Understanding and applying biological resilience, from genes to ecosystems

Authors and affiliations:

* corresponding author (rose.thorogood@helsinki.fi)

§ equal contribution

All other authors listed alphabetically

Rose Thorogood*§[1,2,3], Ville Mustonen§[2,4,5,6], Alexandre Aleixo[7], Pedro J. Aphalo[2], Fred O. Asiegbu[8], Mar Cabeza[2,3], Johannes Cairns[2,4], Ulrika Candolin[2], Pedro Cardoso[7], Jussi T. Eronen[3,9,10], Maria Hällfors[2,11], Iiris Hovatta[12,13,14], Aino Juslén[7], Andriy Kovalchuk[8,15], Jonna Kulmuni[2], Liisa Kuula[11], Raisa Mäkipää[16], Otso Ovaskainen[2,17], Anu-Katriina Pesonen[12], Craig R Primmer[2,6], Marjo Saastamoinen[1,2,11], Alan H. Schulman[6,16], Leif Schulman[7], Giovanni Strona[2,11], Jarno Vanhatalo[2,11,18]

1. HiLIFE Helsinki Institute of Life Science, University of Helsinki, Helsinki, Finland
2. Research Programme in Organismal & Evolutionary Biology, Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland
3. HELSUS Helsinki Institute of Sustainability Science, University of Helsinki, Helsinki, Finland
4. Department of Computer Science, Faculty of Science, University of Helsinki, Helsinki, Finland
5. Helsinki Institute for Information Technology, University of Helsinki, Helsinki, Finland
6. Institute of Biotechnology, HiLIFE Helsinki Institute for Life Science, University of Helsinki, Helsinki, Finland
7. Finnish Museum of Natural History 'Luomus', University of Helsinki, Helsinki, Finland
8. Department of Forest Sciences, Faculty of Agriculture and Forestry, University of Helsinki, Helsinki, Finland
9. Research Programme in Ecosystems and Environment, Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland

10. BIOS Research Unit, Helsinki, Finland
11. Research Centre for Ecological Change, Faculty of Biological and Environmental Sciences, University of Helsinki, Finland
12. SleepWell Research Program, Faculty of Medicine, University of Helsinki, Helsinki, Finland
13. Department of Psychology and Logopedics, Faculty of Medicine, University of Helsinki, Helsinki, Finland
14. Neuroscience Center, HiLIFE Helsinki Institute for Life Science, University of Helsinki, Finland
15. VTT Technical Research Centre of Finland Ltd, Espoo, Finland
16. Natural Resources Institute Finland (Luke), Helsinki, Finland
17. Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science and Technology, Trondheim, Norway
18. Department of Mathematics and Statistics, Faculty of Science, University of Helsinki, Helsinki, Finland

ABSTRACT

Ecosystems are under unprecedented and accelerating pressures. Much work on understanding resilience to these pressures has, so far, focussed on the ecosystem. However, understanding a system's behaviour also requires knowledge of its component parts and their interactions. Here we present a framework for understanding 'biological resilience', or the mechanisms 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 ecological and genomic data are only just beginning. We argue that combining eco-evolutionary knowledge with ecosystem-level concepts of resilience can provide the mechanistic basis necessary to improve management of human, natural and agricultural ecosystems for better resilience.

MAIN TEXT

The Anthropocene is characterised by the pervasive impact of human activity on all aspects of life on earth[1]. Human-driven climate change and overexploitation of natural resources, as well as increasing human population densities and urbanisation, are placing progressively larger land areas and oceans under human influence[2]. Even the world's topology has changed, as global movement of individuals and goods erodes biogeographical barriers[3]. These changes put ecosystems under unprecedented and accelerating pressures, inducing regime shifts[4], causing loss of ecosystem services[5], and even changing the course of evolution[6]. There is therefore an urgent need to better understand why some species, communities or ecosystems decay while others persist or adapt, and whether damage can be reversed or, at least, mitigated through management.

In ecology, 'resilience' has attracted great interest as a concept for describing how ecosystems recover to an antecedent state following a disturbance ('engineering resilience'[7]), or absorb change and resist large shifts in ecosystem function ('ecological resilience'[8]). Both recovery and resistance mechanisms are now recognised to contribute to the resilience of ecosystems[9] but further advances require a better understanding of what determines an ecosystem's response following a perturbation[10], and more accurate predictions of longer-term outcomes[11]. Much work on resilience, however, focuses predominantly at the ecosystem level[12] and still lacks an eco-evolutionary perspective[13]. This is despite the key insight that nothing in ecology makes sense without determining responses within and across *all* biological levels[14]. On the other hand, focusing on how ecology and evolution shapes patterns and processes within individuals and populations has attracted criticism for being too narrow to address broader ecological problems (but see ref.[15] for application of evolutionary concepts). And, although there are increasing calls to make use of evolutionary concepts in addressing biodiversity[12,16] and tipping points[13], for example, eco-evolutionary biologists themselves rarely consider resilience and how it might be conferred by processes that occur within or across the biological levels that form the focus of their studies[13].

