **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 parameters**: Factors that influence the system variables, but are, for the most part, uninfluenced by them (e.g., temperature, precipitation) (Justus, 2007).
- **System variables**: Represent system parts and describe the structure or functioning of a system (Justus, 2007).

- **Tipping point** (or threshold): A limit in a system variable or parameter beyond which a system cannot return to its former state (Dakos et al., 2019; Ives & Carpenter, 2007).
- **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).

The Babylonian confusion about stability and resilience

“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 like 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 & Gradwell, 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 & 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, Donohue, Montoya, & Loreau, 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 stability of systems close to their equilibrium, and one focusing on non-equilibrium behavior and different domains of attraction.

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 the concept of stability in ecology. A bibliometric mapping exercise is then performed to analyze 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.

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 (Fig. 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 behavior of ecological systems close to a stable reference condition, i.e., 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 like Odum (1953) and Elton (1958) in the 1950s on the resistance of communities to environmental perturbations, Pimentel (1961) was the first to publish results of a field experiment testing the stability-diversity relationship in the international literature. 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.

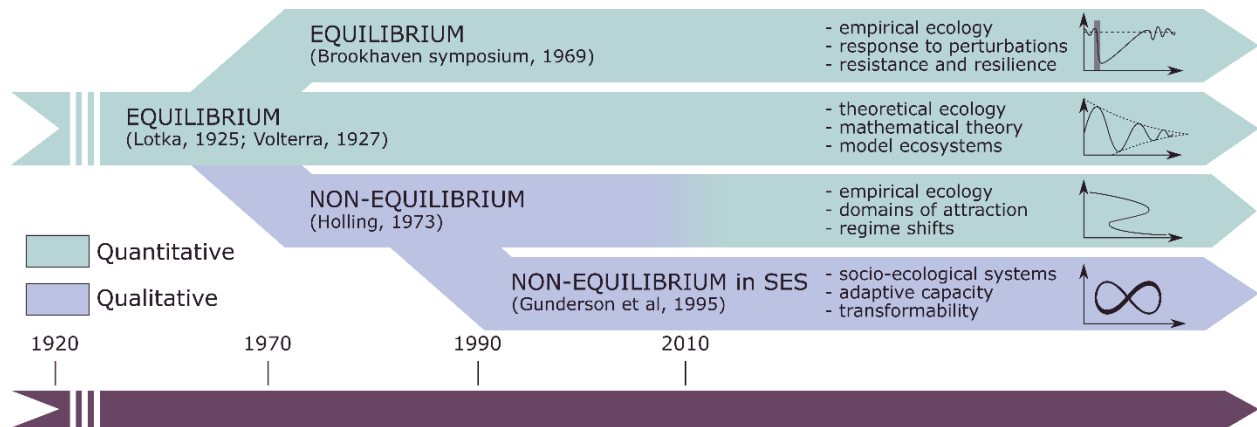


Fig. 1 Evolution of the equilibrium and non-equilibrium concepts of stability in ecology, divided in a ‘quantitative, equilibrium’ and ‘qualitative, non-equilibrium’ view on the behavior of ecosystems. Central themes (with benchmark publications) are indicated in capital letters. Research foci are added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

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 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-centered literature originally defined resilience as a component of stability, Holling used this term to qualitatively describe the behavior 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-centered research, which was therefore considered inappropriate for studying ecosystems with multiple stable states (Nyström, Folke, & Moberg, 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, van de Leemput, & Peeters, 2017). The historical parallel development of different concepts of stability is thus due to them being centered on equilibrium or non-equilibrium systems, respectively. Lastly, by drawing a link between social and ecological systems in his early work (C S Holling, 1969; C S Holling & Goldberg, 1971; C S Holling & Orians, 1971), Holling's definition of resilience went on to permeate the field of socioecology (Fig. 1).

