Understanding and applying biological resilience, from genes to ecosystems

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ABSTRACT

The natural world is under unprecedented and accelerating pressure. Much work on understanding resilience to local and global environmental change has, so far, focussed on ecosystems. However, understanding a system's behaviour requires knowledge of its component parts and their interactions. Here we present a framework for understanding 'biological resilience', or the processes that enable components across biological levels, from genes to communities, to resist or recover from perturbations. Although ecologists and evolutionary biologists have the tool-box to examine form and function, efforts to integrate this knowledge across biological levels and take advantage of big data (e.g. ecological and genomic) are only just beginning. We argue that combining eco-evolutionary knowledge with ecosystem-level concepts of resilience will provide the mechanistic basis necessary to improve management of human, natural and agricultural ecosystems for better resilience.

KEYWORDS Eco-evolutionary dynamics; evolutionary ecology; macroecology; ecology; ecological resilience; applied management; forestry; crops; health

IMPACT STATEMENT

Resilience to environmental change will depend on ecological and evolutionary processes operating across all biological levels of organisation, yet integrating this knowledge for application is only just beginning.

Introduction

The Anthropocene is characterised by the pervasive impact of human activity on all aspects of life on earth (Lewis & Maslin, 2015). Human-driven climate change and overexploitation of natural resources, as well as increasing human population densities and urbanisation, are placing progressively larger areas under human influence (Ellis, 2015), and conspicuous perturbations include increased and/or more variable temperatures (and associated events such as droughts and fires), direct anthropogenic alterations (e.g. pollution, land-use changes, habitat fragmentation), and invasive species. Even the world’s topology has changed, as global movement of individuals and goods erodes biogeographical barriers (van Kleunen et al., 2015). These environmental changes put ecosystems under unprecedented and accelerating pressures, inducing regime shifts (Scheffer, Carpenter, Foley, Folke, & Walker, 2001), causing loss of ecosystem services (Foley, 2005), and even changing the course of evolution (Sullivan, Bird, & Perry, 2017). There is therefore an urgent need to determine why some species, communities or ecosystems decay while others persist or adapt (Sutherland et al., 2013), and then implement this knowledge for improved management practices that can reverse or mitigate damage (Weise et al., 2020).

In ecology, ‘resilience’ has attracted great interest as a concept that describes how ecosystems recover to an antecedent state following a disturbance (‘engineering resilience’; Pimm, 1984), or absorb change and resist large shifts in ecosystem function (‘ecological resilience’; Holling, 1973). Ecological phenomena are the result of a myriad and complex array of responses by different components across biological levels, that may or may not interact. Therefore, resilience has typically been studied at the ecosystem level (Capdevila et al., 2021) with current work recognising that the resilience of ecosystems is likely to depend on both its ability to resist and recover following disturbance (Ingrisch & Bahn, 2018; Capdevila et al., 2021). However, the mechanisms that determine whether an ecosystem resists, or what shapes the trajectory of its recovery, remain largely unknown (Oliver et al., 2015; Capdevila et al., 2021). In part, this may be because studying resilience at the level of the ecosystem reduces our power to identify how and why resistance and/or recovery responses occur (Gladstone-Gallagher et al. 2019): understanding the behaviour and interactions of a system’s component parts is essential to understand and forecast ecology (Levin, 1992). Furthermore, there has been much discussion as to how resilience can be measured, with debate over what metrics are most relevant (e.g. Hodgson et al. 2015). Studying lower biological levels in isolation might make these metrics easier to identify (e.g. population size, individual fecundity, genetic diversity, Figure 1 inset) but it hampers detection of connections between seemingly isolated biological events. How can we deal with this complexity to identify the critical components and indicators of resistance and recovery?

Here we propose that this can be achieved by adopting a ‘biological resilience’ framework (Figure 1) where we (1) test ecosystem-level resilience concepts (i.e. resistance and recovery responses to perturbations; Pimm, 1984; Holling 1973) across lower levels of biological organisation and (2) harness knowledge provided by the eco-evolutionary history of adaptation to past perturbations (Dakos et al., 2019; Sgrò et al., 2011). In this way, biological resilience acknowledges that processes occurring within and between components across biological levels, from genes to communities, shape how systems resist or recover from perturbations. This framework stands out from recent calls to encourage analysis of resilience across systems, scales, and biological levels (e.g. Gladstone-Galagher et al. 2019; Capdevila et al. 2021) as we explicitly acknowledge the crucial role of eco-evolutionary history, and encourage studies of resilience to dive deeper into uncovering the mechanisms and processes that afford resilience within individuals (e.g. genetic diversity, cellular response) and how these scale up to affect populations, communities and ecosystems. We first explore how the eco-evolutionary past provides context for present and future resistance and recovery responses, and then discuss why it is necessary to consider how abiotic and biotic perturbations can affect biological levels differently to detect mechanisms and underlying processes. Next, we outline three testable hypotheses to kick-start research into resilience across levels of biological organisation, from genes to cells, individuals, populations and communities. Collecting and integrating large amounts of data about how every biological component responds to a perturbation is often considered unrealistic. However, here we identify new opportunities emerging from the ongoing infusion of big data into ecology and evolutionary biology and stress the need to combine these data with experimental approaches. Finally, we discuss how considering resilience at the appropriate biological level(s) will enable advances in translating research into practice.

