Scaling up our understanding of tipping points

Sonia Kéfi, Camille Saade, Eric L Berlow, Juliano S Cabral, Emanuel A Fronhofer

To cite this version:

Sonia Kéfi, Camille Saade, Eric L Berlow, Juliano S Cabral, Emanuel A Fronhofer. Scaling up our understanding of tipping points. Philosophical Transactions of the Royal Society B: Biological Sciences, 2022, 377 (1857), 10.1098/rstb.2021.0386 . hal-03759068

HAL Id: hal-03759068
https://hal.umontpellier.fr/hal-03759068v1

Submitted on 23 Aug 2022

Scaling up our understanding of tipping points

Sonia Kéfi*[1,4], Camille Saade[1], Eric L. Berlow[2], Juliano S. Cabral[3], and Emanuel A. Fronhofer[1]

[1]ISEM, CNRS, Univ. Montpellier, IRD, EPHE, Montpellier, France
[2]Vibrant Data Labs, Berkeley CA, USA
[3]Ecosystem Modeling Group, Center for Computational and Theoretical Biology, University of Würzburg, Würzburg, Germany
[4]Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501, USA

***Corresponding author:** sonia.kefi@umontpellier.fr

Keywords: alternative stable states, bistability, catastrophic shifts, hysteresis, global change, resilience

Abstract

Anthropogenic activities are increasingly affecting ecosystems across the globe. Meanwhile, empirical and theoretical evidence suggest that natural systems can exhibit abrupt collapses in response to incremental increases in the stressors, sometimes with dramatic ecological and economic consequences. These catastrophic shifts are faster and larger than expected from the changes in the stressors and happen once a tipping point is crossed. The primary mechanisms that drive ecosystem responses to perturbations lie in their architecture of relationships, i.e. how species interact with each other and with the physical environment and the spatial structure of the environment. Nonetheless, existing theoretical work on catastrophic shifts has so far largely focused on relatively simple systems that have either few species and/or no spatial structure. This work has laid a critical foundation for understanding how abrupt responses to incremental stressors are possible, but it remains difficult to predict (much less manage) where or when they are most likely to occur in more complex real-world settings. Here, we discuss how scaling up our investigations of catastrophic shifts from simple to more complex – species rich and spatially structured – systems could contribute to expand our understanding of how nature works and improve our ability to anticipate the effects of global change on ecological systems.

1 Introduction

The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) recently estimated that approximately one million species are currently threatened with extinction. Meanwhile, the 2021 Intergovernmental Panel on Climate Change (IPCC) report highlights that, even under the most optimistic emissions scenario, we still have decades (at least) of warming ahead. As these and other stressors gradually increase, there is growing concern that many natural ecosystems may exhibit sudden, abrupt, and persistent collapses. While extreme environmental events, such as fires or hurricanes, can have significant, and sometimes irreversible, consequences for ecosystems, we are interested here in ecosystem responses that are much larger and faster that one would intuit from the driver of change. Evidence for these striking, non-linear ecosystem responses to incremental changes in conditions has accumulated from a range of experimental and natural systems, including desertification, eutrophication, the degradation of coral reefs and the collapses of fisheries [1–11]. One of the most pressing scientific challenges of our time is to predict where and when this possibility is likely to be realized [12].

Theoretically, these phenomena are described as ‘catastrophic shifts’ or ‘regime shifts’, which have been well studied using classical ecological models [3, 10, 13–15]. These models show that there are different ways in which a system may respond to gradual changes in external conditions. The response can be gradual, from something almost linear to something that can be highly nonlinear or even abrupt [16]. These latter responses may happen when an ecosystem has more than one possible stable state for the same range of conditions. The ecosystem can then be propelled from its current state to an alternative one, resulting in discrete, surprising changes that can be more or less easily reversed. Such catastrophic shifts between ecosystem states can happen because of a perturbation of the ecosystem state itself or when an environmental condition is changed beyond a threshold value, or ‘tipping point’.

Our current theory of these phenomena is limited to ‘simple’ models that either assume a) very few species, or b) unrealistic spatial settings. In other words, theoretical work on catastrophic shifts has so far largely focused on species-poor systems [3, 10, 13–15, 17] or on species-rich systems in which species interact with each other with a single interaction type (e.g. feeding or pollination) [18, 19]. Further, the vast majority of work has focused on isolated systems ignoring the spatial structure of the landscapes in which ecosystems are embedded. More specifically, there is a good understanding of how alternative stable states can emerge in simple settings but it is less understood how these dynamics occur when embedded in systems that have more realistic complex diversity in species, interaction types, and spatial structure. This means that, despite clear evidence that alternative stable states, catastrophic shifts, and ecological tipping points are possible in a range of ecosystems, we have no strong theory to predict which natural ecosystems on earth are most vulnerable to exhibiting rapid collapses in the context of global changes. This poor understanding of the conditions under which complex ecological systems may exhibit alternative stable states, and thereby catastrophic shifts and tipping points, strongly limits our ability to anticipate and manage natural systems.

Here, we argue that – if we want to predict which ecosystems are vulnerable and prioritize 'at risk' ecosystems before they collapse – current ecological theory on catastrophic shifts and tipping points needs to explicitly address species rich and spatially complex systems. In particular, we need to investigate if, when and how scaling up the current theory from simple – species poor and local – to more complex systems leads to possible emergent alternative ecosystem states as species, interactions or spatial complexity are incorporated. We review the current state of theoretical work and illustrate that these are pieces of a puzzle that still need to be assembled toward a more comprehensive framework of how complex systems can exhibit abrupt transitions to equip our societies to face the challenges to come.

2 Scale up to more complex systems: species diversity

The majority of theoretical studies on catastrophic shifts has focused on 'simple' models, that is, typically either considering a subset of the species of a community while ignoring the rest or lumping species into groups [3, 10, 13, 15, 20]. These models have highlighted early on the importance of reinforcing feedbacks for the emergence of alternative stable states and therefore possible catastrophic shifts between them [14, 15]. A reinforcing feedback occurs when species have positive effects on themselves. For example, in drylands, where water is often the most limiting resource, vegetation can improve local conditions for itself by improving water availability and thus creating a reinforcing feedback: when vegetation growth is increased, vegetation biomass increases, and more water becomes available for plants to grow. This stabilizes an ecosystem state where vegetation is present. However, the feedback loop can work the other way around: if vegetation is lost, for instance, due to perturbations, so that the amount of vegetation falls below a threshold, local conditions will degrade and prevent new vegetation to settle. The loss of vegetation reinforces itself, thereby stabilizing another possible ecosystem state with low or even no vegetation. In these models, a reinforcing feedback loop, often between a biotic and an abiotic component of the ecosystem, creates the possibility for alternative stable states, and therefore for tipping points and catastrophic shifts of the ecosystem.

