ECOLOGY LETTERS

Ecology Letters, (2019) doi: 10.1111/ele.13340

IDEA AND PERSPECTIVE

Advancing our understanding of ecological stability†

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†This article is part of the 20th birthday issue of the journal.

Abstract

The concept of ecological stability occupies a prominent place in both fundamental and applied ecological research. We review decades of work on the topic and examine how our understanding has progressed. We show that our understanding of stability has remained fragmented and is limited largely to simple or simplified systems. There has been a profusion of metrics proposed to quantify stability, of which only a handful are used commonly. Furthermore, studies typically quantify one to two metrics of stability at a time and in response to a single perturbation, with some of the main environmental pressures of today being the least studied. We argue that we need to build on the existing consensus and strong theoretical foundation of the stability concept to better understand its multidimensionality and the interdependencies between metrics, levels of organisation and types of perturbations. Only by doing so can we make progress in the quantification of stability in theory and in practice, and eventually build a more comprehensive understanding of how ecosystems will respond to ongoing environmental change.

Keywords

Permanence, persistence, recovery, resilience, resistance, robustness, variability.

Ecology Letters *(2019)*

INTRODUCTION

What underpins the apparent stability of natural systems? This question has been a core focus of ecologists since the very emergence of the discipline, spurring the parallel development of theory and empirical exploration to a far greater extent than many other topics in the field (Donohue *et al*. 2016). While early work explored fluctuations in population dynamics (Lotka 1925; Volterra 1926), later work evolved to a strong focus on the role of diversity for stability (Odum 1953; MacArthur 1955; Elton 1958; May 1973). The relationship between diversity and stability has continued to engage ecologists ever since (Ives & Carpenter 2007; Allesina & Tang 2012; Hautier *et al*. 2014; Johnson *et al*. 2014; Pennekamp *et al*. 2018), but the growing awareness of the extent of human-induced global change has precipitated exploration of whether and how ecological systems will be able to withstand and recover from intensifying environmental stresses (Holling 1973; May 1977; Pimm 1991; Scheffer *et al*. 2001).

The relatively simple intuitive meaning of stability contrasts with the multiplicity of ways it has been evaluated in theoretical and empirical studies. Grimm & Wissel (1997), for example, identified 163 definitions, 70 different stability concepts and more than 40 measures of stability in the literature. Some of these measures have been more widely used than others with a clear distinction between disciplines and approaches (Donohue *et al*. 2016). Nonetheless, the profusion of metrics together with the misuse of language have fragmented our understanding of ecological stability and jeopardised our ability to make progress in its study.

It has long been acknowledged that there is no stability *per se* but rather that stability is a multifaceted concept characterised by different properties (Fig. S1; Lewontin 1969; Orians 1975; Pimm 1984; Grimm & Wissel 1997; Ives & Carpenter 2007; Donohue *et al*. 2013, 2016). Recurrent attempts at characterising these properties have helped organise our conceptualisation of stability immensely (Fig. S1), but the difficulty in doing so has also opened new questions. First, the multifaceted nature of stability cautions against the use of only some metrics without knowing more about how these metrics are interrelated at the risk of misevaluating the stability of the system (Harrison 1979; Loreau 1994; Donohue *et al*. 2013; Arnoldi *et al*. 2016; Arnoldi & Haegeman 2016). Second, stability's assessment might depend on the organisational scale at which stability is measured (e.g. species vs. total community; Tilman 1996). Third, the concept of stability is intricately related to that of perturbations (Donohue *et al*. 2013), which vary in their nature, temporal extent and spatial scale. Understanding the stability of ecological systems requires addressing these different aspects of stability – the multiple metrics, the various scales of organisation and the diverse perturbations – to investigate their possible interdependencies and relative relevance. Indeed, the question of how to assess the stability of complex ecological systems – What needs to be measured? At what scale? And how does stability scale up across different organisational levels? – remains largely open.

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Here, we review how stability has been assessed in the ecological literature – theoretical and empirical – since the 1950s. We recorded the stability metrics used, the variables on which they were quantified and the perturbations considered. We show that the evaluation of stability in ecological studies has been largely limited to using a single stability metric, on 'simple' species-poor systems, at a single organisational scale, in response to single perturbations. These observations raise a number of questions and challenges that we summarise in order to highlight where research is needed.