FIGURE 1 HERE

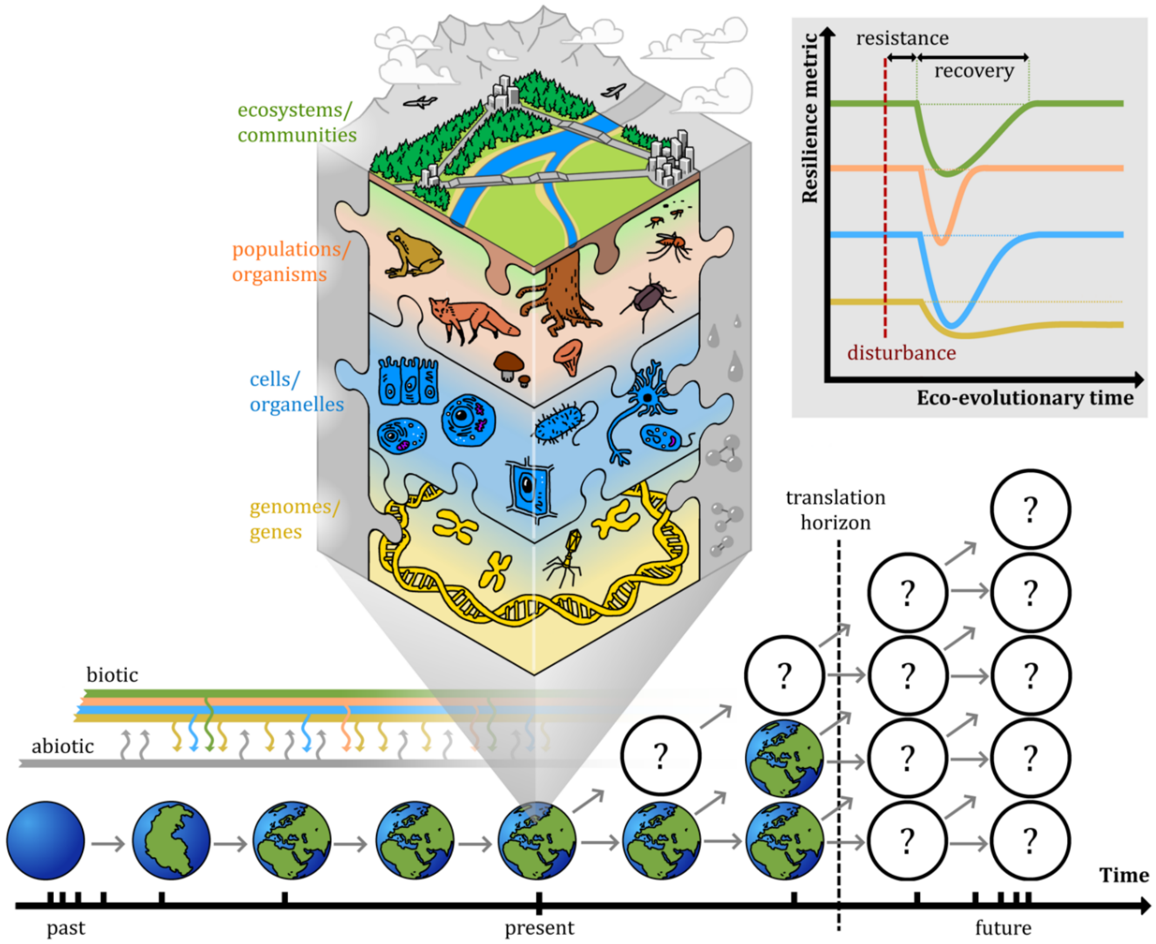

FIGURE 1. Biological resilience, or the mechanisms and processes that enable components across biological levels to resist or recover from perturbations (inset), is mediated by connections within and among levels of life (simplified here to genes and genomes, cells and organelles, organisms and populations, communities and ecosystems). Taking a biological resilience approach requires integrating knowledge about how the present state (centre focus) has been shaped by ecological and evolutionary responses to biotic (depicted by multi-coloured lines and levels) and abiotic (grey) perturbations and selection pressures in the past (time represented by a log-scale). Knowledge of biological resilience can then enhance the translation horizon (vertical dashed line, close in time) by reducing uncertainty in prediction trajectories (grey arrows) and improving accuracy of forecast outcomes (denoted by question marks within circles). Note that the resistance and recovery trajectories of biological levels may differ in both amplitude and temporal scale.

(Re)Placing resilience into an eco-evolutionary context

When Holling introduced ecological resilience in his landmark paper (Holling, 1973), he briefly suggested that a system's resilience is a product of its evolutionary history (1973:p.18). Most research conducted since, however, has lacked an evolutionary perspective (McGill et al., 2019; Oliver et al., 2015) and therefore much of the discussion, theory and examples of resilience in ecology lack a long time horizon. Similarly, eco-evolutionary biologists rarely study resilience explicitly in terms of resistance or recovery from a perturbation, nor do they consider how resilience might be conferred by processes that occur within or across the biological levels that form the focus of their studies (Dakos et al., 2019). This disconnect among fields may be because much of the work on resilience describes patterns at the ecosystem level (Oliver et al., 2015), whereas studies of evolutionary processes rarely scale to complex communities (Tylianakis & Maia, 2020). Indeed, focusing on how ecology and evolution shape patterns and processes within individuals and populations has attracted criticism for being too narrow to address large ecological problems (Carroll et al., 2014; McGill et al., 2019). Nevertheless, here we argue that taking an eco-evolutionary perspective in understanding biological resilience can provide information from the evolutionary past to improve our power to estimate both present and future states (Box 1). Rather than 'reinventing the wheel', this approach to understanding resilience ties into calls to apply 'resilience-thinking' from ecosystems to species (e.g Capdevila et al., 2021) and wider discussions in ecology and evolution about the need to rediscover connections among the fields (e.g. McGill et al., 2019).

Reading the past from the present state

Past perturbations leave their mark on biological entities, creating ecological and evolutionary 'memories' (Desai, 2009; Johnstone et al., 2016) that may influence responses to similar perturbations in future. At the level of genes, evolutionary history is manifested in variation introduced by mutation and/or migration (gene flow) as well as recombination (new combinations of genetic variation) that is filtered by natural selection or fixed by random genetic drift. Some of these variants may provide an advantage against a future perturbation, such as through acquired resistance against a parasite, pest or antibiotic encountered in the past (Bartholomé et al., 2020). On the other hand, perturbations that result in severe population bottlenecks can result in the loss of potentially beneficial variation and/or fixation of maladapted alleles, and thus have negative effects on resilience (Donelson et al., 2019). Similarly, past selection that strongly favoured specific alleles may also limit future resilience due to the loss of genetic variation required for new adaptation to take place (e.g. Afrotropical butterfly experiencing climate change induced variation in seasonality, Oostra, Saastamoinen, Zwaan & Wheat et al. 2018). Responses to past perturbations may also leave heritable epigenetic marks on the genome without causing changes to DNA sequences. These epigenetic ‘stress memories’ can affect how subsequent generations resist or recover from similar disturbances by influencing the regulation of genes (e.g. Holeski, Jander, & Agrawal, 2012; Pazzaglia et al., 2021), although the study of these processes beyond plants is only just beginning.