Understanding the emergence of alternative stable states in relatively simple systems is very useful, especially for ecosystems in which a few strongly interacting species dominate, such as lakes or drylands [10] but what about other ecosystems? Ecological communities in nature are composed of the many species they host and of the network of interactions those species have with each other and with the environment. This raises the question of whether and how increased biotic complexity can allow or prevent the emergence of alternative stable states. Predicting the response of species-richer systems to changes is difficult because the response of the whole system does not only depend on the properties of the entities (the species) but also on the presence, type and strength of the interactions between species and on the way they are arranged, i.e. the structure of the interaction network [21–23]. Addressing the question of how the species interaction network impacts catastrophic shifts therefore requires scaling up our understanding from simple to species-richer systems. Although stability in general, and possible catastrophic shifts in particular, have been understudied in ecological networks [24, 25], some previous works have addressed those questions; We present their insights in what follows.

Large random species interaction networks

Gilpin and Case [26] already discussed in the 70s the theoretical possibility of several stable equilibria in multispecies competition models. Going further, using a modified version of a multi-species Lotka-Volterra model, van Nes and Scheffer [27] confirmed that alternative stable states commonly arise in complex communities that are randomly generated, in agreement with later studies [28]. This implies that such complex communities could occasionally exhibit abrupt responses to gradual environmental changes.

Structured species interaction networks

One shortcoming of the above discussed studies is that they do not take the structure of species interaction networks into account. Decades of work has shown that real ecological networks are far from random and that their structure matters for community dynamics, and in particular for stability (e.g. [21, 23, 29]). For example, food webs (i.e., ecological networks composed of feeding interactions) tend to be organized into compartments [29], that is, groups of species that interact preferentially with each other and less with the rest of the network. This organization in compartments contributes to the reduction of the spread of perturbations by containing them within the compartments [29]. These approaches have, however, largely overlooked the possibility of the emergence of alternative stable states at the network scale (but see examples below). Therefore, until recently, little was know about the species interaction network configurations that favor the emergence of alternative stable states and ecologically significant transitions in species-rich ecological networks.

Hints on underlying mechanisms

As previously mentioned, mathematical models have highlighted early on the importance of reinforcing feedbacks for the emergence of alternative stable states [14, 15]. In a complex network of species interactions, feedbacks are typically composed of a succession of interactions between species as well as between species and their abiotic environment, and the type of the feedback emerges from the interplay between all direct and indirect effects [30].

To investigate the mechanisms leading to alternative stable states in ecological networks, Karatayev et al. [19] studied a multispecies model of consumer-resource interactions with different types of feedbacks: specialized (species-specific feedbacks that occur between a given pair of species) or aggregate (which do not depend on the identity of the species).
They show that alternative stable states are more prevalent under aggregate than specialized feedbacks. Indeed, for species-specific feedbacks, variability among species may desynchronize their dynamics and potentially dissipate the feedback. Conversely, if all species experience the same mechanism (with e.g. the same threshold), this can lead to a synchronization of the feedbacks and the emergence of global tipping points.

In the case of species-specific feedbacks, a model of mutualistic plant-pollinator communities showed that pollinator populations can either collapse partially ('partial collapse') or simultaneously (all pollinator populations collapse simultaneously; 'whole community collapse') as the driver of population decline increases beyond a threshold [18]. The probability of having a single whole community collapse, instead of several partial collapses, is strongly influenced by the structure of the mutualistic networks (connectance and/or nestedness). Indeed, pollinators have direct negative effects on each other through competition, and they also can have indirect positive effects on each other when they pollinate the same plant. Pollinators that depend on the same plant species have increasingly strong positive net effects on each other as stress increases. Increased connectance and nestedness increase the fraction of mutualistic partners shared by pollinators and thereby favor the emergence of reinforcing feedback at the network scale. This means that in highly connected and/or nested networks, pollinators eventually collapse simultaneously as the stress level goes beyond a threshold.

In conclusion, these studies have provided key elements toward understanding the type of ecological mechanisms, and more specifically the structure of the species interaction networks, that can transform pairwise interactions into whole-system feedback that can promote the emergence of alternative stable states. However, how those results expand to other systems, other interaction types as well as to multi-interaction ecological networks is unknown. Therefore, we still lack a more general understanding of the network configurations that can lead to alternative stable states at the system scale, and whether transitions between these alternative stable states correspond to partial or whole collapses.

3 Scale up to more complex systems: space

Most studies discussed up to here have considered ecological systems in isolation, that is, only at one given location in space. However, ecosystems are typically embedded in complex landscapes within which exchanges of energy, materials, and organisms occur [31, 32]. Work on human-made networks (e.g., electricity and internet networks) has shown that the spread of failures can have drastically different, and even opposite, effects in isolated rather than in interdependent networks [33, 34]. In the same vein, a regime shift in one ecosystem of a landscape composed of several, connected ecosystems could trigger shifts in others and possibly lead to a cascade of shifts. If ecosystems exhibiting alternative stable states locally are spatially connected by the movements of species and fluxes of matter, what are the dynamical properties that emerge at the broad spatial scale, or 'meta'-scale? Are global tipping points possible in such spatially connected systems? Recent studies discussed in what follows have started exploring these questions. Note that we are here not interested in the links between spatial structure and tipping points *within* ecosystems (e.g. [17, 35, 36]) but in the role of the spatial connectivity *between* ecosystems.

Implicit space

Investigating the consequences of spatial flows between local systems for functioning at the meta-scale has been the focus of the metapopulation, metacommunity and metaecosystem theoretical frameworks [31]. Space has been found to be stabilizing, for instance in the context of stochastic metapopulations where times to extinctions increase due to the rescue of extinct patches via dispersal [37]. Similar results have been found in classical metacommunity studies (e.g., the patch dynamics paradigm; [38]) and have been scaled up to entire metaecosystems (e.g. [31, 32]). Regarding alternative stable states more specifically, classical work on metapopulation dynamics of the Glanville fritillary has shown that multiple equilibria can exist in connected ecological systems when the effects of dispersal on local dynamics are taken into account [39, 40]. However, these models are spatially implicit and therefore do not take into account the role of the way patches are located in space and connected to others. How the spatial structure of the patches themselves affect the possibility of alternative stable states at the meta-scale remains a largely unresolved question.