Parallel developments of stability concepts

To analyze the impact these different views have on the ecological literature, we therefore 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 analyze and visualize the intellectual and conceptual structure of a research field (Börner, Chen, & Boyack, 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 research 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 main ecological journals Ecology, American Naturalist, Oikos, Ecology Letters, Journal of Ecology, Trends in Ecology & Evolution, Frontiers in Ecology and the Environment, 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 2028 unique articles (Fig. S1).

proportion of articles that treat them together. c) Co-citation network with very weak intellectual linkages between 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 supplementary information (Fig. S2 and S3).

The intellectual structure was analyzed 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. The conceptual structure was analyzed by a Multiple Correspondence Analysis (MCA) and a co-occurrence network. The closer the keywords are situated in the 2-dimensional MCA space, the larger the proportion of articles that treat them together. This analysis is suitable to identify subfields that are revealed by hierarchical cluster analysis (Aria & Cuccurullo, 2017). A co-occurrence network shows the links between keywords based on the co-occurrences in articles with thicker links denoting stronger associations. More information on the bibliographic analysis can be 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 (Fig. 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 behavior of systems close to their equilibrium in response to small perturbations and characterizes the relationship between stability and biodiversity on quantitative grounds (Fig. 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 (Fig. 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 behavior of dynamic systems far from their equilibrium (Folke, 2006; Scheffer, Carpenter, Dakos, & van Nes, 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 (Fig. 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 (Fig. 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 emerged (e.g., Knowlton, 1992; Scheffer, 1989). Within the non-equilibrium literature, two closely connected subfields emerged with a large overlap in authors (Fig. 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 & Holling (2002), Walker et al., (2004), Folke et al. (2005) and Folke (2006). Together with the thematic map showing the level of development of themes (Fig. S4-5), these results 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 (Fig. 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, Trefry, & Swarbrick, 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, Haydon, & Cuddington, 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, Heitzig, Marwan, & Kurths, 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 state \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, McDonald, & Hosken, 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 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.

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 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, integrating definitions of ecological stability and its equilibrium and non-equilibrium properties in ecology. This is fundamental to interpret published results properly, facilitate discussion, and permit 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, Raitsos, Tzanatos, & Maravelias, 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., standing biomass, vegetation cover). The behavior of the system under changing conditions is investigated by means of 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). Secondly, 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' (1974) cyclical and trajectory stability. 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 (1974). While resolving these inconsistencies is beyond the scope of this work (but see Battisti, Poeta, & Fanelli, 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 abovementioned 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, like fire, floods and extreme droughts (Donohue et al., 2016) (Fig. 3). However, to better reflect the reality of ecological systems, there is a need to expand this research to include other types of perturbations (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, Case, & Gilpin, 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 (Domínguez-García et al. 2019)