While genetic information should underpin the capability of an organism to respond (e.g. Waldvogel et al. 2020), there is now abundant evidence that single genotypes can generate different phenotypic responses to the same environmental perturbation (i.e. plasticity). Phenotypically plastic responses can be modified further depending on the composition, structure and spatial context of the perturbed population or ecological community (Thebault & Fontaine, 2010), and plasticity that evolved in the past can shape current distributions (Valladares et al., 2014). Behavioural modifications to a changing world are a common form of plasticity (Wong & Candolin, 2014) and can enable individuals and populations to resist fitness or demographic effects of perturbations. For example, when behavioural repertoires are transmitted within or across species (i.e. via horizontal and/or vertical social learning), individuals can acquire phenotypes that match environmental changes more quickly than by genetic adaptation (although these behaviours can also be maladaptive; Barrett, Zepeda, Pollack, Munson, & Sih, 2019), with potential to feedback on genetic change both within species and across communities if behavioural responses become maintained in space and time (Whitehead, Laland, Rendell, Thorogood, & Whiten, 2019). Current phenotypic responses may therefore reflect past phenotypic resistance or recovery, with or without concomitant genetic change. As a consequence, harnessing knowledge about the past will likely require integrating plasticity, epigenetics and genetic information (e.g. McNamara, Dall, Hammerstein, & Leimar, 2016) and has potential to provide a major advance across these fields.

At the level of the population or community, perturbations can reduce or increase individual or species diversity, and thus impact any future response to disturbances. For example, past climatic fluctuations in the Amazon basin have given rise to areas of more diverse avian fauna in the western parts compared to the south-east. Thus, the south-eastern parts are expected to be more vulnerable to ongoing stress posed by deforestation and climate change (Pontes-da-Silva et al., 2018). Community changes caused by past disturbances may also determine subsequent community assembly through complex cascading effects on species succession. For instance, when species re-colonize an area, or are reintroduced after a perturbation, the order in which species arrive may be important for community assembly (i.e. priority effect or founder control; Fukami, 2015) and future resilience. Disturbances may also fuel rapid evolution of populations, which can, in turn, alter community assembly (Legrand et al., 2017). Discussions regarding the role of genetic diversity and plasticity for resilience are therefore analogous to discussions about how species diversity or functional diversity promotes resilience at the ecosystem-level, and also how in some cases, turnover of species is necessary (e.g. Oliver et al. 2015). Determining whether the effects of past diversity on present states are generalisable across biological levels will be an important step in developing our understanding of biological resilience.

TEXT CONTINUED AFTER BOX 1

Box 1: Integrating ecology and evolution across scales

Evolutionary mechanisms (mutation, drift, migration, natural selection) generate changes in allele frequencies from one generation to another (i.e. microevolution) and, given sufficient time or conditions, can lead to large-scale changes that transcend species boundaries (i.e. macroevolution). Similarly, processes that influence ecology (e.g. density, connectivity, competition, species interactions) at smaller scales (e.g. within populations, communities) give rise to large-scale macroecological patterns (e.g. biodiversity and ecosystem function). Darwin made no distinction between micro and macro scales, nor did he separate ecology from evolutionary processes (see McGill et al., 2019). Over the 20th century, however, research in ecology and evolution specialised to specific scales and processes (McGill et al., 2019). Adopting a biological resilience framework, however, necessitates reintegration. How might this be achieved?

Eco-evolutionary dynamics provides a potential solution to reintegrate ecological and evolutionary processes across scales (Hendry, 2019; Ware et al., 2019; Bassar et al. 2021). Work in this rapidly developing field is increasingly scaling up from population-level studies (Schoener, 2011) to analyse how evolutionary processes impact ecological dynamics (and *vice versa*) in communities and even ecosystems (Ware et al., 2019), with explicit acknowledgement that interactions and feedback can occur across non-adjacent biological levels (e.g. see Figure 1 in Palkovacs & Hendry 2010 and in Ware et al. 2019). For example, a recent *in vitro* study propagated artificial bacterial communities of 34-species to test how initial species-level traits and rapid genetic mutation influenced changes in community-level species and genetic composition following pulses of antibiotic disturbance (Cairns, Jokela, Becks, Mustonen, & Hiltunen, 2020). Although communities appeared to respond to the disturbances according to classic processes of sorting by species' traits, rapid within-species evolution of antibiotic resistance also occurred. Critically, these new variants persisted and left signatures of evolutionary change, despite immigration of additional antibiotic-susceptible species and recovery of community composition. Studies of eco-evolutionary dynamics are also beginning to expand in scope and take a landscape perspective (Legrand et al., 2017; Nadeau & Urban, 2019; Tylianakis & Maia, 2020). Explicit consideration of habitat fragmentation and climate change on both the ecological responsiveness and rapid evolution of dispersal behaviour, for example, might resolve why some species are not experiencing range shifts as expected (Nadeau & Urban, 2019). The role of evolutionary feedbacks on ecosystem-level processes is also now beginning to attract attention, suggesting that evolutionary changes in the variation of traits may play an important role in shaping how and when ecosystems reach tipping points and possibly irreversible ecosystem change (Dakos et al., 2019).

At the macro scale, fusion of ecology and evolution has typically been limited (McGill et al., 2019). For example, phylogenetic ecology attempts to integrate macroevolutionary patterns into studies of community function, with studies suggesting that increased phylogenetic diversity can be critical for ecosystem stability (Cadotte, Dinnage, & Tilman, 2012), but sometimes not (Winter, Devictor, & Schweiger, 2013). There is much scope, however, for evolutionary history to provide further information than as indicators of relatedness (Swenson, 2019). For example, Zitnik and colleagues compared protein interactomes, complex networks of molecular interactions, across the tree of life to reveal how they evolve greater resilience to a loss of network connections over time (Zitnik, Sosič, Feldman, & Leskovec, 2019). At a different level of biological organisation, incorporating historical global temperature records, species-level functional traits, and rates of phylogenetic diversification is also helping to explain how microevolutionary history induces different macroevolutionary responses to temperature change across angiosperms (Sun et al., 2020). Understanding biological resilience will require a step-change from describing macro- or micro- scale patterns to demonstrating how evolutionary and ecological processes shape short- and longer-term responses to environmental change. Bridging ecology and evolution across these scales is still in its infancy (McGill et al., 2019) so adopting this framework could also provide stimulus to return to a more Darwinian integrated approach.