Spatially explicit meta-ecosystems

In analogy to species interaction network topology, one can ask how spatial network topology affects the spread of shifts in a setting where ecosystems are connected to each other in space by the movements of species and fluxes of matter. To answer this question, model studies have included spatial structure explicitly under two paradigms: *i)* models of continuous space are used to describe systems that lack clear spatial patches and where the habitat can be considered relatively homogeneous (see the example of Lake Veluwe in [41]), and *ii)* models of discrete space that are better suited to discontinuous habitats with clear patches connected by dispersal of individuals and flow of resources.

Continuous space

Let's imagine an ecosystem which has two stable states locally. Studies have investigated how local shifts can spread when such ecosystems are connected in continuous space. They have found that the most stable of the two stable states often dominates over the other: a local shift from the dominant state recovers, while shifts to the dominant state spread through space at a constant speed ('travelling wave') [41, 42]. The whole system is generally not expected to exhibit 'spatial bistability' (i.e. the coexistence of the two stable states in space) in a continuous habitat. Because of that, the whole system is expected to exhibit sharp transitions between a fully occupied state and an empty state (i.e. 'regional bistability'). Moreover, hysteresis is expected to be largely reduced at the landscape scale [41].

Discrete space

Because the spatially continuous view can be difficult to analyze mathematically and is often more appropriate for relatively small spatial scales, an option is to consider landscapes as discrete patches connected to each other by fluxes. Such discrete systems, modeled in the form of lines or grids, have been found to behave in a similar way as continuous ones when dispersal is strong: a local shift to the dominant state spreads from patch to patch in a domino effect [42, 43]. Here again, regional scale hysteresis mostly disappears if dispersal is strong. However, as dispersal [42] or flushing rates in aquatic systems [43] decrease, the speed of the travelling wave decreases and can eventually come to a halt (so-called 'pinning' phenomenon). In that case, alternative stable states can coexist in a landscape for intermediate environmental conditions, which can smooth the transition at the regional scale.

Both in discrete and continuous space, several mechanisms have been found to smooth the landscape-scale transitions between the fully occupied and the empty state. Demographic stochasticity [44], spatial heterogeneity in environmental conditions [44, 45] or in dispersal rates [41] facilitate spatial bistability and smooth large scale transitions.

We thus have a relatively good understanding of the whole-system dynamics of spatially connected ecosystems with locally bistable dynamics when the connections between the local systems are simplified to be along a line or a 2-D grid. The whole system will then only have homogeneous stable states (fully empty and fully occupied) and exhibit sharp transitions between them. However, regional bistability and hysteresis being largely reduced, these shifts cannot usually be called catastrophic shifts.

Increasing spatial complexity

As previously mentioned, for practical reasons, studies have so far focused on simplified settings in terms of how ecosystems are connected to each other in space. Real landscapes, however, are discontinuous, heterogeneous and have emergent properties — *e.g.*, terrestrial populations usually show emergent modularity [46] and riverine systems are dendritic [47]. Importantly, the structure of real landscapes have been shown to affect ecological outcomes [48–50]. Ignoring these impacts is an important shortcoming of the current state of the literature as the properties of such habitats — e.g. the heterogeneity in connectivity resulting from local barriers to dispersal — may change how local bistability affects regional scale dynamics and equilibria [41, 45].

Recently, Saade et al. [51] have started to tackle this issue by investigating the landscape-scale stability of more complex discrete landscapes. Comparing the commonly assumed linear (1-D) and grid-like (2-D) landscapes as well as more realistic networks (reflecting riverine and terrestrial systems), they find that local shifts can induce a landscape-scale shift through a domino effect across all landscapes structures. However, the position of landscape-scale tipping points and the extent of hysteresis (*i.e.*, the distance between the degradation and restoration tipping points) is very sensitive to the landscape structure. The reduction of hysteresis documented by Keitt et al. [42] and Hilt et al. [43] is restricted only to landscapes with very low connectivity such as 1-dimensional linear landscapes and dendritic (riverine) networks. Landscapes with a higher connectivity (2-D grids and terrestrial systems) exhibit landscape-scale bistability with a pronounced hysteresis. Moreover, the commonly used linear (1-D) and grid-like (2-D) system do not necessarily reflect the behaviour of more realistic landscapes structures, as 1-D linear systems consistently exhibit smaller hysteresis and 2-D grids consistently exhibit larger hysteresis than more realistic networks. This result may be explained by the fractal dimension of the network. Since the position of landscape-scale tipping points dictates how easy it is to induce a landscape degradation or restoration, we should be wary of overly simplified spatial structure and, when possible, should prefer realistic network structures to study the stability of spatial systems. In the future, one way to link more general theoretical results to real biological systems could be to study explicitly the impact of network properties (*e.g.*, connectivity, modularity, link distribution...) on landscape-scale stability.

In conclusion, ecological systems quasi universally show spatial structure. Existing work has shown that alternative stable states are possible in spatially structured systems. Yet, because most models so far rely on simplified descriptions of space (either implicit, 1-D or grid-like), we don't know how the results may change in the case of more realistic spatial structure. A more explicit inclusion of spatial complexity, meaning the spatial network topology, could help understand when and how this level of complexity contributes to alternative stable states and possible shifts at the meta-scale. It is important to note, however, that studying systems at increasingly larger spatial scales raises the question of whether the environmental conditions are still relatively homogeneous at the scale considered. The existence of alternative stable states, indeed, requires that such states (e.g., species configurations) exist under the same set of environmental conditions, an assumption that becomes less and less likely to hold as scale increases.

4 Opportunities to advance understanding

Both, in the context of biotic interactions and spatial structure, we have argued so far that the current ecological theory of alternative stable states and catastrophic shifts lacks aspects of complexity which are worth exploring. At the same time, complex models become very quickly intractable as the number of dimensions and parameters grow, making it difficult to adequately describe systems with more than three or four interacting components. Yet, perhaps ironically, more complex models can reveal emergent phenomena which constrain system behavior and simplify predictions in ways that are impossible to see with simpler models [52–54]. Therefore, identifying key dimensions of ecological complexity that are lacking in the current theory of tipping points may reveal opportunities to more simply predict when and where they are likely to occur in real-world ecosystems. We next identify a few promising directions in which progress could be made to help get a better understanding of the emergence of shifts in complex ecological systems.

Incorporating the diversity of interaction types

Ecological network studies have so far typically investigated a single interaction at a time, e.g. food webs composed of feeding interactions [21, 22] or mutualistic networks composed of plant-pollinator interactions [23], for example. Yet, in natural communities, species depend on and influence each other in multiple ways: they eat each other, compete for nutrients, light and space, fight for refuges, habitats or common prey, and provide habitat and protection to others [30, 55]. In the last few years, there has been increasing recognition about the need to investigate the consequences of the coexistence of multiple interaction types in nature, i.e. describe ecological communities as 'multi-layer' ecological networks, in which each layer contains information about one type of interactions that link the species of the community [30, 56, 57].