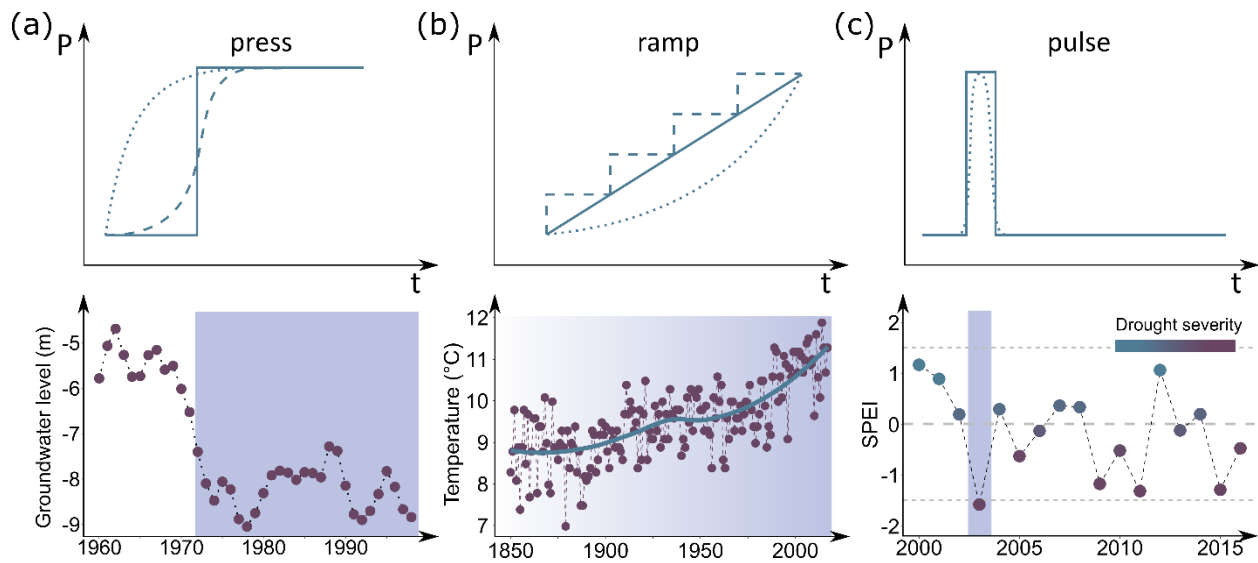


Fig. 3 Different types of perturbations that change system parameters (P) over time (t), i.e., press, ramp and pulse perturbations (top row), with real-world examples from Belgium (bottom row): Permanent lowering of the groundwater table near the nature reserve ‘Kalmthoutse heide’ due to groundwater extraction (De Becker, Van Daele, & Huybrechts, 2004; TNO GDN, 2018); increasing mean annual temperature between 1850-2017 in Uccle (KMI, 2018); and the SPEI (Standardized Precipitation-Evapotranspiration) drought index during growing season (7-month lag in April-October) from 2000 to 2017 (Delvaux, Journée, & Bertrand, 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.

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) and can be measured by a set of ecosystem properties that determine the magnitude, duration and irreversibility of changes in the system variable 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): (1) Resistance is the ability to resist change following a perturbation, (2) resilience is the rate at which a system returns to the reference after change, (3) recovery is the ability to fully return to the reference, (4) latitude is the maximum amount a system variable can be changed before losing its ability to recover, and (5) tolerance is the ability of a system to tolerate perturbations (Justus, 2007). 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 to restrict this term to the return rate as this corresponds to 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, like 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. (2008) define the thermal tolerance as the difference between the minimum and maximum critical temperature.

Note that the definitions of the individual properties imply greater stability as the property increases, which simplifies interpretation. To show the originality of our framework, we highlight the differences with previous work: (1) 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), (2) we do not only describe a system by means of 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), and (3) we expand beyond pulse perturbations to be able study the complexity of real-world perturbations (in contrast to Justus, 2007). Table 1 shows how properties of previous frameworks and newest advances fit in our framework.

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 resist changes	Inertia Reactivity ~Robustness	(Orians, 1974) (Neubert & Caswell, 1997) (Dunne, Williams, & Martinez, 2002)
Resilience	Rate of return after a displacement	Elasticity Resiliency Stability ~Adjustment stability Engineering resilience Recovery Asymptotic stability	(Orians, 1974) (Boesch, 1974) (Holling, 1973) (Connell & Sousa, 1983; Margalef, 1969) (Crawford Stanley Holling, 1996) (Côté & Darling, 2010; Lloret, Keeling, & Sala, 2011) (Donohue et al., 2016)
Recovery	Ability to fully recover	Malleability Resilience	(Westman, 1978) (Lloret et al., 2011)
Latitude	Distance to threshold on the system variable axis	Amplitude Domain of attraction stability ~Adjustment stability Precariousness ~Basin stability ~Horizontal component of resilience Attractor	(Hurd, Mellinger, Wolf, & McNaughton, 1971; Orians, 1974; Westman, 1978) (Grimm & Wissel, 1997) (Connell & Sousa, 1983) (Hodgson et al., 2015; Walker et al., 2004) (Menck et al., 2013) (Vasilakopoulos & Marshall, 2015) (Domínguez-García et al., 2019)
Tolerance	Ability to tolerate perturbations	Resilience Ecological resilience Domain of attraction stability ~Basin stability ~Vertical component of resilience	(Holling, 1973) (Crawford Stanley Holling, 1996) (Justus, 2007) (Menck et al., 2013) (Vasilakopoulos & Marshall, 2015)