Here we argue that the eco-evolutionary history of past adaptation is a critical body of knowledge available to help pinpoint key elements that may scale up to determine the resistance and recovery potential of increasingly managed or perturbed ecosystems. We provide a framework to integrate ecosystem-level concepts of resistance and recovery with knowledge about ecological and evolutionary form and function at each level of biological organisation (Figure 1). This ‘biological resilience’ comprises the processes and functions that enable different components across levels of organisation to persist and/or adapt in the face of environmental perturbations. We first discuss how abiotic and biotic perturbations may affect biological levels differently, and then how the eco-evolutionary past of these component parts provides context for present and future responses. Next, we outline approaches for examining biological resilience, from genes to cells, individuals, populations, and communities, and identify new opportunities emerging from the ongoing infusion of big data into evolutionary biology and ecology. Finally, we discuss how considering resilience at different biological levels will enable advances in translational work that aims to restore, adapt, or preserve human, natural, and agricultural ecosystems.

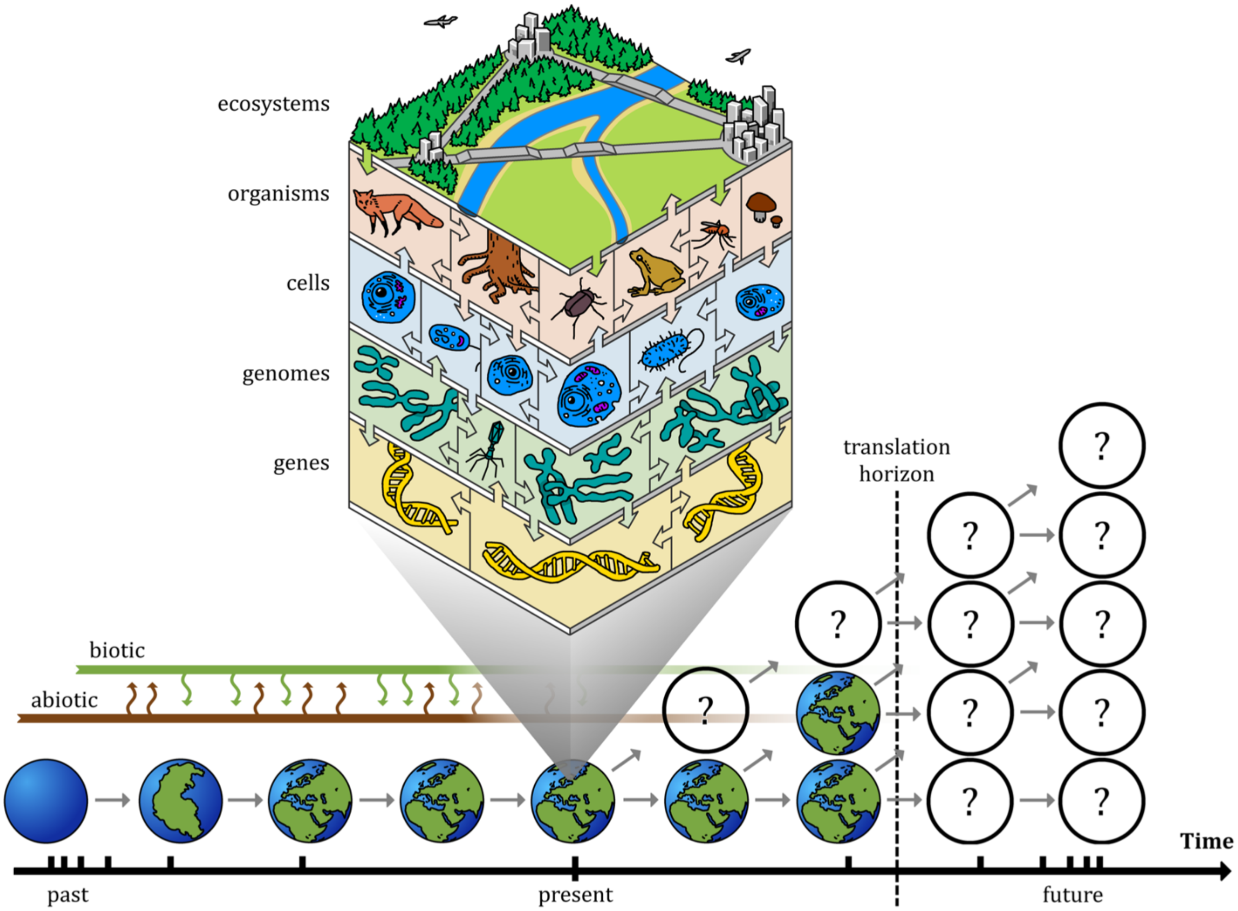

FIGURE 1. Biological resilience is characterised by connections within and among levels of life (simplified here, but not limited to, genes, genomes, cells, organisms and ecosystems). These connections offer a snapshot of the present state, which has been shaped by ecological and evolutionary responses to biotic and abiotic perturbations and selection pressures (indicated by green and brown interactions, respectively) in the past (time represented by a log-scale). Predicting future states, however, has a limited translation horizon (vertical dashed line, close in time) because (i) the long time-scales involved result in reduced incentives for policy makers and in a paucity of management tools and ideas, and because (ii) the understanding of past and present states remains incomplete to forecast outcomes accurately (denoted by question marks within circles). Understanding biological resilience can shift the translation horizon further into the future by reducing uncertainty in prediction trajectories (grey arrows) and facilitating improved evidence-based policy.

