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 resilience.
2. This Special Feature, which spans the *Journal of Ecology*, *Journal of Animal Ecology* and *Functional Ecology*, 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. Almost half of the contributions (48%) study resilience at the community level, with a 30% of them studying resilience at multiple levels of biological organisation. A large proportion of these articles are observational (42%), experimental (14%) or a combination of both (17%), whilst a 17% utilise theoretical or computational approaches. Whilst 38%, 21% and 14% of the studies were based solely on plants, animals or microorganisms respectively, 17% of them incorporated these multiple trophic levels.
4. *Synthesis.* A unified ecological understanding of resilience across systems and taxa requires a trans-disciplinary consensus on what resilience actually is and how to best measure it. Here, we provide an overview of how ecologists define, quantify, compare, and predict resilience across different ecological systems and subdisciplines, with reference to the diverse approaches used by contributions to this Special Feature. We identify four key recommendations to

harmonise future efforts in resilience research: (1) define resilience using existing theoretical frameworks; (2) use common and comparable metrics to measure resilience; (3) clearly contextualise and define the pre- and post-disturbance state of the ecological system; (4) consider explicitly the disturbance type and regime impacting the system.

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

Resumen (Español)

1. La resiliencia ha surgido como un concepto clave en ecología y biología de la conservación para comprender y predecir las respuestas de los ecosistemas al cambio global. En su sentido más amplio, la resiliencia describe la capacidad de un ecosistema para resistir y recuperarse de una perturbación. Sin embargo, la aplicación de este concepto en diferentes subdisciplinas de la ecología y en diferentes sistemas de estudio ha resultado en una gran variedad de definiciones y formas de cuantificar la resiliencia.
2. Este edición especial, que comprende las revistas *Journal of Ecology*, *Journal of Animal Ecology* y *Functional Ecology*, proporciona una descripción general de cómo los ecólogos definen, cuantifican, comparan y predicen la resiliencia en diferentes sistemas de estudio.
3. Las 29 contribuciones a esta edición especial muestran la amplia gama de enfoques utilizados por los ecologistas para estudiar la resiliencia. Casi la mitad de las contribuciones (48%) estudian la resiliencia a nivel de comunidades ecológicas, y un 30% de ellos estudia la resiliencia en múltiples niveles de organización biológica. Una gran proporción de estos artículos son

observacionales (42%), experimentales (14%) o una combinación de ambos (17%), mientras que un 17% utiliza enfoques teóricos o computacionales. Mientras que el 38%, 21% y 14% de los estudios se basaron únicamente en plantas, animales o microorganismos, respectivamente, el 17% de ellos incorporaron estos múltiples niveles tróficos.

4. *Síntesis.* Una comprensión ecológica coherente de la resiliencia entre sistemas y taxones requiere un consenso transdisciplinario sobre qué es realmente la resiliencia y cómo medirla. En esta editorial proporcionamos una descripción general de cómo los ecólogos definen, cuantifican, comparan y predicen la resiliencia en diferentes sistemas ecológicos y subdisciplinas, con referencia a los diversos enfoques utilizados por las contribuciones a esta edición especial. Identificamos cuatro recomendaciones clave para armonizar los esfuerzos futuros en la investigación de la resiliencia: (1) definir la resiliencia utilizando los marcos teóricos existentes; (2) utilizar métricas comunes y comparables para medir la resiliencia; (3) contextualizar y definir claramente el estado anterior y posterior a la perturbación del sistema ecológico; (4) considere explícitamente el tipo de perturbación y el régimen que impacta el sistema.

Introduction

As the impacts of global change continue to unfold worldwide (Díaz et al., 2019; IPCC, 2021; Maxwell et al., 2016), understanding the ability of ecological systems to respond to global threats has become a pressing societal need (CBD, 2010; UNISDR, 2015). 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), with approximately 1 million species predicted to become extinct over the coming decades (Scholes et al., 2018). The on-going loss of species is altering the structure and functioning of ecosystems worldwide (Pecl et al., 2017). As a consequence, preserving resilience, defined as the ability of ecological systems to resist and recovery from disturbances (Hodgson et al., 2015), has become a key conservation priority. For instance, several international environmental policies, such as the Aichi Biodiversity Targets (CBD, 2010), the Sustainable Development Goals (United Nations General Assembly, 2015) or the Sendai Framework (UNISDR, 2015) explicitly include preserving resilience as a target.