AN OVERVIEW OF OUR UNDERSTANDING OF STABILITY

To assess what has been done so far, we reviewed the ecological literature and recorded how stability was quantified in both theoretical and empirical papers. More specifically, we searched for the terms ecolog* AND stability, ecolog* AND resilience, ecolog* AND structural stability on the Web of Science in the period from 1900 to January 2018 in the journals Ecology, American Naturalist, Oikos, Ecology Letters, Science, Proceedings of the National Academy of Sciences of the United States of America (PNAS), Scientific Reports, Nature and Nature Communications.

This search retrieved 995 articles, from which we removed studies that did not explicitly measure, quantify or calculate stability in any form (e.g. review or opinion papers). Our final database consisted of 459 entries (around 46% of the initial search). For each paper, we recorded: (1) the type of study (theoretical, experimental/empirical (hereafter referred to as 'empirical') or both (hereafter referred to as 'mixed'), (2) the system size (number of species or model dimension), (3) the nature (what is perturbed), scale (who is affected: species, group of species, total community), and type (pulse, press, stochastic) of the perturbation(s) performed and (4) the nature (on what variable(s) are the stability metrics measured), scale (on which scale is the metric measured: species, group of species, total community) and type of metric measured. We merged metrics that were named differently in different studies despite having the same definition. The complete list of metrics recorded is summarised in Table S1.

A proliferation of metrics

The number of metrics used in theoretical and empirical studies has increased over time as new metrics keep being suggested in the literature – in papers published between 1970 and 1979, for example, there were 13 different metrics used, while about 34 different ones were used in papers published since 2010 (Fig. 1a). The vast majority of these metrics has received little use in the literature, while only a handful have been used broadly across studies (Fig. 1b). For example, coefficient of variation (CV) and resistance have both been used in more than 100 papers. The diversity of metrics used hinders comparisons among studies, since different metrics are not straightforward to compare. Moreover, the metrics used differ in theoretical vs. empirical studies – dominant eigenvalue, the type of attractor (e.g. alternative stable states, dynamics becoming cyclic), CV and persistence are the most common metrics used in theoretical studies, whereas resistance and CV dominate in empirical studies (Table S1). This creates significant difficulties in linking theory with experiments and observations (Donohue *et al.* 2016).

> These observations raise the question of what metrics to measure, and whether each metric provides complementary information or whether some of them are redundant. Papers typically quantify one to two metrics at a time (1.4 metrics on average in our database). This means that different metrics have rarely been quantified simultaneously and that we do not know much about how stability metrics relate to each other.

A focus on 'simple' (species-poor) ecological systems

The majority of experimental and theoretical studies identified in our literature search focused on relatively simple, species-poor systems. Among the empirical papers studied, 21% involved systems with < 5 species, and 29% with < 10 (Fig. S2a). Among theoretical studies, 39% studied systems with < 5 species, while 45% focused on systems with < 10 (Fig. S2b).

> Clearly, the studied systems are far less diverse and complex than most natural systems. This raises the question of whether our knowledge about the stability

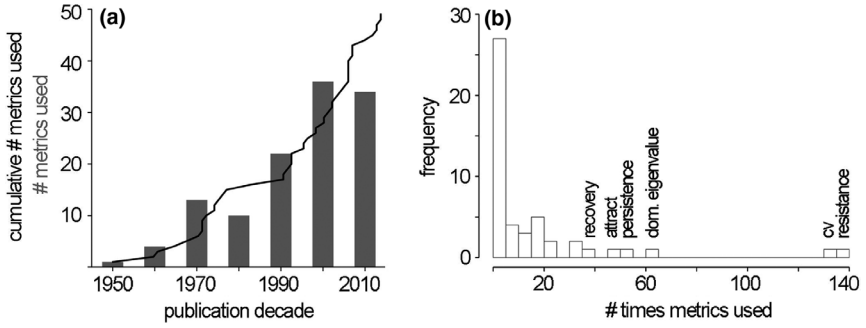

Figure 1 Metrics of stability. (a) Grey bars represent the number of different metrics used in the papers of that decade (e.g. 13 metrics were used in the papers published between 1970 and 1979). The black line displays the cumulative number of metrics used in the papers until a given year (i.e. the total number of metrics used in the papers between 1950 and that year). (b) Distribution of the number of times metrics have been used in the studies of our database (i.e. in how many papers; see Table S1 for a list of stability metrics).

of simplified systems can be extrapolated to systems with more realistic levels of complexity.