Effects of perturbations vary across biological levels

Natural systems face perturbations that may be novel or similar to those experienced in the past[18]. The most conspicuous perturbations are increased temperatures (and associated events such as droughts and fires), direct anthropogenic alterations (e.g. pollution, land use changes, habitat fragmentation), and invasive species. 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[19]. Furthermore, ecosystems commonly face simultaneous perturbations which may be directly related, such as warmer temperatures and increased droughts, or indirectly related, such as invasive species and eutrophication. The end result is often non-linear as simultaneous perturbations can have synergistic effects[20] or generate cascading processes (e.g. co-extinctions[21]). 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[22]. Although increasing theoretical and experimental work suggests that collapse in natural systems can be anticipated by early warning signals[23], detecting these signals in highly variable real world systems remains a great challenge[13].

Biological resilience may provide some insight as responses to perturbations are influenced not only by the intensity of the disturbance and its spatio-temporal scale, but also by the composition, structure, and spatial context of the perturbed ecological communities[24]. For example, fragmented habitats influence the degree to which species can reduce their exposure to perturbations by shifting, shrinking or expanding their range via dispersal[25], or by modifying physiological or behavioural responses[26]. Responses may also vary among species, populations, and even among individuals[27–29]. 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. phenology[30]) and potentially set up cascades of change across other biological levels (e.g. genetic diversity[16]). Spatial context also has fundamental implications for longer-term adaptation to environmental change as it shapes gene flow[31]. Finally, perturbations may be experienced differently at varying levels of biological organization: while outcomes may be catastrophic for some levels, they may also provide stimuli for renewal at other levels. These aspects set biological resilience into a relative perspective: systems that vary in their composition will respond differently to similar perturbations while the same system may respond differently to divergent perturbations.

Past perturbations shaped the present state

Biological resilience is a dynamic and constantly evolving product of long term (co-)evolutionary, ecological and biogeographical processes because past perturbations leave their mark on biological entities, creating ecological and evolutionary ‘memories’[32,33]. This information is often expected to be specific to the features of the disturbance, including its amplitude, duration, frequency, and stochasticity[34], and affect the present state and resilience of the system. Decoding ecological and evolutionary memories at each level, and understanding how they influence interactions among levels (Figure 1), may therefore provide information to better predict future responses (e.g. ref.s[33,34]).

At the level of genes, evolutionary history is manifested in mutations filtered by natural selection or fixed by random genetic drift. Some of these mutations may provide an advantage against a future perturbation, such as through acquired resistance against a parasite, pest or antibiotic seen in the past[35]. At the level of the individual, disturbances may cause reversible marks to the genome via epigenetic effects, which can affect the ability to withstand similar disturbances for subsequent generations, or induce phenotypic plasticity and behavioural modifications that may in some cases spread to others via learning[36]. At the level of the population or community, perturbations can reduce or increase 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[37]. 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[38]). Disturbances may also fuel rapid evolution, which can, in turn, alter population genetic trajectories and community assembly[13].

These effects of perturbations generate general hypotheses concerning the role of historical disturbances in future resilience: (i) past experience primes a biological entity to cope best 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 resilience debt if the magnitude and frequency of the disturbances differ too much from their historical disturbance regimes[33]. 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 diversity or altered species interactions[16].

Approaches to quantify past and present states

Although there is debate over the value of small-scale experimental studies for understanding real-world conditions or problems[39], a growing number of studies are demonstrating how study approaches across biological levels can generate insight into the role of specific processes or mechanisms that confer resilience (see Figure 2 for examples). This development is critical as a major challenge in studying resilience is the need to either induce perturbations experimentally, or coincidentally collect data in the right place at the right time[40,41]. 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 ask predominantly hypothesis-generating questions. For example, which genes contribute to more resilient phenotypes?[42], which populations are more resilient to certain perturbations?[43] or, which species are most affected by which particular aspects of a perturbation?[44]. On the other hand, the results of experiments, particularly into resilience at the cellular[45] or genomic levels[46], are often not interpreted in a broader ecological context or compared to available data from natural populations[47]. Here we survey observational and experimental approaches, how these approaches intersect across biological levels, and how we can use them to test general hypotheses (Table 1).

