**Reconciling resilience across ecological systems,**

**species, and subdisciplines**

Editorial of the cross-journal Special Feature “Reconciling resilience across ecological systems, species, and subdisciplines”, for consideration for publication in *Journal of Ecology*

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## Abstract

1. Resilience has emerged as a key concept in ecology and conservation biology to understand and predict ecosystem responses to global change. In its broadest sense, resilience describes the ability of an ecosystem to resist, and recover from, a disturbance. However, the application of such a concept in different sub-disciplines of ecology and in different study systems has resulted in a wide disparity of definitions and ways of quantifying ecological resilience.
2. This Special Feature, which spans three journals of the British Ecological Society, provides an overview of how ecologists define, quantify, compare and predict resilience across different study systems.
3. The 29 contributions to this Special Feature show the broad range of approaches used by ecologists to study resilience. While most of the contributions study resilience at the community level, a number of them also study resilience at multiple levels of biological organisation. In addition, a large proportion of the articles are observational or in combination with experimental approaches, with theoretical studies being rarely used together with other methods. Most of the studies were based either on plants or animals, with a fewer proportion studying resilience including multiple trophic levels.
4. We provide a summary of the main opportunities and challenges derived from the contributions to this Special Feature. We also provide general guidelines to bring more consensus to the field of resilience to improve future research. This knowledge will ultimately provide crucial guidance to focus effective management actions, informing where to allocate the inherently limited resources allocated to nature conservation.

**Keywords:** Conservation biology, Disturbance,Global change, Recovery, Regime shift, Resistance, Stability.

## Introduction

As the impacts of global change continue to unfold worldwide [(Díaz et al., 2019; IPCC, 2021; Maxwell et al., 2016)](https://www.zotero.org/google-docs/?5l5EKe), understanding the ability of ecological systems to respond to global threats has become a pressing societal need [(CBD, 2010; UNISDR, 2015)](https://www.zotero.org/google-docs/?TtkLVZ). In recent decades, the anthropogenic stressors impacting ecological systems have escalated at unprecedented rates in both number and severity (Barnosky et al., 2012; Díaz et al., 2019; Newbold et al., 2015). Despite efforts to prevent global change impacts, species extinctions have increased 100- to 1,000-fold [(Barnosky et al., 2011; Ceballos et al., 2015)](https://www.zotero.org/google-docs/?IZKI8E), with approximately 1 million species predicted to become extinct over the coming decades [(Scholes et al., 2018)](https://www.zotero.org/google-docs/?Cfmt4d). The on-going loss of species is altering the structure and functioning of ecosystems worldwide [(Pecl et al., 2017)](https://www.zotero.org/google-docs/?FSeKsu). As a consequence, international environmental policies and targets such as the Aichi Biodiversity Targets [(CBD, 2010)](https://www.zotero.org/google-docs/?NzniJW), the Sustainable Development Goals [(United Nations General Assembly, 2015)](https://www.zotero.org/google-docs/?L6LYQQ) or the Sendai Framework [(UNISDR, 2015)](https://www.zotero.org/google-docs/?WrSAFC) include preserving the resilience of ecological systems as a key priority.

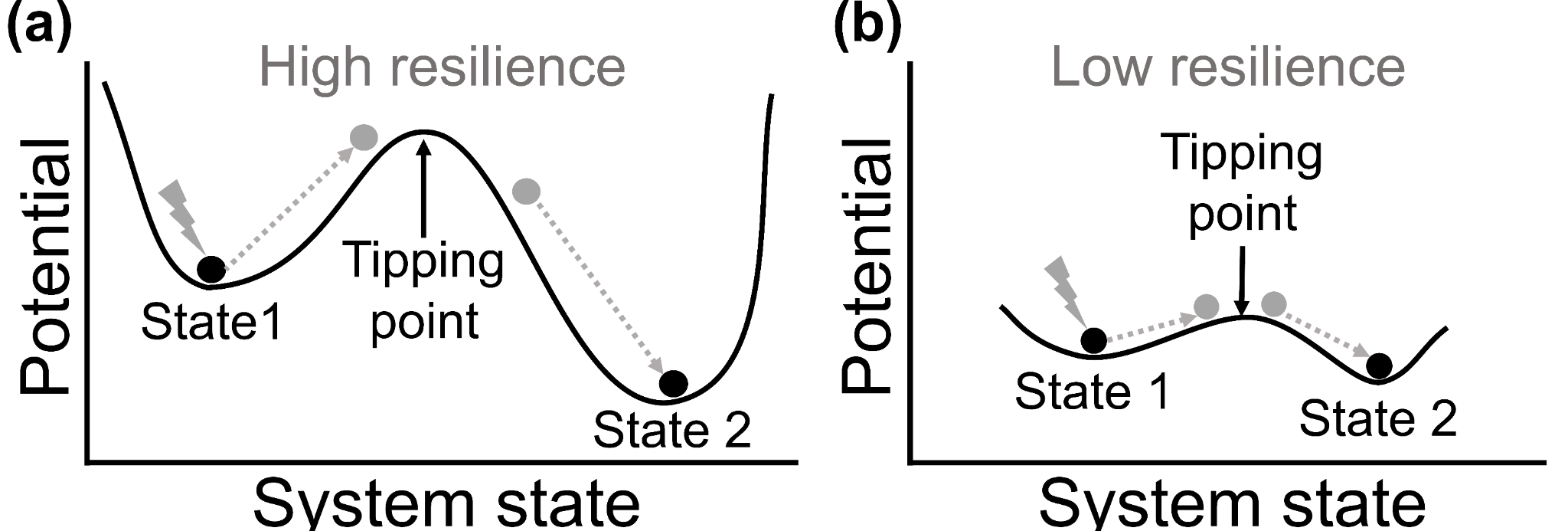
Despite its importance in ecology and conservation, the popularity of resilience is rivalled only by the disparity in its interpretations, definitions, and applications across different ecological subdisciplines [(Hodgson et al., 2015; Ingrisch & Bahn, 2018)](https://www.zotero.org/google-docs/?BeywkT). These discrepancies between approaches mean that ecologists have used a corollary of different ‘indicators’ or ‘metrics’ of resilience [(Angeler & Allen, 2016)](https://www.zotero.org/google-docs/?0Ti45J). As such, *Journal of Animal Ecology*, *Journal of Ecology*,and *Functional Ecology* present this joint Special Feature to provide an updated overview of how ecologists define, quantify, compare, and predict resilience across different ecological systems, species, and subdisciplines. In this Editorial, we discuss current perspectives on resilience, and both theoretical and empirical approaches to study it, across the 29 manuscripts published in this Special Feature. We first provide a brief conceptualisation of resilience and ways to quantify it linking to the approaches used in this Special Feature. Second, we identify the key opportunities and challenges to advance our understanding of resilience in ecological systems, and describe how the Special Feature papers contribute in these new directions. Finally, we propose several steps to move the field further towards an integrated understanding of resilience across ecological scales.