Dynamical models have started investigating such multi-interactions ecological networks [30, 56, 58, 59], showing that the presence, the relative abundance and the structure of the different interaction types can affect our fundamental understanding of how ecological systems work (e.g. [30, 56, 58]). Altogether, these studies suggest that incorporating the diversity of interactions in ecological theory is a worthwhile effort [57]. There is, however, currently no work that we know of about alternative stable states and their implications for the responses of multi-layer ecological systems to environmental changes.

Measuring the resilience of complex systems

The concepts of stability and resilience have received considerable attention in the ecological literature for decades. As originally defined by Holling in 1973, the term resilience was introduced to specifically refer to ecological systems that can exhibit alternative stable states [14]. The concept, however, has faced difficulties in estimating it in real systems [60].

In the same was as the stability of ecological communities has been estimated in a variety of ways using many different metrics [24, 25, 61], this is also true for resilience and more generally for metrics related to catastrophic shifts [62]. This multiplicity of metrics used to quantify the concepts of stability and resilience in ecological studies raises the question of how the different metrics relate to each other [24]. A better understanding of these relationships could help us identify how many and which metrics need to be measured in natural systems [24, 25, 63]. This is especially true for metrics related to abrupt transitions for which we need to understand the relations between each other but also with other stability metrics [62].

As stressed in Carpenter et al. [60], when thinking about the resilience of complex systems, it is not only a matter of deciding on a metric to measure it but also of specifying the ‘resilience *of* what *to* what’. It is indeed important to clarify on what system state resilience is measured (resilience *of* what) as well as the perturbations that are considered (resilience *to* what). Furthermore, one needs to decide on a time period and particular spatial scale since resilience can vary depending on the spatial and temporal scale at which it is measured.

Altogether, despite recent progress, there are still no clear guidelines on how to measure (with which metrics, at what scale and at what level of organization, e.g. species or community) the overall stability and resilience of ecological systems [24, 25]. The concept of resilience has been very useful so far in thinking about ecological systems and their responses to changes, but a more measurable, operational definition of resilience could provide important insights and practical applications in better understanding, quantifying and eventually possibly mapping ecosystem resilience [60].

Predicting the resilience of complex systems: early warning signals

Important changes in stability, especially abrupt ones, are notably difficult to predict. Generic indicators (so-called ‘early-warning signals’) have been proposed in the literature [64]. They are based on a phenomenon referred to as critical slowing down, which states that a disturbed system needs more time to recover when it is closer to a shift, i.e. it becomes slower and therefore less resilient [65]. Signatures of this slowing down can be detected in the temporal or spatial dynamics of ecosystems (increase in recovery time, temporal variance, autocorrelation and skewness of a variable used to quantify the ecosystem’s state, such as total biomass) [64]. Therefore, using temporal or spatial data of a given ecosystem, we should be able to detect whether the system is losing resilience.

The phenomenon of critical slowing down seems to be universal and occurs when any dynamical system approaches a transition. In fact, mathematically, the early warning signals are expected to work when a dynamical system approaches any kind of bifurcation, even when there is a change in stability that is not technically a bifurcation [16]. These signals are therefore generic, as they operate in principle independently of the specific mechanism responsible for the change of resilience, making their potential scope of application very broad. While their generality makes them very promising, it also means that they are not specific to catastrophic shifts [16].

Early-warning signals have been shown to successfully announce a loss of resilience in different models and in controlled laboratory conditions (e.g. [6, 7, 66]). Although more limited in numbers, manipulative field experiments have also demonstrated their ability to test model predictions, identify thresholds and evaluate early warning signals under real-world conditions [8, 67].

Success in real-world observational time series data has, however, been more mitigated [68, 69]. This highlights that we need to better understand the conditions under which early-warning signals work or fail. In particular, because theoretical work on early-warning signals has mainly been based on local models with one or a few species so far, it is unclear how reliable these indicators are in systems with multiple species, locations in space and with multiple interaction types. It is also necessary to understand at which organizational level these indicators should be measured (species or community) and on which variable (e.g. biomass, species number). Investigating this question formally in model ecological communities, Patterson et al. [70] show that the reliability of early-warning signals depends on the species observed as well as on the type of ecological interaction considered. For example, the relevant species to monitor to maximize early-warning signal detection is not the same in a consumer-ressource than in a mutualistic system. Another important limitation of the current ecological theory of catastrophic shifts is that it describes ecosystems at equilibria, which is probably rarely verified in nature [71, 72]. Regime shifts can be caused by non-equilibrium phenomena and early-warning signals are not expected to apply in these cases [72, 73].

Simplifying complexity

Adding new aspects of complexity in current theory comes with practical challenges but there are promising avenues to overcome this challenge. Indeed, recent papers have tried to overcome this issue by describing high-dimensional systems using a few quantities only. For instance, Gao et al. [54] suggested a method of using mean-field approximations to reduce n-dimensional mutualistic networks to a single dimension (the effective average density) and a single control parameter describing structure of the network. This allows getting analytical results on these systems, such as predicting the equilibria from an aggregate of three network metrics (link density, heterogeneity and symmetry). In particular they show how to apply this framework to real ecological networks (plant-pollinator) and gene regulatory networks (from *E. coli* and *S. cerevisiae*), and how to detect if network modifications will trigger a shift.

More recent papers generalized this approach by using spectral analysis of the interaction network to make it applicable to non-random networks [74] and to heterogeneous networks (*i.e.*, where different nodes can have different types of dynamics), providing us with very promising tools for the study of mutualistic interaction networks.

Barbier et al. [53] proposed another reduction method inspired from statistical physics to deal with mutualistic networks, but also with predation and competition networks. It uses aggregate parameters of the interaction network (*i.e.*, the average and variance of the species growth rates, carrying capacities and interaction strengths) to summarize a n-dimensional system in a single stochastic dynamical equation. This single equation predicts aggregate properties of the system, such as the total biomass, the fraction of surviving species, the Simpson's diversity or the temporal variability of the system. While it is best suited for disordered networks (*e.g.*, networks where species associations are seemingly random) with a single interaction type, the authors suggest that extensions of the approach are possible to deal with more structured networks and more than one interaction type. They illustrate this by reducing a strongly compartmentalized bipartite networks (*i.e.*, with competition interactions within and mutualistic interactions between compartments) to two stochastic equations, each corresponding to one compartment. While this method still requires further investigations to determine its applicability, it is extremely promising to simplify the study of complex systems, especially if a more general framework emerges to deal with multi-interaction networks.