TEXT CONTINUED AFTER FIGURE 2 AND TABLE 1

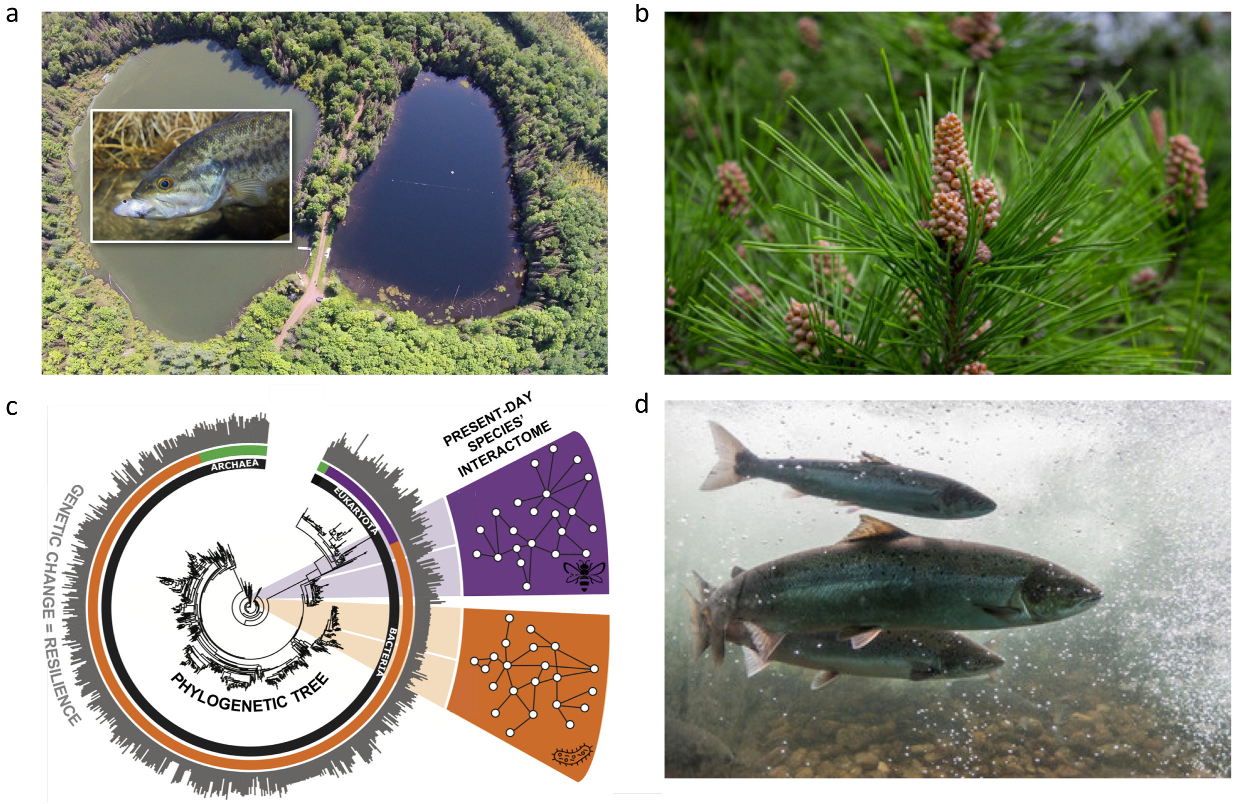

FIGURE 2. Examples of biological resilience (biological levels and approaches in bold): (a) **Communities & ecosystems:** A **semi-natural experiment**, based on knowledge from **long-term monitoring**, tested warning signals of a regime shift, as predicted by **modelling**. Top predators (inset) were introduced into a lake (left) and their biotic and abiotic effects on an aquatic food web (compared to an undisturbed lake, right) were tracked over 3 years[48]. (b) **Individuals & populations:** Various **modelling** methods, coupled with **semi-natural experiment** data from 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[29]. (c) **Cells & proteins:** Over 8 million protein-protein interactions from 1,840 species were **data mined** to **model** protein interactomes. Using species' level evolutionary history and ecological characteristics, the authors then investigated how resilience varies at the protein level[49]. (d) **Genes & genomes:** A **wild survey** of gene-linked loci and gene ontology information in *Salmo salar* populations was conducted to test the hypothesis that loci with immune-related functions have stronger signals of selection than loci with no obvious association with immune function[50]. [Image a with permission from S. Carpenter, inset under licence from Adobe Stock; Image c modified with permission from M. Zitnik; Images b, d under licence from Adobe Stock]

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

General 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[53] • Co-occurrence of taxa before and after Holocene[58]
	Use modelling and simulations to generate testable predictions	• Transgenerational priming[46]
	Perform experimental perturbations in -cosms or field settings	• Experimental evolution with yeast[45] • Legacy effects of drought exposure on microbial communities[64] • Transgenerational acquired resistance in model plants[65] • Resurrection studies[61]
	Interrogate findings with data from natural experiments	• Captive and wild songbirds respond differently to temperature perturbations[47]
(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[57]

	datasets (including ancient DNA) to measure past diversity	• Ecological and evolutionary memory[34,49] • Adaptive genetic diversity[16]
	Use modelling and simulations to generate testable predictions	• Predicting a species response to environmental change when preadaptation of community differs[66]
	Perform experimental perturbations in -cosms or field settings	• Resurrection studies[61]
	Interrogate findings with real-world examples, e.g. natural experiments	• Biological invasions[67]
(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[51]
	Use modelling and simulations to generate testable predictions	• Evolutionary rescue[68]
	Experimentally induce a novel perturbation in cases where rapid adaptation is present vs. absent	• Resurrection studies[61]

Surveys and long-term monitoring of free-living organisms

Surveys of wild populations often include (intentionally or unintentionally) variation in habitats or environmental features. When these features occur along natural gradients (e.g. in temperature, salinity, anthropogenic effects), the surveys provide an opportunity to compare the responses of various biological levels (e.g. genes and genomes of forest trees in response to aridity gradients[51], bacterial diversity and cellular processes in response to salinity[52], individual reproduction and survival in response to parasite infection in Soay sheep[53]). If surveys are conducted in a standardised manner and continue over multiple seasons, years, or generations, this long-term monitoring has the potential to facilitate (i) detection of subtle responses to perturbations, or responses to more subtle perturbations, (ii) replication over time, and (iii) detection of ecological and evolutionary memories[54]. Alternatively, "opportunistic" sampling can follow the (often unexpected) formation of a resilience-relevant gradient/difference. Characteristics at a site that 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[55], or in the event that surveys of the affected sites were conducted prior to the perturbation, a 'before vs. after' analysis can be conducted[56]. The prehistoric and paleoecological record is also an important potential source of survey data, as it is now becoming tractable to incorporate it with extant data[57]. This paleo-perspective could offer natural experiments: data are potentially available to help explain how community assembly (and disassembly) works when time spans are increased[58], 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.