## The concept of resilience across disciplines

Resilience (Lt. *‘resilire’*, to leap or spring back, [OED, 1989](https://www.zotero.org/google-docs/?00N7mB)) is a widely used concept in ecology. Over the course of history, different scientific disciplines have adopted the term resilience to describe different processes. For example, the physician James Carson [(1820)](https://www.zotero.org/google-docs/?GBYglP) used the term to describe the ability of lungs to expand and contract. In psychology, resilience was first coined to describe the capacity of children to endure difficult emotional experiences [(Rutter, 1979)](https://www.zotero.org/google-docs/?HeWozb). In engineering, resilience was first used to describe the stress (in terms of load bearing weight) that timber could sustain before breaking [(Tredgold, 1818)](https://www.zotero.org/google-docs/?PgF4sF). Despite the disparity of the use of resilience in different fields, the commonality among them is that *resilience describes the capacity of a system to deal with change*.

Given the tight link between resilience and change, it is not surprising how resilience has become so fundamental to ecological research. Resilience gained popularity among ecologists because of the rising concern of human impacts on the structures and processes that make up healthy ecosystem functions [(Curtin & Parker, 2014)](https://www.zotero.org/google-docs/?iNjBVE). Early understanding of resilience was predicated on ecosystem stability and persistence despite disturbances [(e.g. MacArthur, 1955)](https://www.zotero.org/google-docs/?qnaZBr), where disturbances represent a/biotic factors displacing the system away from its stationary equilibrium [(Holling, 1973)](https://www.zotero.org/google-docs/?ZsdkvS). Ecological systems were understood to persist in determined states, characterised by various processes typically maintaining some certain structure, and exemplifying stable and equilibrium conditions to which the system is assumed to return back to following any disturbance [(Lewontin, 1969; May, 1977)](https://www.zotero.org/google-docs/?uZa7cA). Though not explicitly linked to the term resilience *per se*, these early works on stability introduced crucial concepts, such as alternative stable states or basins of attraction, which set the foundations of ecological resilience theory.

Holling (1973) was the first -that we are aware of- to explicitly use the term resilience in an ecological context. He suggested that the stability of an ecosystem is a different property than its resilience and argued that ecological systems can exist in multiple, alternative stable states [(Holling, 1996](https://www.zotero.org/google-docs/?8nu8vF); Figure 1). Each state is defined by different stable system structures, compositions, and processes, maintained by forces or feedbacks that represent their basin of attraction (Figure 1; [Folke et al., 2004; Holling, 1973, 1996)](https://www.zotero.org/google-docs/?JwOX4W). When a disturbance displaces the system from its current state, feedback processes draw it back to that initial state (Figure 1). If the system is disturbed beyond the basin of attraction and past a tipping point, however, it may undergo a regime shift and transition to an alternative stable state [(Dakos et al., 2014; Scheffer et al., 2009)](https://www.zotero.org/google-docs/?mx0ts2). As such, Holling defined resilience as *“the size of a stability domain or the amount of disturbance a system could take before it shifted into alternative configuration”* (Figure 1).



**Figure 1. Classical analogy of the rolling ball to represent the resilience of an ecological system according to Holling (1973).** Each black ball represents the stable state of the system, whereas the grey balls illustrate the potential trajectory of the system. The basins represent the potential states. To shift from a stable state to another one, the system must be perturbed sufficiently by a disturbance (lightning) for the ball to surpass a tipping point and roll over from one basin to another (dashed arrow). The width and depth of the basin are related to resilience: a system with a deep and wide pit (**a**) will be more resilient than a system with a flat and narrow pit (**b**), given that more energy will be needed to cause a regime shift.

Due to the rise of discrepancies around the concept of resilience (e.g. Pimm, 1984), Holling distinguished two main approaches to quantify resilience: *engineering resilience* and *ecological resilience* [(Holling, 1996)](https://www.zotero.org/google-docs/?5J39Z3). Engineering resilience defines resilience as the process of *recovery of the system* following a disturbance [(Pimm, 1984)](https://www.zotero.org/google-docs/?4W8aTX). This view considers resilience to be a component of system stability [(Donohue et al., 2013; Pimm, 1984)](https://www.zotero.org/google-docs/?n5VNvo), and often assumes that a system can only have a single stability regime [(Holling, 1996)](https://www.zotero.org/google-docs/?22m2Kw). On the other hand, ecological resilience assumes that a system may have multiple alternative states and defines resilience as *resistance* to change, *i.e.,* the magnitude of disturbance that a system can absorb before shifting from one state to another [(Holling, 1996)](https://www.zotero.org/google-docs/?kEnS8I). These definitions of ecological *vs.* engineering resilience have diverged substantially in the ecological literature [(Brand & Jax, 2007)](https://www.zotero.org/google-docs/?aoHFdI). More recent views consider that resilience encompasses multiple components describing both resistance *and* recovery as described above [(Hodgson et al., 2015; Ingrisch & Bahn, 2018)](https://www.zotero.org/google-docs/?HHA0x5).