Precariousness
Stability threshold
Attractor

(Mitra et al., 2015)
(Klinshov, Nekorkin, & Kurths, 2015)
(Domínguez-García et al., 2019)

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 after being severely displaced by a large perturbation and low resilience, a system 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 – or how much perturbation a system can absorb before it shifts states (C S 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, Hasegawa, & Bailey-Serres, 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 & Sousa (1983), Pimm (1984) and Grimm & 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 & Tilman (2000) would later refer to as temporal stability. The latter 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. However, constancy or persistence do not, by themselves, contribute to ecological stability, as they may simply reflect absence or limited levels of perturbation (Fig. 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 for 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 that caused widespread tree mortality (Crawford S Holling, 1987; Keifer, van Wagtendonk, & Buhler, 2006; Ryan, Knapp, & Varner, 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 and increasing (i.e. flickering) constancy are 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 are useful metrics when studying stability in the face of stochastic perturbation regimes.

Ecological stability is deliberately defined in terms of function, structure and identity. 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 the best strategy for preserving ecosystems on the long run.

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 for 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.

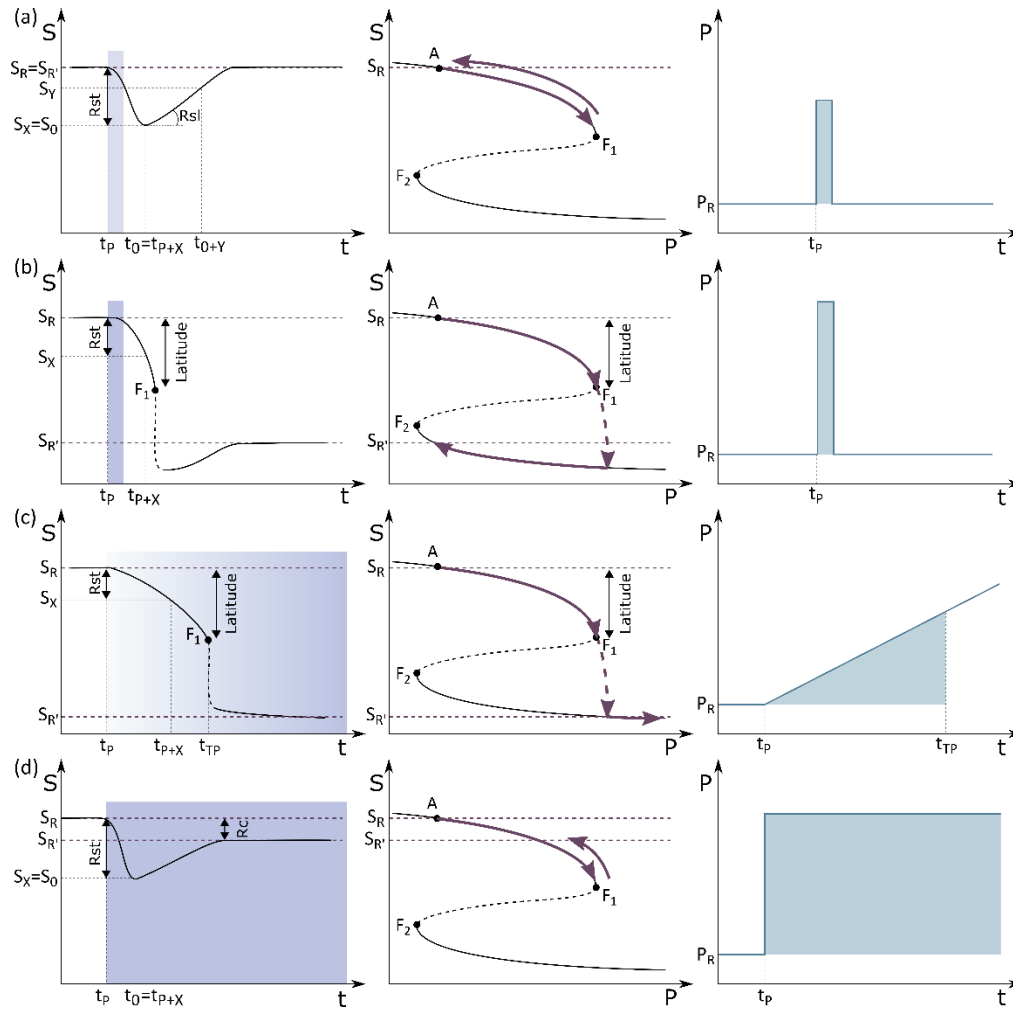


Fig. 4 The behavior of a system in response to different perturbation types (shade of purple denotes the strength of the perturbation). Left column shows the changes of the system variable over time with a stable reference condition S_R (dashed line), the middle column shows the $S \times P$ space and the right column shows parameter (P) changes over time with the green shaded area corresponding to the time 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}). 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 and tolerance. 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.

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): (1) it should be dimensionless and standardized, so that it can be compared across studies; (2) it should be symmetric, capturing both increases and decreases in the system variable (i.e., positive and negative perturbations); (3) it should be a monotonic function of the stability property; (4) it should be bounded for all possible values and not tend to infinity; and (5) 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 & 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:

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

where S_R is the reference value of the system variable and S_X is the value of the response variable at a standardized period of time x (t_{P+X}) after t_P , the time at which the perturbation occurred (Fig. 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_0 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). To take into account the stochasticity of the study system, this time 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 the