Semi-natural and common garden experiments

A major challenge for survey approaches is to disentangle co-varying environmental characteristics (e.g. photoperiod and temperature along a latitudinal gradient, or simultaneous drought and reduced food availability). Experiments in semi-natural (e.g. *in vitro* microcosms or outdoor mesocosm setups) or field settings (e.g. ponds/tanks, forest plots, enclosures suitable for small mammals, or free-ranging individuals and populations) are therefore necessary, 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[39]. Common garden experiments involve rearing individuals of the species of interest under common conditions and can be expanded to study responses to environmental or anthropogenic stressors by adding ‘treatments’ such as thermal stress, disease, or changes in community. They provide an additional level of control as environmental differences can be eliminated or specific environmental factors can be tested, and mean that the extent of resilience that is plastic versus evolutionary (e.g. fish[59], crops[60]) 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[61]. Experiments 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), but only if the selection of individuals, habitats, or species to be moved is designed to test the relative resilience of different characteristics (e.g. social behaviour[62], genetic diversity[63]).

Theory and mathematical models

If each component part of an ecosystem shows variable resilience, how can we integrate knowledge gained by examining resilience at different biological levels? Theory and mathematical models lay the foundations for identifying what to measure from experimental and empirical systems and how to extract these observables from real data (Box 1). For example, a careful normalization of the effect of a perturbation to the undisturbed state is necessary to obtain common metrics that are comparable across biological levels and study systems[11]. As such, theory and models generate new hypotheses and predictions about how systems will likely respond to perturbations, which can then be tested empirically. Therefore, they are a key ingredient for translational work.

TEXT CONTINUED AFTER BOX 1

Box 1: Eco-evolutionary and environmental Big Data

To analyse biological resilience we need:

- data on biotic units (e.g. gene expression, species, communities, ecosystems) and environmental change (stressors of nature) in the same spatial and temporal range
- data that extend over a sufficient timespan (long-term time series data) and/or spatial range
- multiple cases of similar drivers-to-biotic-units pairs.

Data that meet these qualities can be obtained experimentally from simplified systems in single studies, but suitable datasets for real world ecosystems require combining data from different sources. Abiotic data from the last few decades are openly available (e.g. CORINE[69]; USGS[70], WorldClim[71]). At the molecular level, Big Data on genes and genomes (NCBI[72]) and their function (Gene Ontology (GO) database[73]) are rapidly increasing and designed to be taxonomically comparable or even species-neutral (GO). This enables the transfer of functional annotation (molecular function, biological role and cellular location) derived from model organisms for tens of thousands of genes to inferred orthologues in newly sequenced species. It could therefore be a very useful resource for studying the molecular basis of biological resilience, particularly if the current functional focus on medical science broadens to encompass functions in response to ecological stimuli[74].

Big Data on species occurrences (GBIF[75]), traits (TRY[76], Coral Trait Database[77]) and abundances through time[78,79] are also becoming available at an increasing rate. Collecting data of changes in the deeper past requires digitisation of physical collections (natural history specimens, historical landscape photographs, natural resource use statistics, maps, written records etc.) and application and development of new techniques for data extraction (e.g. ref.[80]) and analysis (e.g. ref.[81]). Finding the most potent data sources for reconstructing time series into the past still needs innovation but this approach carries considerable promise for analyses of resilience to changes that have already occurred, thus improving our capability to predict consequences of ongoing and future change.

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 increase. However, most of the global databases at present contain (partially) non-comparable data. Existing data can be analysed by taking advantage of newly developed methods that minimise biases in unrelated or uncertain data (e.g. Bayesian approaches[82]), or when fully comparable data are available, by using mechanistic models that allow moving beyond correlative analyses (e.g. individual-based models[83]). Experimental and observational data can also be combined to increase the credibility of conclusions[84]. 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[85]. Other areas of artificial intelligence, such as evolutionary computation, hold much promise as they can provide both power and interpretability of natural laws[86].

END OF BOX 1

Advancing the translation horizon

Management of ecosystems requires detailed knowledge of the component parts, as competing interests among stakeholders can lead to different aspects being prioritised[87] (e.g. species, services, monetary value). Determining how resilience operates at each biological level has potential to move beyond this stale-mate, by using the ecological and evolutionary history of components of the system to better predict future biological interactions under different management scenarios. Here we provide three examples where biological resilience could have translational impact.