A bias towards measuring stability at the community scale (i.e. on aggregated variables)

Stability can be measured at each of the various levels of ecological organisation, at the species level, at the functional group at the community scale, with aggregated measures such as total biomass or productivity (Fig. 2iii). In our literature analysis, we found a significant bias towards quantifying stability from properties aggregated at the level of the community or meta-community (e.g. total biomass or total cover; 59% of studies, Fig. 2iii). Relatively, few studies quantify stability at finer scales of organisation (i.e. at the level of species or groups of species). Further, the comparison of stability measures performed at different organisational levels in the same system remains poorly studied: 82% of the studies of our database measure stability at only one scale, 16% perform measures at two scales and only 2% consider three different scales when assessing stability.

Because current research focuses on the stability of a single organisation level at a time, these observations raise the question of how stability at a given level of organisation scales to other levels (i.e. how stability depends on the level of organisation).

A restricted examination of perturbations

The idea of stability is intimately linked with how a system responds to perturbations. Traditionally, two broad types of perturbations are distinguished in ecology: *press* and *pulse* (Fig. 2i) (Bender *et al*. 1984). Press perturbations are defined as continuous disturbances causing the abundance or density of species to change permanently, or as long as the perturbation is present (e.g. species extinctions or sustained fishing pressure). Pulse perturbations are defined as instantaneous and short-term disturbances causing a sudden change in species abundances or densities, such as extreme climatic events or fire events. Next to these two types of perturbations, the stability of a system can also be evaluated as its dynamical response to noise (typically sustained random fluctuations), which can take the form of either demographic (intrinsic to the biological system) or environmental (extrinsic to the system) stochasticity (May 1973; Turelli 1978).

Interestingly, we found that a significant portion of studies quantify the stability of ecological systems in the absence of an explicit perturbation (i.e. the 'null' perturbation type in Fig. 3 left). Rather, such studies tend to look at dynamical properties of the system under different conditions, such as contrasting levels of species richness or environmental variables (e.g. nutrients, grazing pressure). This includes most of the studies investigating the links between diversity and community or ecosystem stability (e.g. Yachi & Loreau 1999; McCann 2000; Tilman *et al*. 2006; Downing *et al*. 2014), in which ecosystem variability over time is typically compared across different levels of species richness. These studies have contributed greatly to the understanding of the links between biodiversity and stability, but it is, nonetheless, unclear to what extent these results can help us understand the consequences of biodiversity loss in natural conditions. Indeed, the stability assessed from comparing communities of different diversity levels might not be equivalent to the stability of a community following species removal (Díaz *et al*. 2003). For example, potential cascading effects following extinctions are ignored when comparing diversity treatment levels, and in particular the sequential effects of species loss (i.e. the order in which species are lost). Zavaleta & Hulvey (2004) showed that a realistic species loss scenario decreased grassland resistance to invasions strongly when compared to a random species loss scenario.

In addition, perturbations of different nature (e.g. temperature, nutrient availability, CO_2, light, salinity, rainfall) have attracted different levels of attention (Fig. 3 right). We, for