vegetation in seasonal climates, for example, time period to calculate the reference value should ideally span several 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 S_0 should be taken as $S_X (t_{P+X}= t_0)$ 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 (Fig. 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 one 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, Bideault, Loreau, & Haegeman, 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 & 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:

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

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 standardized period of time y (t_{0+Y}) following t_0 (Fig. 4a). Equation 2 is standardized 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 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 standardized 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, Hinsinger, Dufour, Roy, & Bertrand, 2019; Orwin, Wardle, & Greenfield, 2006; Rivest, Paquette, Shipley, Reich, & Messier, 2015). Standardized time windows to measure resistance and resilience are important to allow for comparison among studies and thus to facilitate synthesis.

Further research is needed to reach a consensus on standardized 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 standardized values.

The third property, recovery, can be measured as the similarity between the new equilibrium condition, established after a perturbation, and the original reference (Fig. 4d; Orians, 1974; Westman, 1978). To measure of recovery, we propose the following formula:

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

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. Non-linear modelling techniques like threshold generalized 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, Holmgren, Van Nes, & Scheffer, 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 is

available, latitude can be calculated at any point in time. At a certain point in time A, the latitude is standardized against the value of the system variable at A (S_A) and is measured as:

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

where S_{TP} is the value of the response variable at the tipping point (Fig. 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 period 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 horizontal distance to the bifurcation 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 intensity and duration of a perturbation into account when quantifying the perturbation (e.g., Granier, Bréda, Biron, & Villette, 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 2000 to 1900 mm. 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 depends not only on the

precipitation, but also on the land cover, soil physical-chemical properties, climatic conditions and the ecophysiological state of the plant among other factors. In contrast to the Standardized Precipitation Index (SPI), the Standardized Precipitation Evapotranspiration Index (SPEI) includes both precipitation and the atmospheric evaporative demand, and thus provides a more reliable measure of drought severity than only considering precipitation (Beguería, Vicente-Serrano, Reig, & Latorre, 2014; Vicente-Serrano, Beguería, & López-Moreno, 2010). Besides drought, the standardization of perturbation metrics has received much less attention. More research is needed to develop standardized metrics for different perturbations and perturbation types (pulse, press, ramp) and find ways to take into account both intensity and duration of the perturbation. Vicente-Serrano et al. (2010), for example, standardized the water deficit (or surplus) based on a log-logistic distribution to calculate SPEI.