END OF BOX 1

Finding the right scale: Effects of perturbations vary across biological levels

Although natural systems can also face novel perturbations to those experienced in the past (Donohue et al., 2016), if we can uncover how elements of the system have responded to past perturbations, then this information will become useful for predicting current and future change. However, perturbations themselves can be complex and perturbations vary in intensity, duration, frequency and spatial extent, and can, depending on their nature, cause gradual changes in ecosystem functions and services, or lead to more drastic regime shifts (Barnosky et al., 2012). The impacts of perturbations can also vary across biological levels; for example, an adaptive mutation enabling a species to exploit the perturbed ecosystem can lead to community effects by outcompeting other species. Furthermore, perturbations are often simultaneous and these may be related directly, such as warmer temperatures and increased droughts, or indirectly, such as invasive species and eutrophication. The end result is often non-linear, with simultaneous perturbations having synergistic effects (Brook, Sodhi, & Bradshaw, 2008) or generating cascading processes (e.g. co-extinctions; Colwell, Dunn, & Harris, 2012). For example, communities often cope with increasing disturbances with minimal apparent signs of stress, but then rapidly collapse when the degree of perturbation reaches a tipping point (e.g. pollinator communities; Lever, van Nes, Scheffer, & Bascompte, 2014). Although increasing theoretical and experimental work suggests that collapse in natural systems can be anticipated by early warning signals (Scheffer et al., 2012), detecting these signals in highly variable real world systems remains a great challenge (Dakos et al., 2019).

Adopting a biological resilience framework could help to predict these events as incorporating a longer time horizon reveals resilience to be a dynamic and constantly evolving product of long term (co-) evolutionary, ecological and biogeographical processes (e.g. Baruah, Clements & Ozgul, 2020). Understanding how these processes operate at different biological levels of organisation is critical, as the rate of evolution for example is constrained by generation times that vary from minutes (e.g. cells and microbes) to centuries (e.g. trees), reproductive strategy influences opportunities for outcrossing and mutation, and migration can diversify or limit local genotypic and phenotypic variation. However, at present it remains unclear whether one level in particular will be of greater importance for predicting responses to current and future perturbations. Furthermore, while it is likely that responses of one level to a given perturbation will influence how multiple other levels respond, investigations into the carry-over effects of perturbations across biological levels are few and mostly focus on adjacent levels (e.g. changes in population influence response of communities, Strona et al. 2021). The composition, structure and spatial context of a perturbed population or ecological community also needs to be taken into account (Thebault & Fontaine, 2010). Range-edge populations, for example, can be comprised of a different set of individual response-types than those found in the range core (e.g. spatial sorting; Massot, Legendre, Fédérici, & Clobert, 2017) and potentially set up cascades of change across other biological levels (e.g. reduced genetic diversity; Sgrò et al., 2011), while fragmented habitats influence the degree to which species can reduce their exposure to perturbations by shifting, shrinking or expanding their range via dispersal (Fahrig, 2003), or by modifying physiological or behavioural responses (Baguette & Van Dyck, 2007). Spatial context also has fundamental implications for longer-term adaptation to environmental change as it shapes gene flow (Anderson et al., 2010). Integrating past and present distributions and habitats is therefore likely to be a key, albeit challenging aspect. Nevertheless, using evolutionary history as a ‘natural experiment’ and integrating information about adaptation explicitly into a resilience framework could provide a previously untapped resource for predicting how ecological systems respond to perturbations.

Biological resilience framework generates testable hypotheses

It is clear that determining how different biological levels resist and recover and buffer other levels from perturbations will be complex, and that harnessing available information from the past is not straighforward. However, theory and mathematical models lay the foundations for identifying what to measure from experimental and empirical systems and how to extract these observations from real data. For example, careful calibration of the effect of a perturbation with respect to the undisturbed state is necessary to obtain common metrics that are comparable across biological levels and study systems (Ingrisch & Bahn, 2018). Efforts to incorporate evolutionary perspectives into models of ecosystem-level responses (e.g. tipping points, Dakos et al., 2019; warning signals, Baruah et al. 2020) are beginning, and there is growing theory surrounding the ecological and evolutionary dynamics of resistance (e.g. antibiotics, Meredith et al., 2018) and rapid genetic adaptation to ecological change (e.g. Waldvogel et al., 2020). New theory is, however, required to bridge resistance and recovery responses across biological levels. A long-term problem in ecological modelling is that theoretical models are good for understanding causality, but difficult to test critically against data, whereas statistical models are correlative, and thus may not identify the relevant underlying mechanisms even if they fit the present data well. Furthermore, incorporating complex processes across many levels of biological organisation within one model is both computationally and mathematically challenging.

Overcoming these shortcomings is especially critical for studying biological resilience, because it is likely to often be driven by the interaction of many complex processes at many levels of biological organization. Nevertheless, considering the effects of perturbations across biological levels in terms of eco-evolutionary form and function helps generate hypotheses concerning the role of historical disturbances in shaping future resilience: (i) past experience primes a biological entity to cope with future disturbances of a similar nature. Alternatively, but not necessarily mutually exclusively, (ii) populations and communities exposed to more variable environments and higher levels of disturbance over the long term are expected to be most resilient. However, even these may accrue a resilience debt if the magnitude and frequency of the disturbances differ too much from their historical disturbance regimes (Waples et al., 2009). Finally, (iii) even without long-term disturbance histories, rapid adaptation may improve resilience against specific stressors. This may, however, come at the cost of decreased resilience in the longer term because of reduced pre-existing diversity after rapid adaptation or altered species interactions (Sgrò et al., 2011; Stange, Barrett, & Hendry, 2020). Aspects of these hypotheses have already begun to be tested (Table 1), but not yet across biological levels within a relevant system.