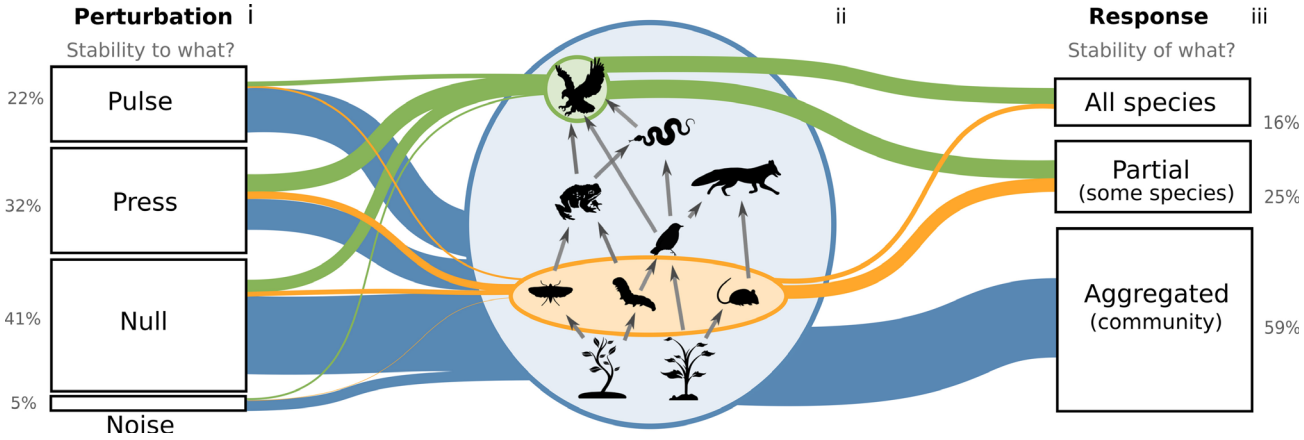

Figure 2 Assessing stability in ecological systems requires identifying i) the nature of the perturbation (the stability 'to what'?) [Pulse, Noise or Press], its intensity and direction, ii) the scale at which it affects the ecological system [individual species in green, groups of species (e.g. functional or trait-based) in orange and whole system in blue] and iii) the scale at which the stability metrics is measured (the stability 'of what'?), which may differ from the scale at which the perturbation occurs. Stability metrics can be quantified on either each of all species of the system ('all species'), some species ('partial') or at the level of the whole community ('aggregated'). The percentages indicate the percentage of studies included in our database. Lines from the perturbation categories on the left indicate the proportion of studies with this type of perturbation applied on each level of organisation.