Another issue when studying ecological systems is that they are often 'networks of networks': a community of species (interaction network) lives in and connects through space a set of inhabitable locations (spatial network). The interactions between these two layers can give rise to complex dynamics such as oscillations and pattern formation [75, 76] analogous to Turing-patterns in reaction-diffusion. These dynamics are unexpected from the study of the interaction network alone and can lead to alternative stable states with abrupt transitions between them when the spatial network topology is altered [75]. Brechtel et al. [77] proposed a method that uses the master stability function [78] of the spatial network to study the stability of such systems. It allows to determine whether a stable state determined from the interaction network alone can form an homogeneous stable state in a given spatial network or if complex pattern formation will arise. It also allows to determine if a modification of the spatial network can result in pattern formation. This method could prove very useful in studying the stability patterns arising of 'networks of networks', and the author suggest other types of systems where it could be applied such as cell biology (where gene regulatory networks determining the state of each cell is nested in the cell interaction network in a tissue).

Innovative methods are also available to reconstruct the whole landscape of possible states of a complex system [79, 80]. Chemical organization theory relies on discretizing the description of species interactions in a way that resembles chemical reactions. Once this is done, the approach provides a set of analytical tools which allows to reconstruct the whole landscape of possible states of the systems and transitions among these states. Obtaining this landscape is very powerful because it provides an overview of all possible states (and their species composition) but also of the possible (and the probability) of transitions between the different states. This shows how a given community is most likely to change when subject to perturbations but also the paths it will take to get there.

Integrating different approaches: beyond modeling

We have so far focused this section on modeling, but progress in understanding catastrophic shifts also requires a better integration of models with observational data and experiments. Although pioneering studies have reported very promising results (see previous section 'Predicting the resilience of complex systems: early warning signals'; [6, 7, 66, 68, 69]), experimental work and particularly manipulative field experiments are largely absent from the catastrophic shifts literature. They, however, have a key role to play in testing predictions from the theory, assess early-warning signals in real world conditions and foster our understanding of the mechanisms behind the reinforcing feedbacks.

In conclusion, we have identified key points of improvement of current catastrophic shift theory in ecology. These are mainly due to the lack of biotic and spatial complexity considered in classical models. We advocate for a multilayer-network perspective, taking into account networks of networks ranging from species interactions to networks of habitats in landscapes. This will allow us to take into account network topology as an important modulator of catastrophic shifts and to understand how disturbances may propagate in realistically complex landscapes of realistically complex ecosystems. While this step forward intrinsically embraces complexity, this does not need to come at a cost of tractability of underlying models. Indeed, highly promising avenues of dimensionality reduction have the potential to facilitate models and theory development. Of course, this list of improvement points is not exhaustive. Taking the influence of multiple stressors and their interactions [81] as well as the importance of stochasticity and transient dynamics [71] into account are examples of further research avenues.

5 Conclusion

Despite the urgency and magnitude of global change threats to humanity's life support system, there is no synthetic, empirically-grounded body of ecological theory to predict which ecosystems and ecological communities are more likely to abruptly shifts in response to upcoming changes. We need to fill that gap. Mathematical models can help us identify and understand the conditions under which species rich, interaction rich and spatially structured ecosystems can exhibit alternative stable states possibly leading to ecologically important catastrophic shifts between them.

Addressing that question is however not trivial. Indeed, the current state of the literature only provides pieces of the puzzle. On the one hand, alternative stable states seem to be a robust phenomenon in large random ecological networks [27]. On the other hand, studies have showed that the structure of real ecological networks deviate from random ones in ways that tends to make them more robust than expected by chance. These studies have however rarely looked at the emergence of alternative stable states. So far, it therefore remains unclear how the structure of real ecological communities constrains (or enables) the emergence of reinforcing feedback loops and therefore possible alternative stable states and associated shifts in species-rich communities.

In a spatial context, where different ecological systems are connected to each other by movement of organisms or matter, alternative stable states at the whole system scale have been shown to be theoretically possible. However, the degree to which biotic complexity amplifies, or dampens, these transitions remains unknown. Moreover, space has usually been described in a very simplified way ignoring important aspects of topology. It is therefore unclear whether and how the spatial coupling between ecological systems may allow for (or prevent) abrupt transitions at the meta-scale.

Making progress along these lines is not only crucial for our basic knowledge of natural systems, but also urgent for the formulation of environmental policies and the prioritization of management efforts on a landscape. We need to understand which of these different aspects of complexity matters for predicting the dynamics of which ecosystems. Expanding the theory of alternative stable states and tipping points toward more complex systems could provide useful tools to map the fragility of ecosystems broadly and to monitor changes in their resilience, which will help manage ecosystems by better anticipating the effects of upcoming perturbations.

This new understanding and indicators could also find applications in a number of complex systems outside of ecology (see Table 1 of Brummitt et al. [34] for an overview). Because of the current state of globalization, complex interdependent networks, involving multiple interaction types between their components as well as several subsystems, are at the core of our modern society as can be seen in the examples of power grids [82], financial systems [83, 84], transportation networks [85] or the internet [86, 87]. A major challenge is the prediction and control of sudden changes (failures) propagating among coupled subsystems, as seen in episodes of cascading electrical blackouts [33], systemic financial crises [84], contagious currency crises [88] or political uprising [89–91].

Understanding stability of ecological systems is a first step in that direction and the knowledge accumulated could prove to be valuable to numerous multi-layer networks outside of ecology.

6 Acknowledgements

SK was supported by the Alexander von Humboldt foundation.

References

[1] Mark Westoby, Brian Walker, and Imanuel Noy-Meir. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management*, 42(4):266–274, 1989. URL `http://www.jstor.org/stable/3899492`.

[2] Ludwig D. Carpenter, S.R. and W.A. Brock. Management of eutrophication for lakes subject to potentially irreversible change. *Ecological Applications*, 9:751–771, 1999.

[3] M. Scheffer, S. Carpenter, J.A. Foley, C. Folke, and B. Walker. Catastrophic shifts in ecosystems. *Nature*, 413:591–596, 2001.

[4] S. Kéfi, M. Rietkerk, C.L. Alados, Y. Pueyo, V.P. Papanastasis, A. ElAich, and P.C. de Ruiter. Spatial vegetation patterns and imminent desertification in mediterranean arid ecosystems. *Nature*, 449:213–217, 2007. doi: 10.1038/nature06111.

[5] Peter J. Mumby, Alan Hastings, and Helen J. Edwards. Thresholds and the resilience of caribbean coral reefs. *Nature*, 450(7166):98–101, 2007.

[6] L. Dai, K.S. Korolev, and J. Gore. Slower recovery in space before collapse of connected populations. *Nature*, 496:355–358, 2013.