TEXT CONTINUED AFTER TABLE 1

TABLE 1. Three hypotheses regarding how the ecological and evolutionary past shapes current and future responses to environmental change, and the multiple study approaches required to understand this biological resilience (with examples).

Hypotheses	Methodological approaches	Examples
(i) past experience primes a biological entity to cope best with future disturbances of a similar nature		
	Describe patterns using correlational or before-after survey data	• Current and future responses are mediated by past infection using long-term data on Soay sheep (Leivesley et al., 2019) • Co-occurrence of taxa before and after Holocene (Lyons et al., 2016)
	Use modelling and simulations to generate testable predictions	• Transgenerational priming (Kokko et al., 2017)
	Perform experimental perturbations in -cosms or field settings	• Experimental evolution with yeast (López-Maury et al., 2008) • Legacy effects of drought exposure on microbial communities (Krause et al., 2018) • Transgenerational acquired resistance in model plants (Holeski et al., 2012) • Resurrection studies (Franks et al., 2008)
	Interrogate findings with data from natural experiments	• Captive and wild songbirds respond differently to temperature perturbations (Verhagen et al., 2020)
(ii) diversity of environments and disturbances in the past generates greater resilience in the future		
	Make use of long-term survey data and/or big ecological and genetic	• Paleological history (Barnosky et al., 2017) • Ecological and evolutionary memory (Waples et al., 2009; Zitnik et al., 2019)

	datasets (including ancient DNA) to measure past diversity	• Adaptive genetic diversity (Sgrò et al., 2011)
	Use modelling and simulations to generate testable predictions	• Predicting a species response to environmental change when preadaptation of community differs (de Mazancourt, Johnson, & Barraclough, 2008)
	Perform experimental perturbations in -cosms or field settings	• Resurrection studies (Franks et al., 2008)
	Interrogate findings with real-world examples, e.g. natural experiments	• Biological invasions (Simberloff et al., 2013)
(iii) rapid adaptation to match current conditions reduces future resilience		
	Compare current resilience of biological entities and search for signs of rapid adaptation in the past	• Genome-wide scans in forest trees to detect adaptation to aridity (Steane et al., 2014)
	Use modelling and simulations to generate testable predictions	• Evolutionary rescue (Bell, 2013)
	Experimentally induce a novel perturbation in cases where rapid adaptation is present vs. absent	• Resurrection studies (Franks et al., 2008)

Approaches to understand biological resilience

Understanding biological resilience will require concerted multidisciplinary research programmes where the effects of a perturbation (or multiple stressors) in terms of resistance and recovery responses are investigated across different levels, and where feedback among levels is also measured explicitly (Table 1, Figure 1). At present, research into coral reef resilience provides a worked example: surveys and experiments have demonstrated that different coral species exhibit different degrees of resistance and recovery to similar stressors (Hughes et al. 2010). Comparing the species' evolutionary history provides some insight into why: a recent study suggests Caribbean corals show lower recovery than Indo-Pacific corals due to an evolutionary bottleneck 2.8 million years ago that favoured large and long-lived species with low rates of recruitment (Roff 2021). Efforts to investigate genomic predictors of coral bleaching (Fuller et al. 2020), and even to assist evolution towards more resilient forms (van Oppen et al. 2015), are also now attracting wide attention (Bay & Guerrero 2020). Furthermore, mapping dependencies of coral-fish species based on natural history and fitting structural equation models has recently suggested that coral loss may lead to substantial negative change in fish diversity and biomass worldwide, with effects extending beyond the fish species directly dependent on corals (Strona et al. 2021).

There are many other studies beyond this example that report genetic-, phenotypic-, or community-level changes along environmental gradients or responses to natural changes, but far fewer either consider more complex environmental scenarios (e.g. multiple or sequential stressors) or how the effects at one biological level may affect others. As such, much of the current work in understanding biological resilience (even if not yet couched in this terminology) relies on surveys and correlations that are carried out at one level. For example, 'which genes contribute to more resilient phenotypes?' (Papakostas et al., 2012), 'which populations are more resilient to certain perturbations?' (Thom et al., 2019) or, 'which species are most affected by which particular aspects of a perturbation?' (Strayer, 2010). Furthermore, the results of experiments, particularly into resilience at the cellular (López-Maury, Marguerat, & Bähler, 2008) or genetic levels (Kokko et al., 2017), are often not interpreted in a broader ecological context or compared to available data from natural populations (Verhagen, Tomotani, Gienapp, & Visser, 2020). Here we explore how we can move beyond studying the effects of single perturbations or single species or levels and progress towards more complex experimental designs and assessments of more complex situations in the wild.