## Measuring resilience across ecological disciplines

Whilst theory helps to conceptualise phenomena such as resilience, empiricism requires specifics. This need is precisely what the title of this Special Feature, “Reconciling resilience across ecological systems, species, and subdisciplines”, alludes to. Ecological systems operate and evolve at different levels of biological organisation (individuals, populations, communities), which correspond to various ecological subdisciplines. All ecological systems have a structure formed of interacting system components (e.g., age structure of a population, [Caswell, 2001](https://www.zotero.org/google-docs/?kn7dg5); functional composition of species in a food web, [Ings et al., 2009](https://www.zotero.org/google-docs/?jYVD6N)). All systems function in terms of how components interact, such as interaction between species (e.g. predation pressure, [Donohue et al., 2017](https://www.zotero.org/google-docs/?eEzZGa)), progression through life history stages (e.g. maturation rate, [Stearns, 1992](https://www.zotero.org/google-docs/?CX3Xoj)), or interaction between individuals (e.g. breeding effort, [Ricklefs, 1977)](https://www.zotero.org/google-docs/?GRS3k3). All systems have measurable system outputs, commonly including size (e.g. population size), growth (e.g. rate of community biomass change), diversity (e.g. species richness), or composition (e.g. sex ratio in a population). System outputs are also often measured using functional traits [(Carmona et al., 2016; Violle et al., 2007)](https://www.zotero.org/google-docs/?YNiCPR), at various output levels (individual, population, community). To quantify resilience, one needs to (1) consider how structure and function are defined, (2) identify relevant measures of system outputs, and (3) develop metrics to quantify those outputs at the appropriate level of organisation that can vary considerably both between and within study species and systems.

In population ecology, resilience has been studied for decades [(Harrison, 1979; Neubert & Caswell, 1997)](https://www.zotero.org/google-docs/?rDlR0J), though not necessarily with the explicit recourse to resilience theory [(e.g. Stott et al., 2011)](https://www.zotero.org/google-docs/?pye4oa). Population models are typically formulated using the (st)age structure of the population, with the life cycle of the species defined by average vital rates (e.g., survival, development, reproduction) clustered into (st)ages. Here, models assume that populations display stable states defined by population structure - *i.e.*, the relative number of individuals in each life cycle (st)age, with commensurate stable numerical growth or size [(Caswell, 2001)](https://www.zotero.org/google-docs/?EJa0NA). Simple (density-independent and non-stochastic) conceptualisations assume that populations converge to a stable rate of increase or decline, with stable relative proportions of life cycle (st)ages over time [(Caswell, 2001)](https://www.zotero.org/google-docs/?fgwHpW). This stable state is maintained by the vital rates of the population, which are determined by the biology of the species and the environmental conditions of the population [(Caswell, 2001)](https://www.zotero.org/google-docs/?5XnxUL). However, populations are subject to disturbances that displace them from their stable structure, thus changing the relative proportions of individuals with high *versus* low survival and/or fecundity [(Caswell, 2001; Stott et al., 2011)](https://www.zotero.org/google-docs/?EK1kmn). These displacements can result in a different post-disturbance population growth [(Caswell, 2001; Stott et al., 2011)](https://www.zotero.org/google-docs/?3ufome). Resistance and return rate of a structured population can be measured relative to its pre-disturbance population size, growth, and/or structure [(Caswell, 2001; Stott et al., 2011)](https://www.zotero.org/google-docs/?WhvvrR). Despite the clear links between these concepts and resilience theory, the connections were not formalised until recently [(Capdevila et al., 2020)](https://www.zotero.org/google-docs/?76N5TY). Similar conceptualisations could reasonably be applied to equilibrium states in density-dependent population dynamics, and expected growth in stochastic population dynamics.

Resilience in communities has received a considerable amount of attention in ecological research. Community ‘structure’ is often understood as the network of interactions of species [(*sensu stricto,* Caswell, 1976)](https://www.zotero.org/google-docs/?xqMhwb), but could also be understood using taxonomic or functional groupings of species [(e.g., Carmona et al., 2016)](https://www.zotero.org/google-docs/?3pC430). Community structure may be measured in a multitude of ways, such as species richness, numerical abundance, evenness of numerical abundance across species, community biomass, or using a variety of graph theoretic means of understanding the interaction network (e.g. interaction strength, feedback loops; [Ings et al., 2009; Tylianakis et al., 2008](https://www.zotero.org/google-docs/?wnGMeX)). Early theory assumed communities to be in a stable state in terms of absolute or relative species abundance, with species interactions being the ‘processes’ underlying community function [(May, 1977)](https://www.zotero.org/google-docs/?IAtUpT). Interactions could be considered negative (such as herbivory, predation, competition, and parasitism), or positive (such as mutualism, facilitation, and cooperation; [Blüthgen, 2010)](https://www.zotero.org/google-docs/?S99sCU). The ‘state’ from which a community departs or to which it may return may be linked to measures of productivity, growth, biomass, abundance, diversity, network, or otherwise, including those mentioned earlier in this paragraph [(e.g. Cole et al., 2014; Yang et al., 2019)](https://www.zotero.org/google-docs/?YQF3jK). Though earlier works often considered limited interaction types (the trophic interactions of food webs being probably the most studied), contemporary research is increasingly concerned with different interaction types and their relative strengths [(Li et al., 2021)](https://www.zotero.org/google-docs/?o2SiOm). A great deal of debate still abounds about the effects of the complexity of the community network on its stability and resilience: while early theoretical works showed complexity to be destabilising [(Magurran, 2013)](https://www.zotero.org/google-docs/?D4JCaV), more recent theory has shown that complexity can be stabilising under many conditions [(Mougi & Kondoh, 2012; Qian & Akçay, 2020)](https://www.zotero.org/google-docs/?d8XoTq)