Case study 1: Measuring stability beyond stable states

Early theoretical work on stability made the assumption 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 (Fig. 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, i.e. when the reference condition changes according to a trajectory (C S 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, is already applied to study vegetation dynamics based on remote-sensing time series (De Keersmaecker et al., 2017; Verbesselt, Hyndman, Newnham, & Culvenor, 2010).

The analysis is based on data from the FunDivEurope 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 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 one year after the drought ($= S_Y$) to quantify the resilience and resistance of each tree using equations (1) and (2).

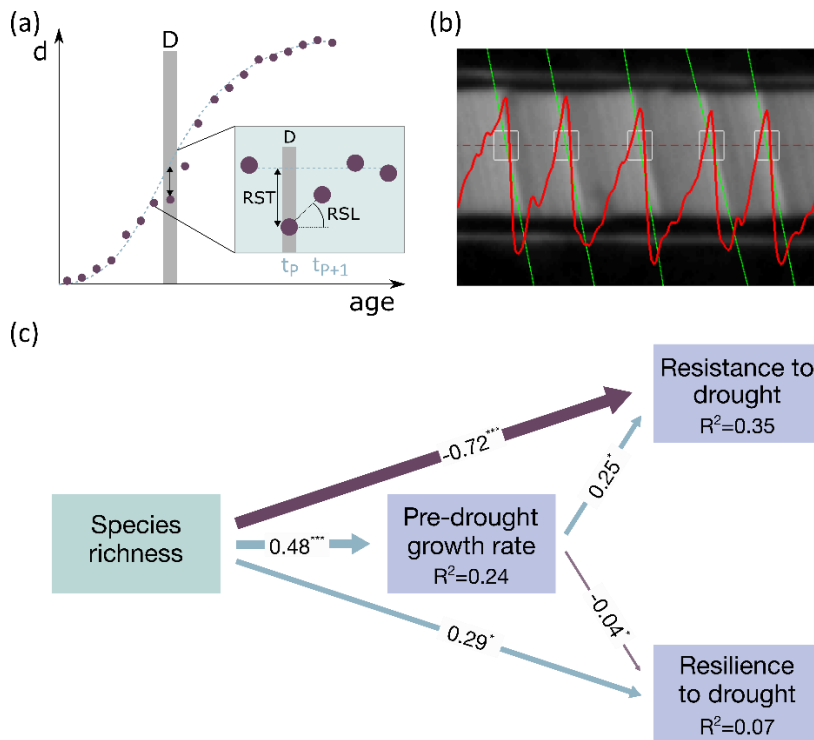


Fig. 5 a) Age-diameter relationship of an individual tree (dashed line, reference dynamic) derived from wood core measurements (purple circles). Inset: Measuring ecological stability to a drought perturbation (grey bar) based on deviations from the modelled overall age-diameter relationship. t_p = time 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 forest diversity on the resistance and resilience to drought of *Pinus sylvestris* trees in central Spain. Green arrows represent positive effects, while purple arrows correspond to negative ones. Arrow width is proportional to the size of the standardized model coefficients (shown on the arrows). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ 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).

Using these data we then explored how a tree's resistance and resilience to drought were influenced by (i) the diversity of its neighbourhood and (ii) 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*: Fig. 5c, *P. nigra*: Fig. 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.

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, Hosper, Meijer, Moss, & Jeppesen, 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 (Fig. 6a), phytoplankton production was limited by low levels of phosphorous, allowing for a well-developed submerged aquatic vegetation (charophyte cover, Fig. 6b). Increasing nutrient loads in the beginning of 1960's induced a regime shift to a turbid state in 1964, characterized by phytoplankton dominance and the loss of submerged vegetation (Fig. 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 (Fig. 6c), after reducing the nutrient load and biomanipulation, showed hysteresis (Fig. 6b).