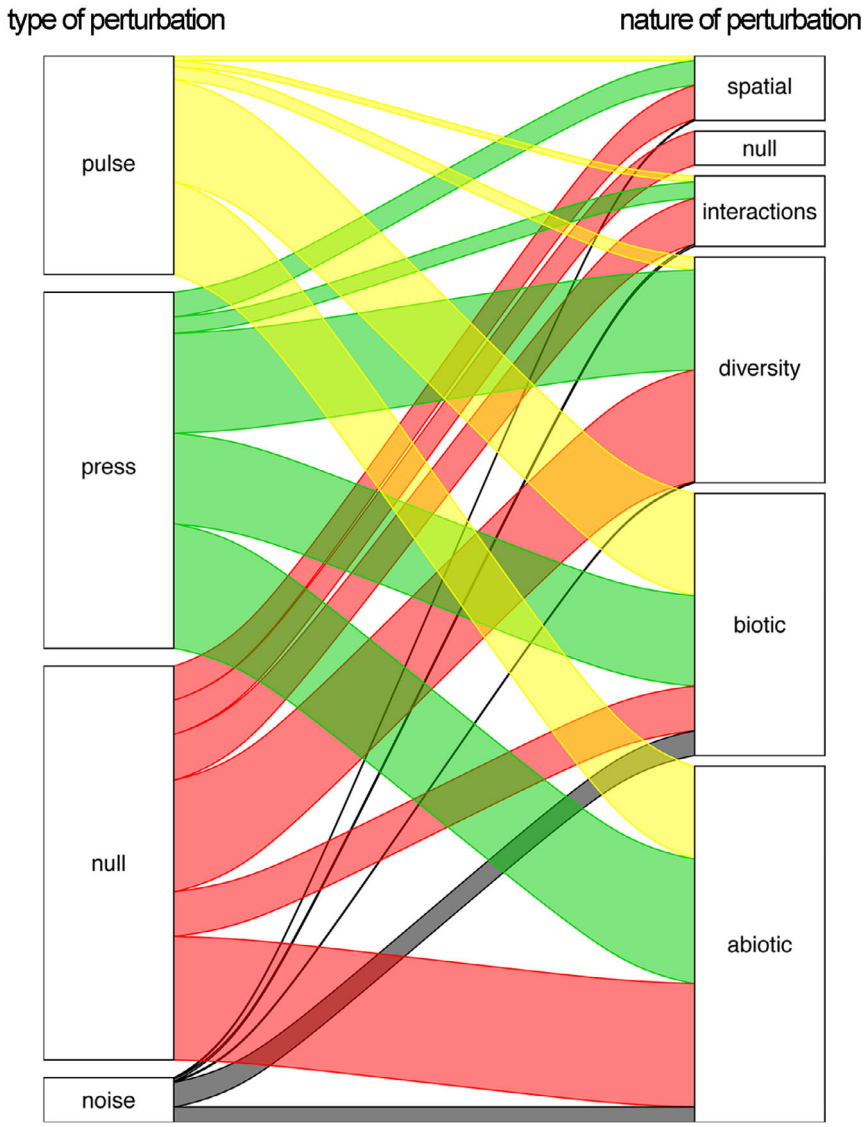

Figure 3 Alluvial plot of the type and nature of perturbations. The 'perturbation types' are defined in the 'A restricted examination of perturbations' part in the main text. 'Null' refers to studies that do not have an explicit perturbation but rather compare treatments (e.g. Biodiversity-Ecosystem Functioning studies or studies comparing persistence of different food web structures); in these cases, we still record the nature of the treatment (which is why there are flows between 'Null' and 'nature of perturbation'). Flow thickness between boxes is proportional to the number of papers, and colours reflect the type of perturbation. Regarding the 'nature of the perturbation': 'spatial' refers to cases where the amount, quality, structure or connectivity of the habitat were affected, 'Null' are the cases where nothing is changed, 'interactions' refers to situations where the interactions between species are changed, 'diversity' are cases where the number and/or identity of species are changed, 'biotic' includes cases where a biotic element other than species diversity is changed (e.g. biomass, abundance, productivity, cover, herbivory) and 'abiotic' refers to cases where an abiotic condition is changed (e.g. pH, temperature).

example, know little about 'spatial stressors', such as habitat destruction and fragmentation, even though they have been identified as critical elements of global change (Millennium Ecosystem Assessment 2005).

Although multiple types of disturbances acting simultaneously are a defining feature of global environmental change (e.g. Millennium Ecosystem Assessment 2005; Piggott *et al.* 2015), this has been largely neglected since studies typically study a system's response to one or two perturbations (1.4 perturbations studied per paper on average in our database; Donohue *et al.* 2016). This finding is consistent with previous work, which highlighted that most studies about the effects of global change on species and their interactions have focused on only one global change driver at a time, while interactive effects are often neglected (Tylianakis *et al.* 2008).

Moreover, different perturbations may affect all or only a subset of the components of a system (Fig. 2ii). For example, harvesting, fishing and hunting typically affect just one or a few species in a system, whereas climate change most likely affects all species in a given community, though probably not in the same way. In our literature review, studies considering perturbations or treatments affecting more than one scale of organisation (i.e. species, group or community) at a time were very rare, suggesting that the interplay of perturbations

affecting different scales of organisation is remarkably understudied (92% of the studies applied perturbations or treatments at only one scale and less than 0.5% considered perturbations affecting more than two different scales of biological organisation).

> Ecologists have neglected some important aspects of disturbances affecting ecosystems. The consequent gaps in our knowledge have led to a remarkably poor understanding of the impacts of many of the most important elements of global change and their interactive effects.

CHALLENGES AND OPPORTUNITIES

Our literature analysis reveals that stability has typically been assessed with one or a few metrics, in species-poor systems, at a given level of organisation, after a single perturbation. These observations raise the worrying question of whether our understanding of stability extends beyond those restricted conditions. Addressing this remains a fundamental challenge that hinders progress towards a more holistic understanding of stability applicable to the natural world. In this section, we highlight some of the challenges that need to be overcome in order to build such understanding.

Elucidating the relationships between stability metrics

Because many different metrics are used in the literature and because they have rarely been assessed simultaneously, a key question is whether they all convey different information or whether some are redundant with each other. Previous studies have proposed various categorisations of stability metrics into groups based on their definition; these groups have been referred to as 'facets', 'properties', 'meanings' or 'components' (e.g. Pimm 1984; Grimm *et al*. 1992; Grimm & Wissel 1997; Ives & Carpenter 2007; Fig. S1). Organising stability metrics into groups is an important but clearly not an easy task. Although recent theoretical advances have started to unravel the mathematical relationships between some of the stability metrics as well as the conditions for these interdependencies (Loreau 1994; Arnoldi *et al*. 2016; Arnoldi & Haegeman 2016; Haegeman *et al*. 2016; Radchuk *et al*. 2019), we are far from having a complete picture of the relationships between stability metrics.

Donohue *et al*. (2013) have suggested a way forward by studying correlations between metrics to estimate what they refer to as 'the dimensionality' of stability. The underlying idea is that if different stability metrics are strongly correlated with each other, this suggests that they bear similar information and that only one (or a few) of them is needed to characterise the system's stability. Conversely, if all the metrics are independent from each other, they all carry different information and they may all be needed to assess the system's stability. In the same vein, another approach could consist in identifying groups of metrics that are redundant with each other within groups but largely independent from each other across groups. Such grouping of the metrics would significantly facilitate the quantification of stability (Donohue *et al*. 2013; Arnoldi *et al*. 2016). Research is, however, needed to identify which categorisations are more meaningful.