While most resilience approaches have focused on quantifying changes in the structure and composition of ecological systems [(Hughes et al., 2003; Lloret et al., 2011)](https://www.zotero.org/google-docs/?9oX606), an emerging area of research is to quantify the resilience of ecosystem functions[(Oliver et al., 2015)](https://www.zotero.org/google-docs/?foPS4C). Focusing on community composition to examine resilience risks rendering an incomplete picture of the extent of the impacts that disturbances might have on the functionality of ecological systems [(Gladstone-Gallagher et al., 2019; Matos et al., 2020; Oliver et al., 2015)](https://www.zotero.org/google-docs/?ljgGot). Species contributions to ecosystems functions are tightly linked to their functional traits —morphological, physiological, phenological, or behavioural features, measurable at the individual level, that have an impact on species fitness (*sensu* Violle et al., 2007). Different species might share similar combinations of traits and so provide similar or equivalent ecosystem functionality, *i.e.* be functionally redundant [(Carmona et al., 2016; de Bello et al., 2010)](https://www.zotero.org/google-docs/?2Wpb2e). Consequently, similar ecosystem functioning might be achieved by different communities [(Gallagher et al., 2013)](https://www.zotero.org/google-docs/?EVt7NY), illustrating the possible independence between structure and composition of ecosystems, and their functionality. This need to distinguish between composition and functionality gave rise to the concept of *functional resilience*, or *“the degree to which an ecosystem function can resist or recover rapidly from environmental perturbations, thereby maintaining function above a socially acceptable level”* (*sensu* Oliver, Heard, et al., 2015).

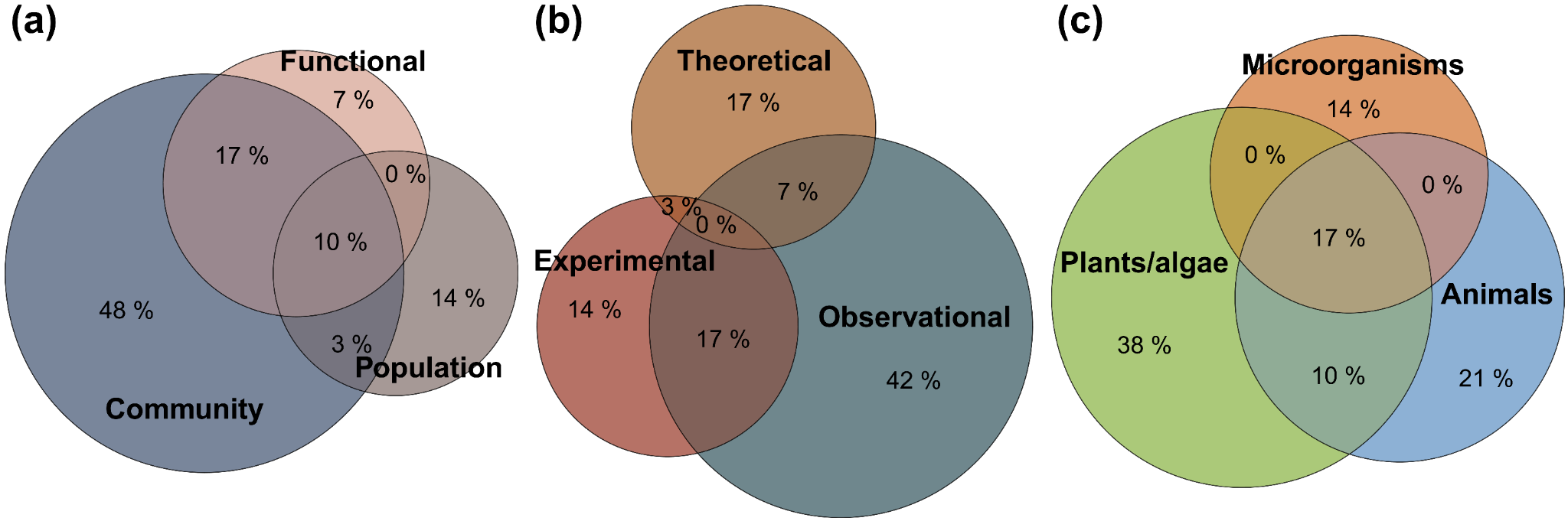
## Contributions to this Special Feature

This Special Feature comprises 29 pieces covering a broad range of topics related to resilience of ecological systems. To better contextualise them, we classified these contributions according to the ecological domain, the approach, and the system through which the authors study resilience (Figure 2). Perhaps as a legacy of early works [(Holling, 1973; Pimm, 1984)](https://www.zotero.org/google-docs/?WEJ8R5), a significant proportion of the contributions in this Special Feature examine resilience at the level of communities (48%), followed by populations (14%) and functional ecology (7%; Figure 2a). Yet, a number of contributions transgress different levels of organisation, with 17% of the works studying resilience both at the community and functional ecology levels, 3% at the community and population level, and 10% at all three levels of organisation (Figure 2a). Curiously, despite recent calls for better integration between population and functional ecology approaches [(Salguero‐Gómez et al., 2018)](https://www.zotero.org/google-docs/?5lESc7), no study here examines links between these two levels of organisation (Figure 2b). The patterns that emerge from this set of publications suggest that ecological research is making progress in breaking previous legacies of focusing only on one level of biological organisation, though more interdisciplinary opportunities lay ahead, as we discuss in the final section of this editorial.