TEXT CONTINUED AFTER FIGURE 2

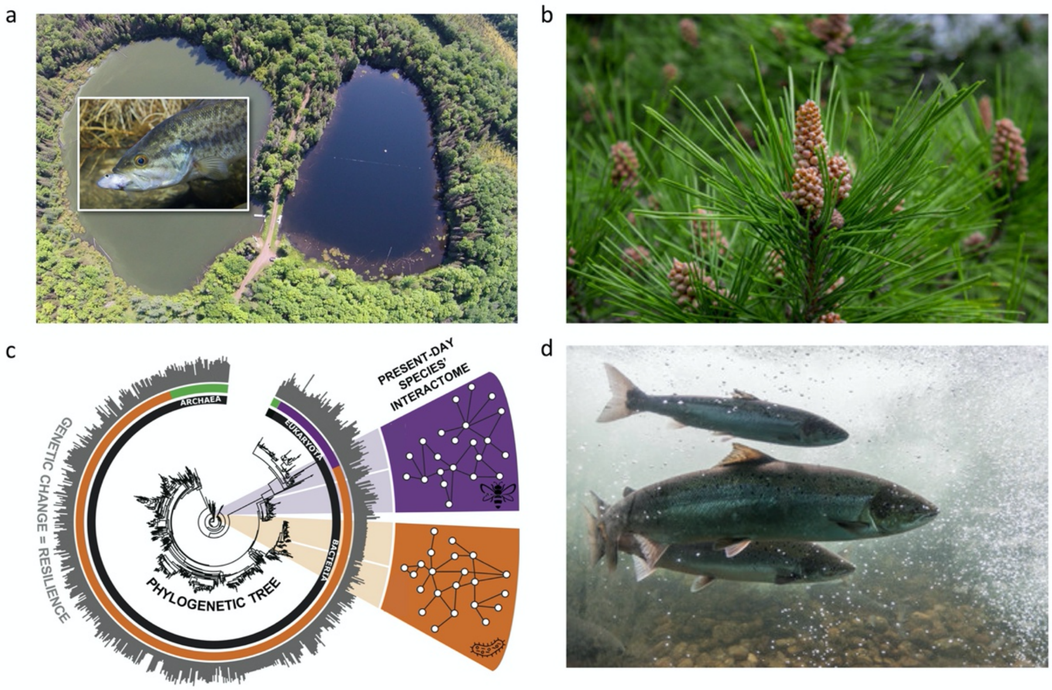

FIGURE 2. Examples of approaches to study biological resilience within biological levels (levels and approaches in bold): (a) **Communities & ecosystems:** Predators (inset) were introduced into a lake (left) in a **semi-natural experiment** and their abiotic and biotic effects were tracked over 3 years to test warning signals of a regime shift in an aquatic food web (compared to an undisturbed lake, right), as predicted by **modelling** after **long-term monitoring** (Carpenter et al., 2011). (b) **Individuals & populations:** Various **modelling** methods, coupled with data from **semi-natural experiment** genetic provenance trials for *Pinus sylvestris*, investigated how variation in population-level responses to environmental change (i.e. phenotypic plasticity and local adaptation) can influence species-level range expansion under climate change (Valladares et al., 2014). (c) **Cells & proteins:** Over 8 million protein-protein interactions from 1,840 species were **data mined** to **model** protein interactomes (examples are shown for a eukaryotic, purple, and bacterial, orange, species). Species' level evolutionary histories and ecological characteristics were then used to investigate how resilience varies at the protein level (Zitnik et al., 2019). (d) **Genes & genomes:** A **wild survey** of gene-linked loci and gene ontology information in *Salmo salar* populations tested the hypothesis that stronger signals of selection occur in loci with immune-related functions (Tonteri, Vasemägi, Lumme, & Primmer, 2010).

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To enable future studies to cover multiple biological levels, incorporating standardized collection of data and sample material from multiple biological levels (e.g. genetic material, phenotype and community structure) into geographical surveys and long-term studies is a good starting point. If these standardised surveys are conducted over multiple seasons, years, or generations, this long-term monitoring has the potential to facilitate (i) detection of subtle responses and/or subtle perturbations, (ii) replication over time, and (iii) detection of ecological and evolutionary memories (Grant et al., 2017). The same recommendation is relevant for “opportunistic” sampling following the (often unexpected) formation of a resilience-relevant gradient/difference. Data for multiple biological levels at sites that have experienced a heat wave for example, or an oil spill or chemical release, can either be compared to those of a nearby site that did not experience the perturbation (Ellegren, Lindgren, Primmer, & Møller, 1997), or in the event that surveys of the affected sites were conducted prior to the perturbation, a ‘before vs. after’ analysis can be conducted (Bergen et al., 2020). Second, the prehistoric and paleoecological record is an important potential source of survey data, as it is now becoming tractable to incorporate it with extant data (Fraser et al., 2020). This paleo-perspective could offer natural experiments: data are available to potentially help explain how community assembly (and disassembly) works when time spans are increased (Lyons et al., 2016), for example, or how genetic structure and adaptations respond to perturbations ranging from major extinctions to rapid climate change or species invasions over long time periods (e.g. Frisch et al. 2014).

A major challenge for survey approaches mentioned above however is to disentangle the effects of co-varying environmental characteristics (e.g. photoperiod and temperature along a latitudinal gradient, or simultaneous drought and reduced food availability). Therefore, experiments in semi-natural (e.g. *in vitro* microcosms or outdoor mesocosm setups) or field settings (e.g. Figure 2a,b; ponds/tanks, forest/field plots, enclosures suitable for small mammals, or free-ranging individuals and populations) are an essential third approach to test how resilience occurs across biological levels, and offer an attractive compromise where ‘real-world’ conditions are partly retained but where some manipulation and/or control is nevertheless possible, together with replicates (Hendry, 2019). These experiments can range greatly across organismal scale, geography, and biological levels (e.g. Figure 2b; Valladares et al., 2014), and can also be conducted alongside interventions to mitigate species decline or change in ecosystem function (e.g. conservation actions including introductions of individuals or translocations of populations, Franks et al., 2020), if the selection of individuals or species to be moved is designed to test the relative resilience of different characteristics (e.g. social behaviour: Goldenberg et al., 2019, genetic diversity: Stange et al., 2020). Although further removed from 'real world' conditions, common garden experiments (i.e. the rearing individuals in a controlled environment under common conditions) could be used to study responses to environmental or anthropogenic stressors by adding 'treatments' such as thermal stress, disease, or changes in community (e.g. flour beetles: Koch & Guillaume, 2020; burying beetles: Sun & Kilner 2020). Here, environmental differences can be eliminated or specific environmental factors can be tested so that the extent of resilience that is plastic versus evolutionary (e.g. fish: Papakostas et al., 2014, crops: Bustos-Korts et al., 2019) can be measured. Resurrection-type experiments are also a promising approach in some taxa, when genotypes that have experienced varying conditions are available for tests under experimental conditions (Franks et al., 2008). Experimental designs like these outlined above have been criticised for over-simplifying ecological processes, however taking an experimental approach will be essential to tease apart the relative effects of multiple stressors, either simultaneously, or sequentially, or at different stages of an organism's life-history. Results of simpler experimental designs or studies at single biological levels may also enable refining hypotheses and study designs for the future study of other biological levels in more complex conditions.