Biological resilience in human health

Ecological systems are also human systems (‘socio-ecological resilience’)[2], yet the idea that the human mind and body can be viewed as a complex ecological system is only just beginning to be recognised[88]. For example, circadian rhythms and sleep/rest-wake cycles are common across species and systems, and serve as processes to enhance resilience by maintaining somatic and psychological health[89]. After prolonged periods of wakefulness, sleep offers a recovery when metabolic balance and network function are restored. Glutamatergic pathways restore attentional capacity, for example, and maximise readiness for the next wake period[90]. Circadian misalignment, where the organism’s inner clock becomes mismatched to environmental or behavioural cues (such as exposure to light or being physically active) is becoming increasingly common in humans living in contemporary societies with increasing artificial light exposure. This disruption to sleep reduces resilience by impairing beta cell function and insulin sensitivity, resulting in impaired glucose tolerance[91]. Understanding time-dependent cyclicity in genes, phenotypes, populations/communities, and human-influenced ecosystems should therefore become a core goal for improved policy-making.

Combatting cancerous cell growth, or infection by microbes and viruses, on the other hand, is made harder by their apparent biological resilience to human interventions. For example, genetic heterogeneity is known to negatively affect treatment success in cancer[92]. However, heterogeneity within cancer reflects the selective pressures endured, and the mutations accumulated, during the whole history of that cancer and can reveal vulnerabilities to therapy[93]. Life-history strategies of cells, such as dormancy, also matter as they can blunt the effects of therapy (e.g. tuberculosis). This suggests that diversity is an important component of resilience in human health, but this requires testing in translational models. Microbiota and antibiotics provide one such system[94]. The human gut is inhabited by a complex and metabolically active microbial ecosystem, where interactions between the host and microbiome are driven by feedback loops and further provide either stabilizing or destabilizing effects. Antibiotics form a particularly important class of perturbations in this system. Compromising the resilience of the microbiota has numerous potential indirect impacts on health[95] whereas antimicrobial resistance has direct impacts on health[96], and both carry a heavy economic burden. Understanding how microbiota form resilient states might allow increasing the resilience of healthy states, and, in turn, decrease the resilience of unhealthy states.

Human-influenced ecosystems: forest management

Ecological disturbances and climate change are forecast to have significant impact on forest productivity and growth, insect and pathogen outbreaks, drought, periodic fires, wind and ice storms and invasive alien species[97,98]. Forest management could enhance resilience if a time-horizon approach across biological levels was integrated into decision-making. Past management of forests has assumed that the effects of climate and other associated factors will remain stable, in spite of the long generation time and individual lifespan of many forest trees and biomes[97]. However, at the community or ecosystem level, 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[99,100]. In tree species with long generation times, resilience is likely to depend strongly on phenotypic plasticity and transgenerational transfer of information[101], as changes to the genome through selection are slow. Better management of forests, therefore, likely requires managers to avoid conversion of forest to monotypic or reduced species plantations[43], and to consider use of alternate genotypes when seeding new forests[102]. Achieving increased resilience, however, will require understanding which features at each biological level are most important to manage, and whether enhanced diversity at one level (e.g. genetic diversity of monotypic plantations or diversity of associated mycorrhizal fungi) can compensate for reduced diversity at another[103]. Evidence-based decisions in forest management are urgently needed to better assess the compromises given limited resources and the competing requirements of resilience and commercial yield.

Agricultural systems: managing crops for drought conditions

Improving the resilience of crop plants to abiotic stress is becoming increasingly important as climate change increases variability in precipitation and temperature and associated episodes of drought and heat waves. The consequences of these perturbations, however, may be complex because drought leads to decreased transpirational cooling of the plant, which in turn intensifies the effects of heat[104]. A plant's response to drought (e.g. stomatal closure, early flowering) affects multiple organs across all levels of biological organization, ranging from transcription to metabolism, energetics, and plant development[105]. This means that past drought leaves an abiotic 'stress memory', encoded in DNA methylation and chromatin marks, which may increase resilience over multiple generations[106,107] in a process of acquired transgenerational resistance[65]. Therefore, recovery following drought in the past is an especially important process to understand future resilience. Can we 'future-proof' crop plants to resist or recover from predicted drought conditions?

While most advances have been made with model systems such as *Arabidopsis*, genetic and genomic approaches combined with precision phenotyping are now making it possible to translate this understanding into practical advances for food crops[65]. At the population level, studies of local adaptation may also help to understand how we can best buffer food production against drought. A critical measure of success for the wild ancestor of a crop plant was its ability to set viable seed following a perturbation (i.e. period of drought). Before the 20th century, farmers kept seed to sow in successive years and produced heterozygous "landraces" of crop plants that were locally adapted to prevailing conditions and stressors; the seeds may have been smaller or fewer, but the diversity contributed to the yield stability of the local population. Modern plant breeding, however, selects for yield under high inputs, relying in many cases on hybrid seed that does not remain true to type across generations. To prepare for the future, the likelihood of the timing, severity, and length of reduced precipitation must be balanced against the need for productivity. Accurate crop models and genomic prediction approaches[108], together with appropriate allelic diversity, will be required to meet the challenge.