Early developments of resilience research were mostly based on theoretical works [(e.g. Harrison, 1979; Holling, 1973)](https://www.zotero.org/google-docs/?m9wNSG). These theoretical approaches have sometimes challenged their application to “real world” systems, hampering the use of resilience in applied disciplines [(Hodgson et al., 2015; Ingrisch & Bahn, 2018)](https://www.zotero.org/google-docs/?8RDFX3). In this Special Feature, most of the contributions are observational studies (42%), with 17% being theoretical and 14% experimental (Figure 2b). Importantly, 18% of the contributions combine experimental and observational approaches, 7% theoretical and observational, and 3% experimental and theoretical approaches. Such a combination of approaches is important to provide a better understanding of the resilience of ecological systems (Figure 2b). For example, experiments might help to unravel processes promoting resilience, which might be more difficult to observe through classical observations [(Hoover et al., 2021; Jones et al., 2020; Lipoma et al., 2021)](https://www.zotero.org/google-docs/?avPX9i). Combining theoretical studies with experiments and/or observational studies can also help to test the validity of resilience concepts [(Li et al., 2021; Medeiros et al., 2021)](https://www.zotero.org/google-docs/?VrCVmC). This strength contrasts with the lack of contributions tackling all three approaches (Figure 2b), a clear area of future research.

Because natural systems are complex, it is challenging to study all their components. In this Special Feature, most of the studies focus on plants or algae (38%), with a 21% focusing on animals and 14% on microorganisms (Figure 2c). Of the 29 contributions, 10% studied resilience in both plants/algae and animals, while 17% included the three taxonomic systems, though these are mostly theoretical studies (Figure 2c). While focusing on a single system can simplify experimental and observational studies, incorporating multiple systems will render a more clear picture of the resilience of the entire system.

Overall, the different representations of studies in this Special Feature render a general idea of how ecologists study resilience. While biases might exist with the submissions to *Journal of Ecology*, *Journal of Animal Ecology*, and *Functional Ecology*, we argue that these illustrate knowledge gaps in our understanding about the resilience of ecological systems, thus representing key opportunities for research. In the following section we briefly highlight the opportunities and challenges in resilience research in ecology, drawing from the key contributions of the 29 publications within this Special Feature.

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## Figure 2. Venn diagrams showing the domain of operation of the 29 manuscripts included in the joint Special Feature “Reconciling resilience across ecological systems, species, and subdisciplines”. The different panels show the proportion of contributions according to: (a) The ecological domains of study, including population ecology, community ecology, and functional ecology.. (b) Whether the approach used to study resilience was experimental, theoretical, and/or observational approaches. (c) The study system, classified as plants/algae, animals, and/or microorganisms. Conceptual contributions are here assigned to the three ecological domains in panel a and the three taxonomic groups in panel c due to their cross-applicability.

## Opportunities and challenges in the Special Feature

## *Conceptualising and operationalising resilience*

A unified ecological understanding of resilience across systems and species requires a trans-disciplinary consensus on what resilience actually is and how to best measure it. As such, one of the most pressing challenges ahead is to bring consensus across traditionally disparate fields. In this Special Feature, two key contributions, [Delettre (2021)](https://www.zotero.org/google-docs/?z5RJ6m) and [Van Meerbeek et al. (2021)](https://www.zotero.org/google-docs/?bdX2qm), provide complementary perspectives on current definitions and quantifications of views of resilience, given historical divergences in its study. Both contributions recognise the importance of semantics in furthering the study of resilience, and make key suggestions regarding ways to overcome conflicting consensus of definitions. [Delettre (2021)](https://www.zotero.org/google-docs/?238tJD) stresses that the different concepts of resilience used in the literature do not represent degrees of resilience but rather types of behaviour of a system. Hence, it is important to choose the appropriate definition of resilience depending on the research questions or management goals, the processes by which persistence is achieved, and the types of disturbance and spatio-temporal scales considered. Semantics aside, understanding commonalities across systems in terms of how they are structured, how they function, and how they can be measured, may be a good start towards reconciling how we ecologists study resilience.

One casualty of diverse and divergent parlances is an inability to compare results between studies asking similar questions. Synthesis and meta-analysis in ecology have proven extremely powerful tools [(Koricheva & Gurevitch, 2014)](https://www.zotero.org/google-docs/?blDm64); but the current state of the art in resilience research is one that makes finding generality challenging. As pointed out by Van Meerbeek et al. (2021), it would be advantageous to standardise metrics depicting resilience/stability components to facilitate comparisons across studies. Over the last decades, ecological research has made significant methodological advances, with an increasing number of statistical techniques (e.g. time-series analyses, [Dennis et al., 2006](https://www.zotero.org/google-docs/?footkN); network analyses, [Blüthgen, 2010](https://www.zotero.org/google-docs/?TD8JKg); spatial analyses, [Dale & Fortin, 2014)](https://www.zotero.org/google-docs/?ghlZpq), and sharing of methods and tools will be advantageous to everyone. Using common “currencies” of resilience/stability -or at least determining “conversion factors” across different metrics of resilience- will make comparisons among studies possible, opening up the possibility of much-needed global assessments of resilience.

*Understand resilience at different disturbance regimes*

Resilience research is inherently linked to the properties of the disturbances altering ecological systems [(Bender et al., 1984)](https://www.zotero.org/google-docs/?2w5iNw). Historically, resilience research has predominantly focused on sudden events or pulse disturbances (Holling, 1973; Pimm, 1984). However, disturbances can occur at different intensities (low to high) and frequencies (pulse to chronic) (Jentsch & White, 2019). Hence, to understand the resilience of ecological systems to global change, accounting for different disturbance regimes is crucial. This is particularly so because a change in the disturbance regime due to global change can have profound impacts in the systems’ resilience. To this end, two contributions to this Special Feature demonstrate that changes in sea temperature, acting as a chronic stressor, can have major impacts on the functioning [(Tsimara et al., 2021)](https://www.zotero.org/google-docs/?XUH9Nm) and stability [(Miner et al., 2021)](https://www.zotero.org/google-docs/?Iu3Aen) of marine communities. Tsimara et al. (2021) combine data on Mediterranean fisheries landings over 31 years (1985-2015) and species traits to infer the resilience dynamics and build stability landscapes. On the other hand, Miner et al. (2021) utilise a decade-long data set covering the whole of the U.S. West coast, alongside comprehensive multinomial descriptors that describe whole communities, rather than statistical descriptors of their composition. Similarly, Serra et al. [(2021)](https://www.zotero.org/google-docs/?pMvK6U) show that forest age has a stronger influence than clearing frequency in the recovery of the number and diversity of soil macrofaunal communities of the Brazilian Amazon.