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). These discrepancies between approaches mean that ecologists have used a variety of different ‘indicators’ or ‘metrics’ of resilience (Angeler & Allen, 2016). As such, *Journal of Animal Ecology*, *Journal of Ecology*, and *Functional Ecology* present this joint Special Feature to provide an updated overview of the different ways 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 studying it, across the 29 manuscripts published in this Special Feature. We first provide a brief conceptualisation of resilience and ways of quantifying 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 subdisciplines

Resilience (Lt. *'resilire'*, to leap or spring back, OED, 1989) 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) 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). In engineering, resilience was first used to describe the stress (in terms of load bearing weight) that timber could sustain before breaking (Tredgold, 1818). 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 that resilience has become fundamental to ecological research. Early understanding of resilience was predicated on ecosystem stability and persistence despite disturbances (e.g. MacArthur, 1955), where disturbances represent a/biotic factors displacing the system away from its stationary equilibrium (Holling, 1973). Ecological systems were understood to persist in determined states, representing stable and equilibrium conditions to which the system is assumed to return back to following any disturbance (Lewontin, 1969; May, 1977). 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.

The first formalisation of the term resilience in ecology - that we are aware of - was made by Holling (1973), although he already used the term in some of his earlier studies (e.g. Holling & Goldberg, 1971; Holling & Orians, 1971). Holling 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; 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). 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). 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"* (*sensu* Holling, 1973).

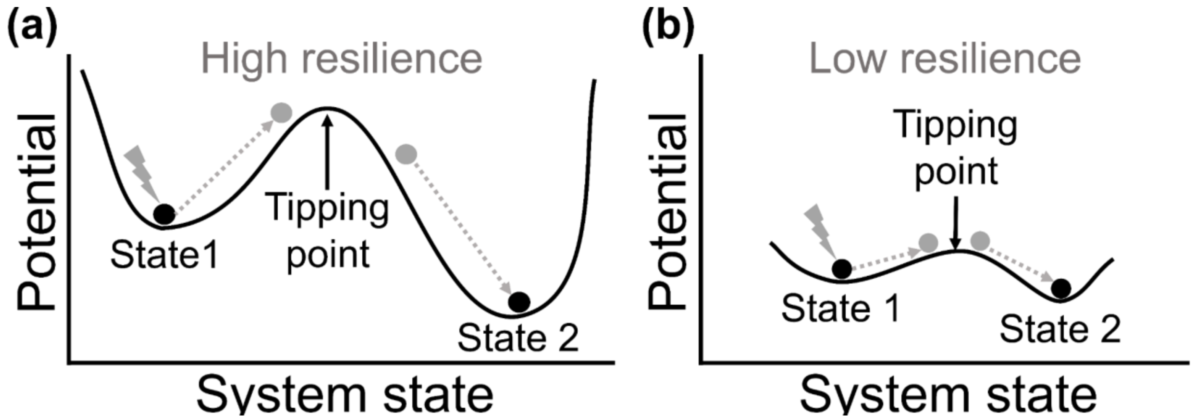

Figure 1. Classical analogy of the rolling ball to represent the resilience of an ecological system according to Holling (1973). Each black ball represents the stable state of the system, whereas the grey balls illustrate the potential trajectory of the system. The basins represent the potential system states. Lightning symbols represent a disturbance to the system. 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 a more extreme disturbance will generally 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). Engineering resilience defines resilience as the process of *recovery of the system* following a disturbance (Pimm, 1984). This view considers resilience to be a component of system stability (Donohue et al., 2013; Pimm, 1984), and often assumes that a system can only have a single stability regime (Holling, 1996). 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). These definitions of ecological *vs.* engineering resilience have diverged substantially in the ecological literature (Brand & Jax, 2007). More recent views consider that resilience encompasses multiple components describing both resistance *and* recovery as described above (Hodgson et al., 2015; Ingrisch & Bahn, 2018).

Measuring resilience across ecological systems

Whilst theory helps to conceptualise phenomena such as resilience, empiricism requires specifics. This need is precisely what the title of this Special Feature alludes to: “Reconciling resilience across ecological systems, species, and subdisciplines”. Ecological systems operate 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; functional composition of species in a food web, Ings et al., 2009). All systems function in terms of how components interact, such as interaction between species (e.g. predation pressure, Donohue et al., 2017), progression through life history stages (e.g. maturation rate, Stearns, 1992), or interaction between individuals (e.g. breeding effort, Ricklefs, 1977). 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), at various output levels (individual, population, community). To quantify resilience (i.e. the capacity of a system to deal with change), one needs to (1) consider how structure and function are defined, as well as in which ways these are affected by disturbance (i.e. “change” imposed on the system), (2) identify relevant measures of system outputs (i.e. the best understanding of system “capacity”), and (3) develop metrics to quantify those outputs at the appropriate level of organisation, which can vary both between and within study species and systems (i.e. best ways to measure capacity of the system to respond to change).