Fourth, eco-evolutionary and environmental Big Data, from the molecular to the ecosystem level, provides a broad and expanding scope, particularly when datasets span space and/or time. At the molecular level, Big Data on genes and genomes (NCBI; National Library of Medicine (US) & National Center for Biotechnology Information, 1988) and their function (Gene Ontology (GO; Ashburner et al., 2000) and Kyoto Encyclopaedia of Genes and Genomes (KEGG; Kanehisa, Sato, Furumichi, Morishima, & Tanabe, 2019) databases are rapidly increasing. These databases are designed to be taxonomically comparable, or even species-neutral, to enable transfer of functional annotation (molecular function, biological role and cellular location) or gene network information derived from model organisms to inferred orthologues in newly sequenced species. If the current focus on medical science or morphological characters broadens to encompass functions in response to ecological stimuli (Primmer et al., 2013), then big genomic data will become an even more useful resource for studying the molecular basis of biological resilience (e.g. Figure 2c,d). Similarly, finding the most potent data sources for reconstructing time series into the past still requires innovation, but this approach carries considerable promise for analyses of resilience to changes that have already occurred. For example, abiotic data from the last few decades are now openly available (e.g. CORINE (Copernicus Land Monitoring Service, 2018), USGS (USGS, 2020), WorldClim (Fick & Hijmans, 2017)) and big data on species occurrences (GBIF (GBIF.org, 2020)), traits (TRY (Kattge et al., 2020), Coral Trait Database (Madin et al., 2016)) and abundances through time (Ovaskainen et al., 2020) are becoming available at an increasing rate. Collecting data of changes in the deeper past requires continued efforts in digitising physical collections (museum specimens; The NOW Community, 2020) and application and development of new techniques for data extraction and analysis (Fraser et al., 2020).

As the resolution and density of data increases, and new algorithms that make use of large-scale computational resources become available, the possibilities to find and match comparable drivers-to-biotic-units cases will increase. However, most of the global databases at present contain (partially) non-comparable data, and experimental data are rarely combined with observational data despite potential to increase credibility of conclusions (Kotta et al., 2019). Existing data can be analysed by taking advantage of newly developed methods that minimise biases in unrelated or uncertain data (e.g. Bayesian approaches; Ovaskainen & Abrego, 2020), or when fully comparable data are available, by using mechanistic models that allow moving beyond correlative analyses (e.g. individual-based models; DeAngelis & Grimm, 2014). Any data analysis must, however, be based on theoretically sound models as blindly applying black-box machine learning algorithms to interpret data may lead to conclusions that are not biologically sensible (Hartmann, et al., 2017). Moreover unbalanced sampling may lead to incorrect interpretations if not accounted for in analyses (Foster et al., 2021) – a problem similar to discriminatory biases in social data applications of machine learning. Other areas of artificial intelligence, such as symbolic regression (Udrescu & Tegmark, 2020), hold much promise to improve our ability to predict the consequences of ongoing and future change as they can provide both power and interpretability of natural laws.

Translating biological resilience from research to management and conservation

While there have been many calls to adapt management and conservation of natural resources to improve resilience to environmental change, substantial obstacles remain before this can be realised. First, managers require indicators at levels most appropriate for decision-making. Many of the indicators currently available, however, are system-wide or remain challenging to quantify (Dunbar et al., 2020; Ingrisch & Bahn, 2018; Standish et al., 2014). Indicators based on species diversity and habitat connectivity, for example, allow assessment of large-scale patterns (Dunbar et al., 2020), but they are less helpful for management of more tractable system components. Similarly, current discussions around genetic diversity are often difficult to reconcile with ecosystem health as they operate at different timescales (but see Kettenring et al. 2014 for a notable example in plants). Second, attempts to manage 'for resilience' typically focus on avoiding thresholds or tipping points. Rather, managers need to compare alternative choices, assess potential outcomes with greater certainty than is currently possible, and manage adaptively (Weise et al., 2020). Third, management approaches largely aim for current or historical states, rather than attempting to forecast outcomes according to novel future conditions. This is especially problematic when the time horizon is long (Weise et al., 2020), for example in forestry and agriculture where long or uncertain time horizons play a large part in the difficulty to translate recommendations (Dhankher & Foyer, 2018; Millar, Stephenson, & Stephens, 2007). Determining how resilience operates at different biological levels has potential to move beyond this stalemate, by using the ecological and evolutionary history of components of the system (Fraser et al., 2020; Yang et al., 2019) to better predict future states under different management scenarios (e.g. Box 2).

TEXT CONTINUED AFTER BOX 2

BOX 2.

Here we highlight the broad potential for the applicability of a biological resilience approach by briefly exploring how it could influence translation and management in two divergent examples: (i) forestry and agriculture, and (ii) human health.

(i) Biological resilience in forestry and agriculture

In the past, forest managers have assumed that the climate and other associated factors will remain stable, in spite of the long generation times and individual lifespans of many forest tree species and biomes (Millar et al., 2007). However, soil degradation (for example) can occur rapidly compared to the lifespan of the forest and then impact on the ability of trees to withstand other environmental perturbations (Swinfield et al., 2020). Similarly, modern plant breeding selects for yield potential under high and stable resource supply, and generally relies on genetically uniform cultivars. A biological resilience framework, however, encourages a different approach. For example, studies of local adaptation at the population level would help to understand how we can best buffer food and/or timber production against perturbations, perhaps by combining long-term data series and targeted experiments informed by historical farming practice or evolutionary processes (Millar et al., 2007). In a context with clear applications for management, Ives and colleagues recently discovered that spatial heterogeneity in crop-harvesting is a major driver of the ecological and evolutionary feedbacks that limit resistance of pea aphids to parasitoid wasps, an important biological control agent (Ives et al., 2020). Past perturbations also leave abiotic ‘stress memory’, encoded in DNA methylation and chromatin marks, which may increase resilience over multiple generations (Chang et al., 2020; Friedrich, Faivre, Bäurle, & Schubert, 2019) in a process of acquired transgenerational resistance (Holeski et al., 2012). Similarly, interactions across trophic and biological levels are well-known features of plant growth and health, with key work demonstrating that these also influence resilience (e.g. plant-microbe interactions influence resistance to climate change; Rudgers et al., 2020). Harnessing this information could lead to improved crop plant and tree breeding programmes (e.g. Messier et al., 2019), but much of this work remains embedded in model plant systems, such as *Arabidopsis*. Understanding which features at what biological level are most important to manage (e.g. managing for genetic diversity of monotypic plantations versus diversity of associated mycorrhizal fungi) will require combined approaches and translation of work from model species to natural systems.