Disturbances rarely impact ecological systems in isolation, but they often act in combination with other disturbances (Côté et al., 2016; Orr et al., 2020). A number of contributions to this Special Feature explore the interactive effects of multiple disturbances on systems. [Lipoma et al. (2021)](https://www.zotero.org/google-docs/?xHu1ZG) explore the interactive effects of land-use exclusion and weather variability on the vegetation engineering resilience in the Chaco forest. Their findings also suggest that long-term land use might induce long-term changes in the ecological system hampering their engineering resilience in a short period of time (five years after disturbance cessation). Nowiciki et al. [(2021)](https://www.zotero.org/google-docs/?4kmFeJ) highlight how trophic cascades, through the loss of predators, can exacerbate the impacts of extreme climatic events by reducing the resilience of seagrass meadows to such disturbances. Similarly, Nelson et al. [(2021)](https://www.zotero.org/google-docs/?3C8dr0) report the interactive effects of warming and drought on invertebrate communities resilience in food webs with different energy channel configurations. Their results suggest that communities inhabiting streams with large amounts of organic matter and more complex substrates are more resilient to the loss of surface water than communities inhabiting streams with simpler, more homogeneous substrates.

Accounting for the temporal and spatial scale at which disturbances occur is also crucial. A large proportion of the ecological literature has focused on studying the immediate response of ecological systems to disturbances [(e.g. Cole et al., 2014; de Vries et al., 2012; DeSoto et al., 2020)](https://www.zotero.org/google-docs/?EzDczI). Yet, the effects of such disturbance on the system might take several years or even decades to manifest [(Hughes et al., 2013; Johnstone et al., 2016)](https://www.zotero.org/google-docs/?wn4POK). In this Special Feature, a number of contributions show the importance of the “legacy effects” of disturbances into the present resilience of ecological systems [(Johnstone et al., 2016)](https://www.zotero.org/google-docs/?9jX5vB). In this sense, [Leizeaga et al. (2020)](https://www.zotero.org/google-docs/?8dE0ie), using a functional resilience approach, report a lower sensitivity to droughts in microbial communities that have been historically affected by a higher drought frequency in a gradient of precipitation. [(Hoover et al., 2021)](https://www.zotero.org/google-docs/?Px4ihl), on the other hand, demonstrate that the long-term effects of seasonal droughts on soil moisture can impact plant biomass and phenology. Likewise, [Webster et al. (2021)](https://www.zotero.org/google-docs/?yCrmCG)show how the resilience of seagrass populations to extreme rainfall events depends on the salinity levels to which these have been exposed previously. In their meta-analisis, [Leverkus et al. (2020)](https://www.zotero.org/google-docs/?6GGe0c) highlight how local environmental factors also play a key role in the resilience of trees to logging. Also, [Ovenden et al. (2021)](https://www.zotero.org/google-docs/?WH0OJg) report a high sensitivity of different metrics of forest resilience to the period of time considered as baseline, which calls into caution the need for a clear definition of the stable state of the system under examination. Finally, Steel et al. (2021) high-resolution LiDAR data, field data, and a natural experiment in California’s Sierra Nevada mountains to explore the factors promoting forest resilience to secondary wildfires. For example, they show that forests that survived past fires were more resistant to subsequent high-severity fire when they were characterized by dense but heterogeneous upper strata and a sparse understory, located in variable and mesic terrain, and burned under milder fire weather conditions.

*Integrating multiple levels of biological organisation*

## Individual organisms are - in extremely basic terms - an amalgamation of their traits (including, but not limited to, anatomy, physiology, behaviour) and their emergent properties. These traits are determined by their genes, environment, and interactions. Populations are composed of a number of interacting conspecific organisms. Communities are composed of interacting populations. The study of each level of biological organisation in isolation does a disservice to the interconnectedness of the natural world: changes at a particular level can and do often cascade to other levels (e.g. [Barbour & Gibert, 2021; Mrowicki et al., 2016)](https://www.zotero.org/google-docs/?hHc2JD). For example, individual responses to environmental change mediate population abundance and resulting interactions with other species, thus affecting community structure and composition as well as the functions that these provide (Gladstone-Gallagher et al., 2019; Oliver et al., 2015). Whilst examining resilience in the context of processes happening at specific levels of organisation, we may miss important drivers of a system’s resilience emerging from bottom-up or top-down processes in constituent sub-systems or overarching super-systems. We are approaching a turning point where we have the requisite knowledge, the methodological maturity, data sufficiency, and the computational firepower to begin understanding how resilience at any one level of biological organisation has ripple effects on resilience at levels both above and below.

In this Special Feature, a number of contributions provide key examples of how to integrate data, framework, and methods to examine resilience in a holistic manner. Lisovski et al. [(2020)](https://www.zotero.org/google-docs/?BxhXwS) show that specific traits can impact resilience at a population level. The authors show that migration behaviours in two shorebird species differentially affect individual survivorship, which has implications for population resilience. Populations lie at the intersection between processes that directly shape individual and community performance [(Griffith et al., 2016)](https://www.zotero.org/google-docs/?YOwcea). In this context, Paniw et al. [(2021)](https://www.zotero.org/google-docs/?l6MbV9) demonstrate how both functional traits and demographic processes complement each other in determining the resilience of a Mediterranean shrubland community to extreme droughts. The authors show a high degree of complementarity between demographic and functional traits in providing community resilience. For example, vital rates are more important in explaining total and individual species resilience, while functional traits matter more to explain compositional resilience.