Better understanding of relationships among metrics could also help bridge the gaps between theoretical and empirical studies. Not only do the metrics used in these studies differ (Donohue *et al*. 2016; Table S1), but only 2% of the papers in our literature analysis combine theory and empirical measurements (Fig. S2b). These important disparities between theoretical and empirical studies result in much of the theoretical advances remaining untested and hinder the mechanistic understanding of empirical studies and our capacity to generalise them. Although there have been some success stories of the gaps between theory and empirical studies being bridged (Mazancourt *et al*. 2013; Sanders *et al*. 2015, 2018; Donohue *et al*. 2017), these remain rare.

Unraveling the interdependency of stability across scales of organisation

Because species influence each other through networks of interactions in natural communities, even localised perturbations can spread rapidly through the whole community (Mrowicki *et al*. 2016). This interdependency between organisation levels raises the question of the level of organisation (e.g. species, group of species, community; Fig. 2ii) at which stability metrics should be measured.

For example, how does stability at the species level relate to community stability and *vice versa*? Many theoretical and experimental studies have found destabilising effects of diversity on variability at species level but stabilising effects of diversity at community or ecosystem level (e.g. Tilman 1996; Thébault *et al*. 2005; Jiang & Pu 2009; Gross *et al*. 2014). Such differences between the variability at species and community level result from the fact that variability at community level is not only determined by species variability but also by the synchrony of species temporal dynamics (Yachi & Loreau 1999). If species have asynchronous responses to environmental changes, community variability may decline with increasing species richness even if species variability increases. While variability has been investigated at different levels of organisation, this has very rarely been the case for other stability measures (but see e.g. Haegeman *et al*. (2016) who showed that asymptotic resilience at the aggregated community level was unrelated to that calculated at the corresponding species level).

Furthermore, some stability metrics only reflect the response of a single (or a few) species, despite the fact that they are typically measured at the 'system' scale. For example, resilience (the asymptotic return rate to equilibrium after a pulse perturbation, i.e., the long-term return rate) is determined by rare species, while the short-term return rate is determined by abundant species (Arnoldi *et al*. 2018). In case of very uneven species abundance or biomass distributions, community variability might also be determined by the variability of the most abundant species (e.g. Thébault & Loreau 2006). So, the knowledge of a few species could be enough to infer the stability of whole communities, and these few species could be used as indicator species for community wide responses, as long as they can be identified.

Accounting for the multidimensional nature of disturbances

Despite the high diversity in the nature of the disturbances used in stability studies (Fig. 3), disturbances are generally characterised as one-dimensional, affecting at most a couple of ecological scales and acting in isolation from each other. Few studies have focused on interactive effects of disturbances acting on more than one scale of biological organisation (e.g. community vs. species). The main reason for this is the difficulty in conducting experiments that include multiple disturbance effects. Donohue *et al.* (2013, 2016) describe how this large one-dimensional perspective has led to confused communication about stability and to increased risks of significantly underestimating the impacts of perturbations. Multiple disturbances can indeed have synergistic or antagonistic effects. For example, in an increasingly hotter climate, the chance of wildfire events may also increase (Jolly *et al.* 2015). The combined detrimental effect of multiple disturbances was well exemplified by coral reefs that have been lost because of the synergistic effects of coastal eutrophication, global warming and hurricane disturbances (Hughes *et al.* 2017). Clearly, the question of how to best integrate different types and properties of disturbances when studying the stability of a given system is a significant challenge. A general solution may lie in recently developed frameworks for incorporating both the strength and duration of combined pulse and press disturbances to better understand the stability of ecosystems such as shrublands (Ratajczak *et al.* 2017).