(ii) Biological resilience in human health

While ecological systems are increasingly becoming viewed as socio-ecological systems (Ellis, 2015), the idea that the human mind and body can be viewed as a complex ecological system is only just beginning to be recognised (Bernstein, 2019). Understanding how circadian misalignment of sleep/wake cycles leads to a mismatch between abiotic cues and internal cellular functions (e.g. impairment of beta cell function and insulin sensitivity; Mason, Qian, Adler, & Scheer, 2020), and then scales up to affect system health via resilience to disease and other stressors, could help to provide more appropriate guidelines for managing shift work, for example. Recent experiences with COVID-19 also demonstrate the need to consider how resilience operates across biological levels: identifying what makes an individual more resilient to a virus at the cellular level (e.g. vaccine development) is not enough if insufficient people take up the vaccine (i.e. population level), or if the virus itself evolves resistance. Indeed, understanding the biological resilience of viral infections, or cancerous growths for example, to medical interventions could assist in progress with treatment. Genetic heterogeneity is known to negatively affect treatment success in cancer (Maley et al., 2006), yet this heterogeneity reflects the selective pressures endured, and the variation accumulated, during the whole history of that cancer and can reveal vulnerabilities to therapy (Alexandrov, Nik-Zainal, Siu, Leung, & Stratton, 2015). Furthermore, life-history strategies of cells, such as dormancy, can blunt the effects of therapy (e.g. tuberculosis). This suggests that diversity could be an important component of resilience in human health, but this requires testing in translational models.

END OF BOX 2

Challenges of implementing a biological resilience framework

Here we have argued that understanding and managing for biological resilience requires moving away from the approach of considering function or resilience only at the level of ecosystems, or of focusing studies within a single biological level. We have also stressed how the resilience of the present state not only relies on perturbations experienced in the past (whether contemporary, transgenerational, or deeper in evolutionary time) but that we can also access information about these past responses. Nevertheless, incorporating evolutionary history and complex interactions within and across biological levels is non-trivial, and key challenges exist for modelling complexity and broadening the scope of data collection, as well as setting the temporal and spatial boundaries of the systems or components being studied.

Firstly, in both theoretical and empirical work, we need to identify which connections among what levels are most critical to study. A top-down view of ecosystems works best when considering change over a relatively short period of time, and reduces power for forecasting future responses, either to predicted environmental change or potential management interventions. In ecosystem ecology, species, for example, are normally classified into functional types that leave out valuable information about evolutionary responses to specific perturbations in the past. These responses can however be searched for by mining existing data (e.g. Figure 2c; Zitnik et al., 2019) or by experiment (e.g. Oostra et al., 2018). Similarly, we need to move beyond research focusing on what makes an individual, or a species, resistant or tolerant to some perturbation without assessing its relevance to systems or communities. Research in eco-evolutionary dynamics is already beginning to tackle these interactions (Box 1), and adapting this approach to investigate resilience provides a model for moving forwards. While it is not tractable to measure everything, well-controlled experiments can provide critical data to understand the mechanisms that drive biological resilience – or the lack of it. However, as experiments entail at least some simplification of natural complexity, results will need to be linked conceptually to surveys of the relevant organisms and ecosystems.

Considering multiple levels of biological organisation will also necessitate data collection that tracks responses and maximises phylogenetic, functional, spatial and temporal coverage with minimum monetary cost (Cardoso & Leather, 2019). This is a challenging task for independent research groups as the acquisition of uninterrupted and consistent time series of ecological and environmental data depend on continued funding. Therefore, coordinated multidisciplinary research projects would enhance data collection and optimise funding streams, making it possible to expand the scope from single- to multiple levels. Some types of data are already available to inform about responses to past conditions, but if we are to make better use of existing and future available datasets, these will require high quality metadata annotations including as many potential ecological variables as possible (and not only the ones directly related to the analyses data were collected for) and easy and open access (e.g. following the FAIR principles; Wilkinson et al., 2016).

Providing the evidence necessary to make the case to policy makers is perhaps the most important challenge. For example, accumulating knowledge on ecosystem resilience is yet to change the principles of forestry or cropland management dramatically, which is alarming given that we know many current management practices compromise the ability of future generations to meet their own needs. This may be because resilience is currently difficult to quantify, and a lack of resilience is easier to recognise than a successful management practice. A biological resilience framework could improve identification of 'resilience indicators' at scales in which management decisions are made. Tracking genetic diversity at a species level, for example, is a feasible method to collect robust data, and could enable modelling of which actions are likely to be most successful. A critical further step, however, will be improved monitoring of the impact of potential indicators so that we are able to learn from both successful and less successful implementations. Similarly, there are still substantial gaps to bridge between scientists, policymakers and other stakeholders. For example, in commercial farming and forestry widespread adoption of science-led practices depends on short-term economic benefits, so adoption will require policy-based incentives. A deeper understanding of management practices, and co-creation of research questions with stakeholders that will apply management practices, is essential, particularly if we are to implement decisions using an experimental approach.

In summary, biological resilience requires shifting our perspective in eco-evolutionary studies towards investigating terms of resistance versus recovery (the key conceptual outcomes in ecosystem resilience) while also incorporating an eco-evolutionary perspective to better understand ecosystem-level processes (Figure 1, Box 1). This requires real multidisciplinary coordinated actions. But we can also begin to take small steps within existing research programmes. Researchers should consider reframing current research to test theory regarding types of responses to perturbations under study. Or, we could consider how influences from evolutionary history may impact ecological responses being detected under current conditions. Although challenging, this approach should provide the advances in data collection, modelling, and testing of hypotheses across levels that are urgently needed to improve resilience in the face of current and future environmental challenges.

Author contributions

All authors were involved in Conceptualisation, Writing – original draft preparation, and Writing – review & editing. R.T. and V.M. were responsible for preparation of the final version.

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