Merging the equilibrium-centered 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 parameter (Fig. 6b, c). With time series of charophyte cover and phosphorous concentration, the latitude and tolerance can be quantified (see formulas 4, 5). For the onset of the phosphorous increases (year 1959), they are 0.4 and 1.25 respectively (with $S_R = 80\%$ and $P_R=0.05 \text{ mg L}^{-1}$), meaning that a relative change less than -100% in charophyte cover and/or an average increase of 125% in phosphorous inputs over six years were necessary to provoke a regime shift. Such regime shifts perfectly fit in the quantitative framework of ecological stability (Fig. 6c). The resistance to the phosphorous input equals 0 (macrophytes almost disappeared completely, with $t_0=1973$ in formula 1), and as the system did not recover at all during the first year after t_0 , the resilience was 0 (formula 2). In response to the restoration, the resilience of the system was 0.08 (with $t_Y=1990$, 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.

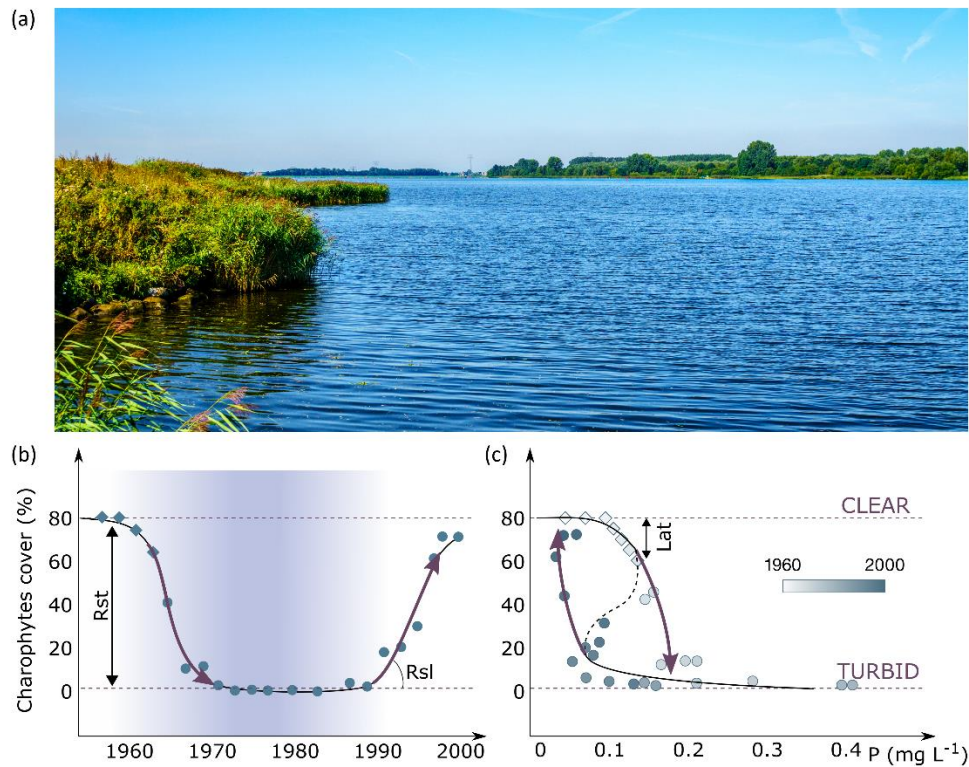


Fig. 6 a) The Veluwe lake in the Netherlands, created in 1957 as a result of land reclamation (Picture: Harry Beugelink). b) A regime shift occurred in the Veluwe lake (The Netherlands) in the 1960s from a clear state with extensive cover of charophytes to a turbid state in response to increasing nutrient 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 increasing 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 description in Ibelings et al. (2007)

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 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 with examples the broad applicability of our framework. A next step could be to work towards a set of standardized, operational and easy-to-use metrics of the stability components, to allow for comparisons across studies and for the summary of ecological evidence through meta-analyses. 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, Fornara, Yang, Peng, Li, 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, Fornara, Yang, Peng, Peng, et al., 2017) further complicate the study of ecological stability. Expanding the framework to multi-directional change with

appropriate metrics and baselines is the next big hurdle to take. 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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Authorship

KVM and JCS conceived the idea of the study. KVM performed the review and bibliometric analysis, TJ analysed the tree ring data. KVM wrote the manuscript. All authors contributed substantially to the revisions.

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