In the same way as multiple simultaneous disturbances are understudied in spite of their known relevance in the current context of global change, the study of certain specific perturbations has lagged far behind – in particular those due to habitat fragmentation or destruction (Fig. 3 right) – even though these have clearly been identified as major ongoing pressures on species worldwide (Pimm & Raven 2000; Foley et al. 2005; Millennium Ecosystem Assessment 2005). Recent studies have started tackling this issue. Using an original network approach and simulating the sequential removal of different habitats, Evans *et al.* (2013) identified key habitats whose degradation would lead to disproportional species losses. Blüthgen *et al.* (2016) showed that land use intensity in forests and grasslands could decrease the temporal variability of bird and bat communities in an empirical study, while Gravel *et al.* (2016) and Guelzow *et al.* (2017) highlighted the critical role played by dispersal and ecological connectivity in moderating stability. These studies suggest that a better integration of the spatial dimension of perturbations and ecosystems might be fruitful to understand stability, not only because many important ecological process related to stability has a spatial component, but also because considering perturbations at the landscape scale might be a way to study more realistic perturbation cocktails.

CONCLUSION

Reviewing the literature on ecological stability since the 1950s helped us identify three gaps of knowledge as key challenges. (1) We need to better understand the relationships between stability metrics to clarify what needs to be measured and in what context. Among other things, this could help bridge gaps between empirical and theoretical studies, which have used different metrics for practical reasons. (2) We need to investigate how a given metric changes depending on the level of biological organisation considered, but also how different metrics may best characterise certain levels of organisation. (3) We need to focus on multiple types of perturbations and especially those that are common and known to affect ecological systems particularly strongly. Addressing these challenges means that we need to embrace the multidimensionality of the stability concept by studying several stability metrics and perturbations simultaneously, and this at different scales (temporal, spatial and organisational).

Nonetheless, we also found that in recent decades the number of papers tackling multiple metrics of stability simultaneously has increased, albeit slowly (Fig. S3a). Multiple perturbations and, to a lesser extent, perturbations affecting multiple scales have also attracted more recent attention (Fig. S3b,d). Finally, more papers are quantifying stability at several scales (Fig. S3c). These encouraging trends suggest that we are slowly starting to fill the gaps in our understanding of the stability of complex ecological systems.

Of course, these challenges are not the only gaps in our knowledge of the stability of ecological systems. For example, recent work has explored how stability changes from local to larger spatial scales (Peterson *et al.* 1998; Wang & Loreau 2014, 2016) using invariability-area relationships (Wang *et al.* 2017). Moreover, a key challenge is to understand how eco-evolutionary dynamics, and in particular the ability of ecological systems to adapt to changes through evolution, can affect ecological responses to stress and the stability of ecological systems (Orians 1975). A recent experiment has shown how evolution can influence species coexistence in a pondweed community (Hart *et al.* 2019), for example. Lastly, it remains a challenge to deal with non-equilibrium dynamics, oscillations or even alternative states as most metrics of stability still assume an equilibrium viewpoint. Nonetheless, recent approaches are taking advantage of the increasing availability of data derived from remote-sensing or long-term monitoring to estimate ecological stability via proxies (Scheffer *et al.* 2009; Dakos *et al.* 2012; Kéfi *et al.* 2014) and to quantify nonlinear dynamics (Ushio *et al.* 2018). A challenge is to translate these approaches into practical and accessible tools for quantifying stability in real ecological systems.

When thinking about stability, the simple metaphor of a ball rolling in a landscape that stabilises at the bottom of a valley comes to mind. This metaphor has served well its purpose for 'simple' (i.e. low dimensional) systems, where there was no ambiguity about the definition and choice of state variables, reference states and disturbances. Ecological systems are, however, clearly not simple (Grimm *et al.* 1992). In an ecological community composed of many species, the multiple levels of organisation involved, the multiple types of perturbation and scales of the system's response imply multiple ways in which stability can be quantified and interpreted, depending on the variable measured and the type of perturbation applied. Moving towards such a multidimensional consideration of stability appears as a key ingredient currently

missing to improve our understanding of the stability of natural systems.

ACKNOWLEDGEMENTS

VD-G and SK were funded by the ANR project ARSENIC (ANR-14-CE02-0012). ET and CF were funded by the ANR project ECOSTAB (ANR-17-CE32-0002/ECOSTAB).

AUTHORSHIP

SK, VDo and VDa developed the original idea, SK, VDo, CF, ET and VDa performed the literature analysis, SK, VDo and CF analysed the results, SK wrote the first full draft of the paper with the help of all co-authors.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.c0t1892.

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Additional supporting information may be found online in the Supporting Information section at the end of the article.

Editor, Tim Coulson
Manuscript received 24 May 2019
Manuscript accepted 26 May 2019