In population ecology, resilience has been studied for decades(Harrison, 1979; Neubert & Caswell, 1997), though not necessarily with explicit recourse to resilience theory (e.g. Stott et al., 2011). 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). Simple (density-independent and non-stochastic) conceptualisations assume that populations converge to a stable state defined by the relative proportions of life cycle (st)ages and maintained by the vital rates of the population (Caswell, 2001). However, populations are frequently 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). Resistance and return rate of a structured population can thus be measured relative to its pre-disturbance population size, growth, and/or structure (Caswell, 2001; Stott et al., 2011). Despite the clear links between these concepts and resilience theory, the connections were not formalised until recently (Capdevila et al., 2020). 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* Caswell, 1976), but could also be understood in terms of “composition” using taxonomic, phylogenetic or functional groupings of species (Carmona et al., 2016; Pérez-Valera et al., 2018). Community structure and composition may be measured in a multitude of ways, such as measures of species richness, numerical abundance, biomass, or phylogenetic diversity (Ings et al., 2009; Tylianakis et al., 2008). 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). The ‘state’ from which a community departs or to which it may return may be linked to those measures mentioned earlier in this paragraph or others (e.g. Cole et al., 2014; Yang et al., 2019). 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). 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), more recent theory has shown that complexity can be stabilising (Mougi & Kondoh, 2012; Qian & Akçay, 2020).

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), an emerging area of research is to quantify the resilience of ecosystem functions (Oliver et al., 2015). Focusing on community structure and/or 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). 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). Consequently, similar ecosystem functioning might be achieved by different communities (Gallagher et al., 2013), 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* (Oliver et al., 2015). Functional resilience, *"the degree to which an ecosystem function can resist or recover rapidly from environmental perturbations"* (*sensu* Oliver et al., 2015), incorporates a more recent view of resilience.

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 subdiscipline, the approach, and the system through which the authors study resilience (Figure 2). Perhaps as a legacy of early works (Holling, 1973; Pimm, 1984), almost half of the contributions in this Special Feature examine resilience at the level of communities (Figure 2a). Yet, a number of contributions cut across different levels of organisation, with a large proportion of the works studying resilience levels at the interfaces of community, population and functional perspectives (Figure 2a). 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 lie 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). These theoretical approaches have sometimes been challenging to apply to “real world” systems, hampering the use of resilience in applied disciplines (Hodgson et al., 2015; Ingrisch & Bahn, 2018). In this Special Feature, most of the contributions are observational studies, with a large proportion combining experimental and observational approaches (Figure 2b). Such a combination of approaches is important to provide a better understanding of the resilience of ecological systems. For example, experiments might help to unravel processes promoting resilience, which might be more difficult to observe in the field (Hoover et al., 2021; Jones et al., 2020; Lipoma et al., 2021). 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).

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, with a relatively large proportion studying resilience by including multiple taxonomic groups, though these are mostly theoretical studies (Figure 2c). While focusing on a single system can simplify experimental and observational studies (e.g. only primary producers in a community), where feasible, incorporating multiple components of the system (e.g. further trophic levels) will render a better understanding of it as a whole.