Challenges for future research

Here we have argued that understanding and managing biological resilience requires moving away from the reductionist approach of considering function only at the level of ecosystems. A simplified view of ecosystems only works when considering change over a relatively short period of time, and reduces power for forecasting future response, either to predicted environmental change or potential management interventions. In ecosystem ecology, species, for example, are normally classified into functional types. However, this leaves out valuable information about evolutionary responses to specific perturbations in the past (unless specifically searched for, e.g.[49]). This represents a lost opportunity to learn more about current response and reduce uncertainty in predictions. Nonetheless, incorporating evolutionary history and complex interactions within and across biological levels is non-trivial, and key challenges exist for data collection, as well as setting the temporal and spatial boundaries of the systems or components being studied.

Firstly, data is still expensive and heterogeneous in time and space, even in the era of Big Data. Considering multiple levels of biological organisation will require data collection that tracks responses and maximises phylogenetic, functional, spatial and temporal coverage with minimum monetary cost[109]. If we are to make better use of these data, it will require high quality metadata annotations and easy and open access (e.g. following the FAIR principles[110]), while the acquisition of uninterrupted and consistent time series of ecological and environmental data depend on continued funding. Coordinated multidisciplinary research projects would enhance data collection, and optimise funding streams; these are likely to be necessary if we are to expand the scope from single- to multiple levels. Some types of data are already available to inform about responses to past conditions, relieving the need to wait for Big Data to accrue (Box 1).

Second, we need to move beyond studying the effects of single perturbations to single species, both in theoretical and empirical work, if we are to measure and understand the effects of multiple perturbations to multiple-species. It is not tractable to measure everything, but well-controlled experiments at intermediate scales will provide critical data for understanding the mechanisms that drive biological resilience – or the lack of it. However, the removal or simplification of aspects of natural complexity means that experiments will need to be linked conceptually to surveys of the relevant organisms and ecosystems to understand biological resilience. Integrating survey data and interpreting experimental data in the light of environmental Big Data provides a broader scope, particularly when datasets span space and/or time (Box 1). Finding ways to integrate all these data with rapidly accumulating genomic data will likely facilitate significant advances in the assessment of past and current indicators of biological resilience. Similarly, incorporating complex processes across many levels of biological organisation within one model is both computationally and mathematically challenging, even with recent advances[13]. 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. These shortcomings are especially critical for studying biological resilience, because it is driven by the interaction of many complex processes at many levels of biological organization. Thus, a major challenge will be expanding, but still setting, theoretical and empirical boundaries in terms of mechanism detail and range of validity.

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. Taking a biological levels approach may help if it enables identification of ‘resilience indicators’, elements that are best suited for developing management practices for resilience. Tracking genetic diversity at a species level, for example, is a feasible method for collecting robust data that can be used to identify which actions are likely to be most successful, and monitor their impact. Identifying others will require bringing together expertise across biological levels and different scientific disciplines. Similarly, there are still substantial gaps to bridge between scientists and policymakers. Co-creation of research questions with the stakeholders that will apply management practices is essential, particularly if it facilitates decisions to be implemented using an experimental approach. In summary, biological resilience requires viewing eco-evolutionary studies in terms of resistance vs. recovery (the key conceptual outcomes in ecosystem resilience) and incorporating an eco-evolutionary perspective to better understand ecosystem-level processes. 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 future environmental challenges.

Author contributions

All authors conceived the idea, contributed to the writing of the manuscript, and approved the submitted version written by R.T. and V.M.

Acknowledgements

This manuscript is a contribution by members of the HiLIFE (Helsinki Institute for Life Science) Grand Challenge programme in Understanding Biological Resilience (BIORESILIENCE), funded by the Academy of Finland funding instrument PROFI1 (awarded to the University of Helsinki). Further funding support provided to (in alphabetical order) F.A. (Academy of Finland grant no. 307580), J.C. (Jenny and Antti Wihuri Foundation), P.C. (Kone Foundation), M.H. (Jane and Aatos Erkko Foundation), J.K. (HiLIFE fellowship, Academy of Finland grant no. 328961), L.K. (Academy of Finland grant no. 12871741), R.M. (Academy of Finland Strategic Research Council decision no. 312912), O.O. (Academy of Finland grant no. 309581, Jane and Aatos Erkko Foundation, Research Council of Norway CoE grant no. 223257), C.R.P. (Academy of Finland grant no. 314254), M.S. (HILIFE start-up grant, Jane and Aatos Erkko Foundation, European Research Council Independent Starting grant no. 637412 'META-STRESS'), A.H.S. (Academy of Finland grant no. 314961), G.S. (Jane and Aatos Erkko Foundation), R.T. (HILIFE start-up grant), J.V. (Academy of Finland grant no. 317255, Jane and Aatos Erkko Foundation).