[7] J.M. Drake and B.D. Griffen. Early warning signals of extinction in deteriorating environments. *Nature*, 467:456–459, 09 2010. URL `http://dx.doi.org/10.1038/nature09389`.

[8] S.R. Carpenter, J.J. Cole, M.L. Pace, R. Batt, W.A. Brock, T. Cline, J. Coloso, J.R. Hodgson, J.F. Kitchell, D.A. Seekell, L. Smith, and B. Weidel. Early warnings of regime shifts: A whole–ecosystem experiment. *Science*, 332(6033):1079–1082, 2011. ISSN 0036-8075. doi: 10.1126/science.1203672.

[9] K.N. Suding, K.L. Gross, and G.R. Houseman. Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution*, 19(1):46–53, 2004. ISSN 0169-5347. doi: https://doi.org/10.1016/j.tree.2003.10.005.

[10] P. Petraitis. *Multiple stable states in natural ecosystems.* Oxford University Press, 2013.

[11] A.C. Newton. *Ecosystem collapse and recovery.* Cambridge University Press, 2021.

[12] Timothy M. Lenton. Tipping positive change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 375(1794):20190123, 2020.

[13] Imanuel Noy-Meir. Stability of grazing systems: An application of predator–prey graphs. *Journal of Ecology*, 63(2):459–481, 1975. ISSN 00220477, 13652745.

[14] C.S. Holling. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, 4:1–23, 1973. doi: https://doi.org/10.1146/annurev.es.04.110173.000245.

[15] R.M. May. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature*, 269:471–477, 1977. doi: 10.1038/269471a0.

[16] S. Kéfi, V. Dakos, M. Scheffer, E.H. Van Nes, and M. Rietkerk. Early warning signals also precede non–catastrophic transitions. *Oikos*, 122(5):641–648, 2013. doi: 10.1111/j.1600-0706.2012.20838.x.

[17] S. Kéfi, M. Rietkerk, M. van Baalen, and M. Loreau. Local facilitation, bistability and transitions in arid ecosystems. *Theoretical Population Biology*, 71(3):367–379, 2007. ISSN 0040-5809. doi: https://doi.org/10.1016/j.tpb.2006.09.003.

[18] J. Jelle Lever, Egbert H. van Nes, Marten Scheffer, and Jordi Bascompte. The sudden collapse of pollinator communities. *Ecology Letters*, 17(3):350–359, 2014.

[19] Vadim A. Karatayev, Marissa L. Baskett, and Egbert H. van Nes. Quantifying the relevance of alternative stable states in many-species food webs. *bioRxiv*, 2021.

[20] M. Rietkerk and J. Van de Koppel. Alternate stable states and threshold effects in semi–arid grazing systems. *Oikos*, 79(1):69–76, 1997. doi: doi:10.2307/3546091.

[21] P.C. de Ruiter, A.M. Neutel, and J.C. Moore. Energetics, patterns of interaction strengths, and stability in real ecosystems. *Science*, 269:1257–1260, 1995.

[22] Jennifer A. Dunne, Richard J. Williams, and Neo D. Martinez. Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters*, 5(4): 558–567, 2002.

[23] J. Bascompte, P. Jordano, C.J. Melián, and J.M. Olesen. The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences*, 100(16):9383–9387, 2003. doi: 10.1073/pnas.1633576100.

[24] I. Donohue, O.L. Petchey, J.M. Montoya, A.L. Jackson, L. McNally, M. Viana, K. Healy, M. Lurgi, N.E. O'Connor, M.C. Emmerson, and M. Gessner. On the dimensionality of ecological stability. *Ecology Letters*, 16(4):421–429, 2013. doi: 10.1111/ele.12086.

[25] S. Kéfi, V. Domínguez-García, I. Donohue, C. Fontaine, E. Thébault, and V.Dakos. Advancing our understanding of ecological stability. *Ecology Letters*, in press, 2019. doi: doi:10.1111/ele.13340.

[26] M. Gilpin and T. Case. Multiple domains of attraction in competition communities. *Nature*, 261:40–42, 1976.

[27] Egbert H. van Nes and Marten Scheffer. Large species shifts triggered by small forces. *The American Naturalist*, 164(2):255–266, 2004.

[28] G. Biroli, G. Bunin, and C. Cammarota. Marginally stable equilibria in critical ecosystems. *New Journal of Physics*, 20(8):083051, 2018.

[29] Daniel B. Stouffer and Jordi Bascompte. Compartmentalization increases food-web persistence. *Proceedings of the National Academy of Sciences*, 108(9):3648–3652, 2011.

[30] S. Kéfi, V. Miele, E.A. Wieters, S.A. Navarrete, and E.L. Berlow. How structured is the entangled bank? the surprisingly simple organization of multiplex ecological networks leads to increased persistence and resilience. *PLoS Biology*, 14(8):e1002527, 2016. doi: 10.1371/journal.pbio.100252.

[31] Michel Loreau, Nicolas Mouquet, and Robert D. Holt. Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. *Ecology Letters*, 6(8):673–679, 2003.

[32] Isabelle Gounand, Eric Harvey, Chelsea J. Little, and Florian Altermatt. Meta-ecosystems 2.0: Rooting the theory into the field. *Trends in Ecology Evolution*, 33(1):36–46, 2018.

[33] Sergey V Buldyrev, Roni Parshani, Gerald Paul, H Eugene Stanley, and Shlomo Havlin. Catastrophic cascade of failures in interdependent networks. *Nature*, 464(7291):1025–1028, 2010.

[34] Charles D Brummitt, George Barnett, and Raissa M D'Souza. Coupled catastrophes: sudden shifts cascade and hop among interdependent systems. *Journal of The Royal Society Interface*, 12(112):20150712, 2015.

[35] M. Rietkerk, M.C. Boerlijst, F. van Langevelde, R. HilleRisLambers, J. van de Koppel, L. Kumar, H.H.T. Prins, and A.M. de Roos. Self–organization of vegetation in arid ecosystems. *The American Naturalist*, 160(4):524–530, 2002. doi: 10.1086/342078.

[36] J. van de Koppel, J.C. Gascoigne, G. Theraulaz, M. Rietkerk, W.M. Mooij, and P.M.J. Herman. Experimental evidence for spatial self–organization and its emergent effects in mussel bed ecosystems. *Science*, 322(5902):739–742, 2008. ISSN 0036-8075. doi: 10.1126/science.1163952.

[37] Ilkka Hanski. *Metapopulation Ecology.* Oxford University Press, Oxford, 1999.

[38] M. A. Leibold, M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, 7(7):601–613, 2004.