Similarly, [Carnicer et al. (2021)](https://www.zotero.org/google-docs/?5jO4Zn) combine ecophysiological and demographic metrics to determine the resilience of sessile oaks (Quercus patraea) to droughts and heatwaves. A great deal of population variation was found regarding individual secondary growth, recruitment, and thermal exposure of saplings to heatwaves, mostly driven by microhabitat conditions. Their research highlights the importance of understanding the role of abiotic and biotic disturbances at meso- and micro-habitat scales. Finally, [Muñoz et al. (2021)](https://www.zotero.org/google-docs/?6eCGZP) by combining demographic and community dynamics data they highlight the importance of autogenic regulation for tropical forests as a basic component of its resilience. The authors used long-term community data from old-growth and secondary forests in southern Mexico to analyse three key state variables (basal area, tree density, species richness), their annual rates of change, and their underlying demographic processes (recruitment, growth, mortality). They find a negative relationship between state variables, their rates of change and their underlying demographic processes, supporting that forest dynamics is driven by autogenic factors.

*Unravelling the relationship between the multiple components of resilience*

Some of the current views in ecological research define resilience as the result of multiple processes, particularly resistance and recovery [(Capdevila et al., 2020; Hodgson et al., 2015; Ingrisch & Bahn, 2018)](https://www.zotero.org/google-docs/?nuEXcF). Because of the multifaceted nature of resilience, a key question ahead is whether and how its components are related to each other. In this Special Feature, Medeiros et al. [(2021)](https://www.zotero.org/google-docs/?m9VihD) reveal experimental microbial communities show negatively correlated recovery and resistance, supporting theoretical models which showed the same and indicating a complementarity which would mean information on one may be inferred from knowledge of the other. [Jones et al., (2020)](https://www.zotero.org/google-docs/?934T2K) show that both the resistance and recovery of plant communities to punctual disturbances are similarly affected by flooding stress gradients in salt marshes in Louisiana, USA. Moreover, it is key to understand whether the linkages between the different components of resilience hold when the systems are exposed to disturbances (Donohue et al., 2013). Eagle et al. [(2021)](https://www.zotero.org/google-docs/?YEvsfH) demonstrate that flood events can alter the correlations between different metrics of stability on freshwater macroinvertebrate communities. The authors use a 18-year time series (2000-2017) of macroinvertebrate community dynamics from a southeast Alaskan river, illustrating how stability can be examined in natural ecosystems time series data.

*What makes a system resilient?*

A key challenge in ecology is to predict the resilience of ecological systems to future, and potentially novel, disturbances and environmental conditions [(Sutherland et al., 2013)](https://www.zotero.org/google-docs/?ToVfzb). Global threats, such as global warming [(IPCC, 2021)](https://www.zotero.org/google-docs/?3hVDk4) or habitat loss [(Newbold et al., 2015)](https://www.zotero.org/google-docs/?rBf9Oa), are likely to continue to impact ecosystems worldwide even in the most optimistic conservation policy scenarios [(Leclère et al., 2020)](https://www.zotero.org/google-docs/?1ilZPI). However, predicting resilience is not an easy task, not only because of the abovementioned discrepancies in the field, but also because it is an emergent property of complex systems [(Scheffer et al., 2018)](https://www.zotero.org/google-docs/?iQpyMw). Hence, we need to develop frameworks that can help us to anticipate the potential consequences of the current ongoing global change into the future resilience of ecological systems.

Trait-based approaches could provide a solution to this challenge. Indeed, these approaches are becoming more accessible to ecologists, with standardised protocols for data collection (Moretti et al. 2017) and global databases already at hand (e.g TRY, Kattge et al., 2011; Amniote, Myhrvold et al., 2015). Bonhomme et al. ([2020)](https://www.zotero.org/google-docs/?Yy7pzP) report that drought applies selection pressures on invertebrate species living within water pools in bromeliad plants, according to feeding traits and ability to tolerate drought stress. Resilience, as measured using both functional and taxonomic diversity, is more dependent on these traits, and particularly stress-tolerance of resting stages such as eggs and cysts, than on meta-community dynamics of post-disturbance immigration. Su et al. [(2020)](https://www.zotero.org/google-docs/?2izbuF) show that trait-based early warning signals can be used to anticipate both the collapse and the recovery of a lake ecosystem in the Yangtze floodplain to multiple disturbances (warming, eutrophication, and biotic interactions). Studies such as these may be pivotal in informing management, and [De Battisti (2021)](https://www.zotero.org/google-docs/?kgZdKn) proposes a conceptual framework for predicting functional resilience of communities. The author illustrates how different suites of plant traits can help predict the resistance and recovery of salt marshes and sand dunes to pulse, chronic, and rapid onset disturbances. De Battisti argues that, by linking plant functional traits to the resilience of coastal ecosystem properties, we can provide actionable plans for resource managers.

Some network structures will be more disposed to high resilience than others, and specific “keystone” species, species groups, interactions, cascades or feedback loops may indicate greater capacity for a system to withstand environmental disturbances or change. Maia et al. [(2021)](https://www.zotero.org/google-docs/?htZO9v) use adaptive population-dynamics models to indicate that herbivory networks and their high degree of specialisation are inherently resilient against extinction cascades. Pollination networks, on the other hand, show high generalisation which appears to make them more vulnerable to species loss in the short term. However, their structure confers an adaptive capacity that could be leveraged in efforts designed to restore or maintain key ecosystem functions like pollination. Thakur et al. [(2021)](https://www.zotero.org/google-docs/?OgQhJZ) show that heat shocks applied to rhizosphere microcosms decreased prey biomass to a far greater extent than predator biomass, with prey biomass relatively low through the recovery period. These results highlight how the same disturbance due to difference in the resilience of the components of a system can promote imbalance in the structure of food webs.