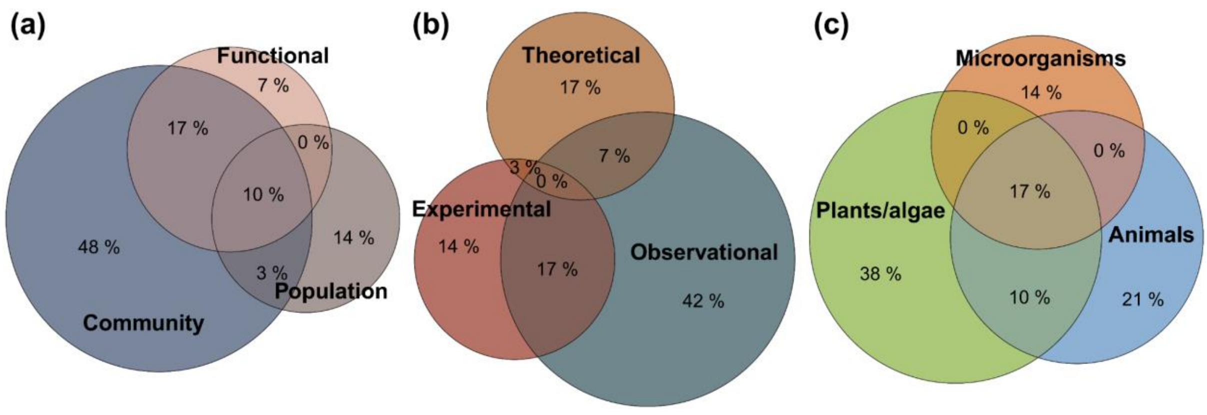

Figure 2. Venn diagrams showing the domain of operation of the 29 manuscripts included in the joint Special Feature "Reconciling resilience across ecological systems, species, and subdisciplines". The different panels show the proportion of contributions according to: **(a)** the ecological subdisciplines, 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 species or taxa studied, classified as plants/algae, animals, and/or microorganisms. Conceptual contributions are assigned to the three ecological subdisciplines 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) and Van Meerbeek et al. (2021), 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 definitions. Delettre (2021) 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); 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; network analyses, Blüthgen, 2010; spatial analyses, Dale & Fortin, 2014), and sharing of methods and tools will be advantageous to everyone. Using common “currencies” of the components of resilience/stability (e.g. Capdevila et al., 2020; Clark et al., 2021; Ingrisch & Bahn, 2018) -or at least determining “conversion factors” across different metrics - will make comparisons among studies possible, opening up the possibility of much-needed global assessments of resilience.

Understand resilience under different disturbance regimes

Resilience research is inherently linked to the properties of the disturbances altering ecological systems (Bender et al., 1984). 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 press) (Jentsch & White, 2019). Hence, accounting for different disturbance regimes is crucial to understand the resilience of ecological systems to global change, particularly so because a change in the natural disturbance regime can have profound impacts on 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) and stability (Miner et al., 2021) 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 of rocky intertidal communities from the whole of the U.S. West coast, to quantify the temporal and spatial community changes as a measure of stability. Likewise, Serra et al. (2021) explore the influence of vegetation clearing frequency and forest age on the recovery. The authors quantify resilience as a measure of the recovery of the number and diversity of soil macrofauna in the Brazilian Amazon.

The effects of multiple disturbances often compound one another in ecological systems (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) explore the interactive effects of land-use and weather variability on the rate of change of vegetation towards the primary forest, which they consider to be the reference state of the system. Their findings 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). Nowicki et al. (2021) highlight how trophic cascades, through the loss of predators, can exacerbate the impacts of extreme climatic events on the temporal changes in seagrasses and macroalgae cover in Western Australia, using initial cover as reference state. Similarly, Nelson et al. (2021) report the interactive effects of warming and drought on both resistance and recovery of invertebrate community abundance 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). 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). 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). In this sense, Leizeaga et al. (2020), report a low sensitivity to droughts in bacterial growth, fungal growth and respiration that have been historically affected by high drought frequency in a gradient of precipitation in Texas, USA. Hoover et al. (2021), demonstrate that the long-term effects of seasonal droughts on soil moisture can impact the resistance and recovery of plant biomass and phenology in Colorado, USA.

Webster et al. (2021) show how following extreme rainfall events the resistance to changes in biomass and leaf density of seagrass populations, and the recovery to pre-disturbance historical values, depends on the salinity levels to which these have been exposed previously. Leverkus et al. (2020) use a meta-analysis approach to highlight how local environmental factors also play a key role in the resilience of trees to logging. Also, Ovenden et al. (2021) 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) show that topography and vegetative structure influence of on the resistance and recovery of forest vegetation cover and heterogeneity in California's Sierra Nevada mountain.

Integrating multiple levels of biological organisation

Ecological systems are often studied at different levels of biological organisation (individuals, populations, communities). However, by 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. 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) show that specific traits can impact resilience at a population level: 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). In this context, Paniw et al. (2021) show a high degree of complementarity between demographic and functional traits in facilitating community composition and cover resilience to droughts. For example, vital rates are more important in explaining total and individual species resilience, while functional traits matter more to explain compositional resilience.