[39] Ilkka Hanski, Juha Pöyry, Timo Pakkala, and Mikko Kuussaari. Multiple equilibria in metapopulation dynamics. *Nature*, 377(6550):618–621, 1995.

[40] Mats Gyllenberg and Ilkka Hanski. Single-species metapopulation dynamics: A structured model. *Theoretical Population Biology*, 42(1):35–61, 1992.

[41] Ingrid A van de Leemput, Egbert H van Nes, and Marten Scheffer. Resilience of alternative states in spatially extended ecosystems. *PloS one*, 10(2):e0116859, 2015.

[42] Timothy H Keitt, Mark A Lewis, and Robert D Holt. Allee effects, invasion pinning, and species' borders. *The American Naturalist*, 157(2):203–216, 2001.

[43] Sabine Hilt, Jan Köhler, Hans-Peter Kozerski, Egbert H van Nes, and Marten Scheffer. Abrupt regime shifts in space and time along rivers and connected lake systems. *Oikos*, 120(5):766–775, 2011.

[44] Paula Villa Martín, Juan A Bonachela, Simon A Levin, and Miguel A Muñoz. Eluding catastrophic shifts. *Proceedings of the National Academy of Sciences*, 112(15):E1828–E1836, 2015.

[45] Egbert H van Nes and Marten Scheffer. Implications of spatial heterogeneity for catastrophic regime shifts in ecosystems. *Ecology*, 86(7):1797–1807, 2005.

[46] Luis J Gilarranz. Generic emergence of modularity in spatial networks. *Scientific reports*, 10 (1):1–8, 2020.

[47] Luca Carraro, Enrico Bertuzzo, Emanuel A Fronhofer, Reinhard Furrer, Isabelle Gounand, Andrea Rinaldo, and Florian Altermatt. Generation and application of river network analogues for use in ecology and evolution. *Ecology and Evolution*, 10(14):7537–7550, 2020.

[48] Luis J Gilarranz, Bronwyn Rayfield, Gustavo Liñán-Cembrano, Jordi Bascompte, and Andrew Gonzalez. Effects of network modularity on the spread of perturbation impact in experimental metapopulations. *Science*, 357(6347):199–201, 2017.

[49] Florian Altermatt and Emanuel A Fronhofer. Dispersal in dendritic networks: Ecological consequences on the spatial distribution of population densities. *Freshwater Biology*, 63(1): 22–32, 2018.

[50] Francesco Carrara, Florian Altermatt, Ignacio Rodriguez-Iturbe, and Andrea Rinaldo. Dendritic connectivity controls biodiversity patterns in experimental metacommunities. *Proceedings of the National Academy of Sciences*, 109(15):5761–5766, 2012.

[51] Camille Saade, Emanuel A Fronhofer, Benoît Pichon, and Sonia Kéfi. Landscape structure and dispersal rate drive large scale catastrophic shifts in spatially explicit metapopulations. 2021.

[52] Eric L. Berlow, Jennifer A. Dunne, Neo D. Martinez, Philip B. Stark, Richard J. Williams, and Ulrich Brose. Simple prediction of interaction strengths in complex food webs. *Proceedings of the National Academy of Sciences*, 106(1):187–191, 2009.

[53] Matthieu Barbier, Jean-François Arnoldi, Guy Bunin, and Michel Loreau. Generic assembly patterns in complex ecological communities. *Proceedings of the National Academy of Sciences*, 115(9):2156–2161, 2018.

[54] Jianxi Gao, Baruch Barzel, and Albert-László Barabási. Universal resilience patterns in complex networks. *Nature*, 530(7590):307–312, 2016.

[55] S. Kéfi, Eric L. Berlow, Evie A. Wieters, Lucas N. Joppa, Spencer A. Wood, Ulrich Brose, and Sergio A. Navarrete. Network structure beyond food webs: mapping non-trophic and trophic interactions on chilean rocky shores. *Ecology*, 96:291–303, January 2015. ISSN 0012-9658. doi: 10.1890/13-1424.1. URL `http://www.esajournals.org/doi/abs/10.1890/13-1424.1`.

[56] S. Kéfi, E.L. Berlow, E. a. Wieters, S. Navarrete, O.L. Petchey, S. Wood, A. Boit, L.N. Joppa, K.D. Lafferty, R.J. Williams, N.D. Martinez, B. Menge, C. Blanchette, A.C. Iles, and U. Brose. More than a meal: integrating non-feeding interactions into food webs. *Ecology Letters*, pages 291–300, February 2012. ISSN 1461023X. doi: 10.1111/j.1461-0248.2011.01732.x. URL `http://doi.wiley.com/10.1111/j.1461-0248.2011.01732.x`.

[57] S. Pilosof, M.A. Porter, M. Pascual, and S. Kéfi. The multilayer nature of ecological networks. *Nature Ecology & Evolution*, 1:0101, 2017.

[58] C.J. Melián, J. Bascompte, P. Jordano, and V. Krivan. Diversity in a complex ecological network with two interaction types. *Oikos*, 118(1):122–130, 2009.

[59] A. Mougi and M. Kondoh. Diversity of interaction types and ecological community stability. *Science*, 337(6092):349–351, 2012. ISSN 0036-8075. doi: 10.1126/science.1220529. URL `http://science.sciencemag.org/content/337/6092/349`.

[60] Steve Carpenter, Brian Walker, J. Marty Anderies, and Nick Abel. From metaphor to measurement: Resilience of what to what? *Ecosystems*, 4(8):765–781, dec 2001. ISSN 1432-9840. doi: 10.1007/s10021-001-0045-9.

[61] Stuart L. Pimm. The complexity and stability of ecosystems. *Nature*, 307:321–326, 1984.

[62] V. Dakos and S. Kéfi. Ecological resilience: what to measure and how. *Environmental Research Letters*, 17(4):43003, 2022.

[63] V. Dominguez-Garcia, V. Dakos, and S. Kéfi. Unveiling dimensions of stability in complex ecological networks. *PNAS*, 51(116):25714–25720, 2014.

[64] M. Scheffer, J. Bascompte, W.A. Brock, V. Brovkin, S.R. Carpenter, V. Dakos, H. Held, E.H. van Nes, M. Rietkerk, and G. Sugihara. Early–warning signals for critical transitions. *Nature*, 461:53–59, 2009. URL `http://dx.doi.org/10.1038/nature08227`.

[65] C. Wissel. A universal law of the characteristic return time near thresholds. *Oecologia*, 65(1): 101–105, 1984. doi: 10.1007/BF00384470.

[66] A.J. Veraart, E.J. Faassen, V. Dakos, E.H. van Nes, M. Lürling, and M. Scheffer. Recovery rates reflect distance to a tipping point in a living system. *Nature*, 481:357–359, 2012.