Similarly, Li et al. [(2021)](https://www.zotero.org/google-docs/?kTqCve) demonstrate that energetic constraints at the trophic group and food web level enhance resilience by dampening the strength of destabilizing positive feedback loops. The authors quantified the resilience of the food web using the real part of the maximum eigenvalue of the Jacobian matrix based on empirical data from a seagrass bed in the Yellow River Delta. [Jia et al. (2020)](https://www.zotero.org/google-docs/?LcFd7F) reveal that the presence of arbuscular mycorrhizal fungi (AMF) in grassland ecosystems promotes resistance and improves resilience to drought. AMF aided recovery of the community following drought, and promoted resistance to drought as measured using plant productivity and nitrogen cycling, particularly ameliorating compounding adverse effects of N deposition. Finally, [Mungi et al. (2021)](https://www.zotero.org/google-docs/?w80JKN) demonstrate that the role of protected areas in providing resistance to species invasions is context dependent. The authors use data on plant communities (species richness and abundance) from five tropical forest types inside and outside protected areas, also accounting for other covariates such as climate, forest type, anthropogenic disturbance and native plant richness.

**Conclusions**

Despite decades of research, important knowledge gaps remain in our understanding regarding the resilience of ecological systems. The contributions to this joint Special Feature certainly address these gaps, using a mix of theoretical and empirical means, using natural and experimental case studies, across ecological systems within and across scales of biological organisation. They also naturally open up new and exciting research avenues. For the field of ecological resilience to move forward, we identify four recommendations to harmonise future research efforts.

(1) *Define resilience using existing frameworks.* Existing frameworks currently provide both clear definitions and ways to quantify the resilience and the stability of ecological systems [(Capdevila et al., 2020; Donohue et al., 2013; Hodgson et al., 2015; Ingrisch & Bahn, 2018; Oliver et al., 2015)](https://www.zotero.org/google-docs/?lEEWdI). Future studies would benefit from making it clear where their resilience approach sits within the existing resilience frameworks, distinguishing whether they are studying resilience, stability, or any of their sub-components. Artificial distinctions such as ecological *vs.* engineering resilience may not be helpful given contemporary frameworks for holistically understanding components of resilience [(Capdevila et al., 2020; Hodgson et al., 2015; Ingrisch & Bahn, 2018). Thus](https://www.zotero.org/google-docs/?iWBmeb), identifying the variables of interest and how they are measured, within such frameworks, will help cohesion and aid comparison across studies.

(2) *Use common metrics to measure resilience.* Studies should aim to use common and standardised metrics to measure resilience, both theoretically and empirically applicable. This unified approach will facilitate comparisons among different systems and scales of biological organisation [(Clark et al., 2021; Ingrisch & Bahn, 2018)](https://www.zotero.org/google-docs/?FsLuRw), as well as linking theoretical and observational studies. Beyond that, common metrics will help to find global patterns of resilience across different systems (e.g. [Capdevila et al., 2021](https://www.zotero.org/google-docs/?n1eALQ)), as well as contributing to improve our mechanistic understanding of how ecological systems achieve resilience.

(3) *Define the pre- and post-disturbance state*. Independently of the scale and level of organisation at which resilience is measured, all systems have a given structure and composition with measurable outcomes (e.g. size, diversity). It is then crucial to define such a reference state from which resilience and/or its components will be measured for better contextualisation. For example, if one wants to measure resistance as the ability of the system to remain unchanged after a disturbance, it is crucial to have a reference state of the system before the disturbance. This can be achieved either by characterising the system before the disturbance or by using undisturbed control treatments [(Ingrisch & Bahn, 2018)](https://www.zotero.org/google-docs/?OKVBIV).

(4) *Define the disturbance type and regime.* The resilience of a system is sensitive to the kind of disturbance [(Bender et al., 1984; Johnstone et al., 2016)](https://www.zotero.org/google-docs/?Lw0vDk). It is therefore important to clearly define the nature of the disturbance affecting that determined system. That is, distinguishing whether that disturbance represents a sudden event (e.g. storm, fire), or if it represents a chronic disturbance (e.g. global warming, ocean acidification). This distinction is important to also define the trajectory of the system towards its “recovered state”. For instance, a chronic disturbance might cause a permanent system change, where a return to stability can only be achieved through adaptation [(Hodgson et al., 2015)](https://www.zotero.org/google-docs/?zQA5PH). Furthermore, frequency and intensity of disturbance events will have a strong impact on system recovery, dependent on (non)linearity of system resistance to disturbance intensity, and the recovery time required following a disturbance event as compared to disturbance frequency. This is particularly important given existing and expected increases in intensity and frequency of large disturbance events given climate change [(IPCC](https://www.zotero.org/google-docs/?YKi9rT), 2021).

Resilience is a common component of how we understand the response of the natural world to global threats and change. Moreover, conserving resilience in nature is an explicit goal of global conservation efforts [(CBD, 2010; UNISDR, 2015; United Nations General Assembly, 2015)](https://www.zotero.org/google-docs/?xExiyX). Bringing consensus to how resilience is conceptualised will render a better understanding of resilience across diverse ecological systems by framing resilience in terms of consistent components. This of course requires clarity in how these are measured. In doing so, barriers -which in our views are artificial- between ecological subdisciplines, and indeed between different schools of thought within resilience research, may begin to dissolve. This will bring commensurate benefits to ecology as we begin to understand the ripple effects of resilience up and down systems at different levels of biological organisation. This knowledge will ultimately provide crucial guidance to focus effective management actions, informing where to allocate the inherently limited resources allocated to nature conservation.

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