Carnicer et al. (2021) combine ecophysiological and demographic metrics to determine the resilience of sessile oaks (*Quercus petraea*) 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. The authors use 20 different resilience, resistance and recovery indices comparing secondary growth before and after disturbance. Muñoz et al. (2021) combine demographic and community data to show that the resilience of tropical forests is driven by autogenic regulation. 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

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) reveal that recovery and resistance are negatively correlated with one another using both experimental microbial systems and theoretical models, suggesting that resistance could be inferred from recovery and *vice versa*. Likewise, Jones et al. (2020) show that both the resistance and recovery of plant communities to pulse disturbances (*i.e.* sudden events) are similarly affected by flooding stress gradients in salt marshes in Louisiana, USA. Moreover, it is key to understanding 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) demonstrate that flood events can alter the correlations between five 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). Global threats, such as global warming (IPCC, 2021) or habitat loss (Newbold et al., 2015), are likely to continue to impact ecosystems worldwide even in the most optimistic conservation policy scenarios (Leclère et al., 2020). 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). 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., 2020; Amniote, Myhrvold et al., 2015). In this Special Feature, Bonhomme et al. (2020) 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. They show that resilience, 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) 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) 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) use adaptive population-dynamics models to indicate that herbivory networks and their high degree of specialisation show robustness 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. Likewise, Thakur et al. (2021) 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 can promote imbalance in the structure of food webs due to differences in the resilience of the components of a system. Li et al. (2021) demonstrate that energetic constraints at the trophic group and food web level enhance resilience by dampening the strength of destabilizing positive feedback loops. Jia et al. (2020) 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)

demonstrate that the role of protected areas in providing resistance to species invasions, measured indirectly as the lack of invasive species, 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 address some of 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). 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. While distinctions such as ecological *vs.* engineering resilience have been helpful in the past, contemporary frameworks might provide a more holistic approach to integrate the different components of resilience (Capdevila et al., 2020; Hodgson et al., 2015; Ingrisch & Bahn, 2018). Thus, identifying the variables of interest

and how they are measured, within such frameworks, will help cohesion and comparison across studies.

(2) *Use common metrics to measure resilience.* Studies should aim to measure resilience using standardised metrics that are applicable both in theoretical and empirical studies, and that are comparable among different systems. For example, measuring the relative change in abundance before and after a disturbance could represent a measure of resistance in both communities and populations. In this sense, Ingrisch & Bahn (2018), provide an extensive review on how to standardise measures of resilience across systems. Using a unified approach will facilitate comparisons among different systems and scales of biological organisation (Clark et al., 2021; Ingrisch & Bahn, 2018), 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), as well as contributing to improve our mechanistic understanding of how ecological systems achieve resilience.

(3) *Define the pre- and post-disturbance state*. Independent 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. Defining a reference state can be achieved either by characterising the system before the disturbance or by using undisturbed control treatments (Ingrisch & Bahn, 2018).

(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). It is therefore important to clearly define the nature of the disturbance affecting that determined system. That is, distinguishing whether these are pulse (e.g. storm, fire), or press disturbances (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). 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. Understanding the impact of different disturbance regimes on resilience is therefore particularly important, given existing and expected increases in intensity and frequency of large disturbance events due to climate change (IPCC, 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). Bringing consensus to how resilience is conceptualised will render a better understanding of resilience across diverse ecological systems by framing it in terms of consistent components. This consensus of course requires clarity in how these components 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 develop and apply effective management actions, informing where to allocate the inherently limited resources for nature conservation.

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Authors contributions

P.C., I.S., and R.S.-G. set the foundations to the special feature. P.C. coordinated its development and integration. I.O.M., D.B.S., R.L.G.R., H.W. and M.B. summarised most of the contributions to the Special Features and provided feedback to initial and final versions of the manuscript. P.C., I.S. and R.S-G. wrote the first version of the editorial and integrated feedback from co-authors and reviewers. All authors contributed to the article and gave final approval for publication.

Data availability statement

No new data were used in this manuscript

Conflict of interest statemen

Imma Oliveras Menor and Iain Stott are Associate Editors of Journal of Ecology, but took no part in the peer review and decision-making processes for this paper. Matthew Barbour, Rafael Raimundo, Daniel Stouffer, and Hannah White are Associate Editors and Roberto Salguero-Gómez is Commissioning Editor of Journal of Animal Ecology, but took no part in the peer review and decision-making processes for this paper.

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