[67] Luca Rindi, Martina Dal Bello, Lei Dai, Jeff Gore, and Lisandro Benedetti-Cecchi. Direct observation of increasing recovery length before collapse of a marine benthic ecosystem. *Nature Ecology & Evolution*, 1(6):0153, 2017.

[68] S.J. Burthe, P.A. Henrys, E.B. Mackay, B.M. Spears, R. Campbell, L. Carvalho, B. Dudley, I.D.M. Gunn, D.G. Johns, S.C. Maberly, L. May, M.A. Newell, S. Wanless, I.J. Winfield, S.J. Thackeray, F. Daunt, and C. Allen. Do early warning indicators consistently predict nonlinear change in long–term ecological data? *Journal of Applied Ecology*, 53(3):666–676, 2015. doi: 10.1111/1365-2664.12519.

[69] A.S. Gsell, U. Scharfenberger, D. Özkundakci, A. Walters, L.-A. Hansson, A.B.G. Janssen, P. Nõges, P.C. Reid, D.E. Schindler, E. Van Donk, V. Dakos, and R. Adrian. Evaluating early-warning indicators of critical transitions in natural aquatic ecosystems. *Proceedings of the National Academy of Sciences*, 113(50):E8089–E8095, 2016. ISSN 0027-8424. doi: 10.1073/pnas.1608242113.

[70] Amy Chian Patterson, Alexander G. Strang, and Karen C. Abbott. When and where we can expect to see early warning signals in multispecies systems approaching tipping points: Insights from theory. *The American Naturalist*, 198(1):E12–E26, 2021.

[71] Alan Hastings, Karen C. Abbott, Kim Cuddington, Tessa Francis, Gabriel Gellner, Ying-Cheng Lai, Andrew Morozov, Sergei Petrovskii, Katherine Scranton, and Mary Lou Zeeman. Transient phenomena in ecology. *Science*, 361(6406):eaat6412, 2018.

[72] Karen C. Abbott. Non-equilibrium dynamics and stochastic processes. In Kevin S. McCann and Gabriel Gellner, editors, *Theoretical Ecology: concepts and applications*, chapter 4, pages 40–52. Oxford University Press, Oxford, 2020.

[73] C. Boettiger and A. Hastings. No early warning signals for stochastic transitions: insights from large deviation theory. *Proceedings of the Royal Society of London B: Biological Sciences*, 280(1766), 2013. ISSN 0962-8452. doi: 10.1098/rspb.2013.1372.

[74] Edward Laurence, Nicolas Doyon, Louis J Dubé, and Patrick Desrosiers. Spectral dimension reduction of complex dynamical networks. *Physical Review X*, 9(1):011042, 2019.

[75] Hiroya Nakao and Alexander S Mikhailov. Turing patterns in network-organized activator–inhibitor systems. *Nature Physics*, 6(7):544–550, 2010.

[76] Lucas D Fernandes and MAM De Aguiar. Turing patterns and apparent competition in predator-prey food webs on networks. *Physical Review E*, 86(5):056203, 2012.

[77] Andreas Brechtel, Philipp Gramlich, Daniel Ritterskamp, Barbara Drossel, and Thilo Gross. Master stability functions reveal diffusion-driven pattern formation in networks. *Physical Review E*, 97(3):032307, 2018.

[78] Louis M Pecora and Thomas L Carroll. Master stability functions for synchronized coupled systems. *Physical review letters*, 80(10):2109, 1998.

[79] C. Gaucherel and F. Pommereau. Using discrete systems to exhaustively characterize the dynamics of an integrated ecosystem. *Methods in Ecology and Evolution*, 10:1615–1627, 2019.

[80] T. Veloz. The complexity?stability debate, chemical organization theory, and the identification of non-classical structures in ecology. *Foundations of science*, early online, 2019.

[81] James A. Orr, Rolf D. Vinebrooke, Michelle C. Jackson, Kristy J. Kroeker, Rebecca L. Kordas, Chrystal Mantyka-Pringle, Paul J. Van den Brink, Frederik De Laender, Robby Stoks, Martin Holmstrup, Christoph D. Matthaei, Wendy A. Monk, Marcin R. Penk, Sebastian Leuzinger, Ralf B. Schäfer, and Jeremy J. Piggott. Towards a unified study of multiple stressors: divisions and common goals across research disciplines. *Proc. R. Soc. B.*, 287(1926):20200421, 2020.

[82] Paul Hines, Seth Blumsack, E Cotilla Sanchez, and Clayton Barrows. The topological and electrical structure of power grids. In *2010 43rd Hawaii International Conference on System Sciences*, pages 1–10. IEEE, 2010.

[83] Thomas Ho and Anthony Saunders. A catastrophe model of bank failure. *The Journal of Finance*, 35(5):1189–1207, 1980.

[84] Kartik Anand, Prasanna Gai, and Matteo Marsili. Rollover risk, network structure and systemic financial crises. *Journal of Economic Dynamics and Control*, 36(8):1088–1100, 2012.

[85] Shangjia Dong, Alireza Mostafizi, Haizhong Wang, Jianxi Gao, and Xiaopeng Li. Measuring the topological robustness of transportation networks to disaster-induced failures: A percolation approach. *Journal of Infrastructure Systems*, 26(2):04020009, 2020.

[86] Reuven Cohen, Keren Erez, Daniel Ben-Avraham, and Shlomo Havlin. Breakdown of the internet under intentional attack. *Physical review letters*, 86(16):3682, 2001.

[87] Reuven Cohen, Keren Erez, Shlomo Havlinl, Mark Newman, Albert-László Barabási, Duncan J Watts, et al. Resilience of the internet to random breakdowns. In *The Structure and Dynamics of Networks*, pages 507–509. Princeton University Press, 2011.

[88] Barry Eichengreen, Andrew K Rose, and Charles Wyplosz. Contagious currency crises. Working Paper 5681, National Bureau of Economic Research, July 1996. URL `http://www.nber.org/papers/w5681`.

[89] Philip N Howard, Aiden Duffy, Deen Freelon, Muzammil M Hussain, Will Mari, and Marwa Maziad. Opening closed regimes: what was the role of social media during the arab spring? *Available at SSRN 2595096*, 2011.

[90] Philip N Howard and Muzammil M Hussain. The upheavals in egypt and tunisia: The role of digital media. *Journal of democracy*, 22(3):35–48, 2011.

[91] Muzammil M Hussain and Philip N Howard. What best explains successful protest cascades? icts and the fuzzy causes of the arab spring. *International Studies Review*, 15(1):48–66, 2013.