REFERENCES

1. Lewis, S. L. & Maslin, M. A. Defining the Anthropocene. *Nature* **519**, 171–180 (2015).
2. Ellis, E. C. Ecology in an anthropogenic biosphere. *Ecol. Monogr.* **85**, 287–331 (2015).
3. van Kleunen, M. *et al.* Global exchange and accumulation of non-native plants. *Nature* **525**, 100–103 (2015).
4. Scheffer, M., Carpenter, S., Foley, J. A., Folke, C. & Walker, B. Catastrophic shifts in ecosystems. *Nature* **413**, 591–596 (2001).
5. Foley, J. A. Global consequences of land use. *Science* **309**, 570–574 (2005).
6. Sullivan, A. P., Bird, D. W. & Perry, G. H. Human behaviour as a long-term ecological driver of non-human evolution. *Nat. Ecol. Evol.* **1**, 0065 (2017).
7. Pimm, S. L. The complexity and stability of ecosystems. *Nature* **307**, 321–326 (1984).
8. Holling, C. S. Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.* **4**, 1–23 (1973).
9. Hodgson, D., McDonald, J. L. & Hosken, D. J. What do you mean, ‘resilient’? *Trends Ecol. Evol.* **30**, 503–506 (2015).
10. Standish, R. J. *et al.* Resilience in ecology: abstraction, distraction, or where the action is? *Biol. Conserv.* **177**, 43–51 (2014).
11. Ingrisch, J. & Bahn, M. Towards a comparable quantification of resilience. *Trends Ecol. Evol.* **33**, 251–259 (2018).
12. Oliver, T. H. *et al.* Biodiversity and resilience of ecosystem functions. *Trends Ecol. Evol.* **30**, 673–684 (2015).
13. Dakos, V. *et al.* Ecosystem tipping points in an evolving world. *Nat. Ecol. Evol.* **3**, 355–362 (2019).
14. Levin, S. A. The problem of pattern and scale in ecology: The Robert H. MacArthur award lecture. *Ecology* **73**, 1943–1967 (1992).
15. Carroll, S. P. *et al.* Applying evolutionary biology to address global challenges. *Science* **346**, 1245993–1245993 (2014).
16. Sgrò, C. M., Lowe, A. J. & Hoffmann, A. A. Building evolutionary resilience for conserving biodiversity under climate change. *Evol. Appl.* **4**, 326–337 (2011).
17. Jiang, J. *et al.* Predicting tipping points in mutualistic networks through dimension reduction. *Proc. Natl. Acad. Sci.* **115**, E639–E647 (2018).

18. Donohue, I. *et al.* Navigating the complexity of ecological stability. *Ecol. Lett.* **19**, 1172–1185 (2016).

19. Barnosky, A. D. *et al.* Approaching a state shift in Earth's biosphere. *Nature* **486**, 52–58 (2012).

20. Brook, B., Sodhi, N. & Bradshaw, C. Synergies among extinction drivers under global change. *Trends Ecol. Evol.* **23**, 453–460 (2008).

21. Colwell, R. K., Dunn, R. R. & Harris, N. C. Coextinction and persistence of dependent species in a changing world. *Annu. Rev. Ecol. Evol. Syst.* **43**, 183–203 (2012).

22. Lever, J. J., van Nes, E. H., Scheffer, M. & Bascompte, J. The sudden collapse of pollinator communities. *Ecol. Lett.* **17**, 350–359 (2014).

23. Scheffer, M. *et al.* Anticipating critical transitions. *Science* **338**, 344–348 (2012).

24. Thebault, E. & Fontaine, C. Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* **329**, 853–856 (2010).

25. Fahrig, L. Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.* **34**, 487–515 (2003).

26. Baguette, M. & Van Dyck, H. Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. *Landsc. Ecol.* **22**, 1117–1129 (2007).

27. Saastamoinen, M. *et al.* Genetics of dispersal. *Biol. Rev.* **93**, 574–599 (2018).

28. Wong, B. B. M. & Candolin, U. Behavioral responses to changing environments. *Behav. Ecol.* **26**, 665–673 (2014).

29. Valladares, F. *et al.* The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecol. Lett.* **17**, 1351–1364 (2014).

30. Massot, M., Legendre, S., Fédérici, P. & Clobert, J. Climate warming: a loss of variation in populations can accompany reproductive shifts. *Ecol. Lett.* **20**, 1140–1147 (2017).

31. Anderson, C. D. *et al.* Considering spatial and temporal scale in landscape-genetic studies of gene flow. *Mol. Ecol.* **19**, 3565–3575 (2010).

32. Desai, M. M. Reverse evolution and evolutionary memory. *Nat. Genet.* **41**, 142–143 (2009).

33. Johnstone, J. F. *et al.* Changing disturbance regimes, ecological memory, and forest resilience. *Front. Ecol. Environ.* **14**, 369–378 (2016).

34. Waples, R. S., Beechie, T. & Pess, G. R. Evolutionary history, habitat disturbance regimes, and anthropogenic changes: What do these mean for resilience of Pacific salmon populations? *Ecol. Soc.*

14, (2009).

35. Bartholomé, J. *et al.* The genetics of exapted resistance to two exotic pathogens in pedunculate oak. *New Phytol.* nph.16319 (2019). doi:10.1111/nph.16319

36. Barrett, B., Zepeda, E., Pollack, L., Munson, A. & Sih, A. Counter-culture: does social learning help or hinder adaptive response to human-induced rapid environmental change? *Front. Ecol. Evol.* **7**, 1–18 (2019).

37. Pontes-da-Silva, E. *et al.* Extinction risks forced by climatic change and intraspecific variation in the thermal physiology of a tropical lizard. *J. Therm. Biol.* **73**, 50–60 (2018).

38. Fukami, T. Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Annu. Rev. Ecol. Evol. Syst.* **46**, 1–23 (2015).

39. Hendry, A. P. A critique for eco-evolutionary dynamics. *Funct. Ecol.* **33**, 84–94 (2019).

40. Thibault, K. M. & Brown, J. H. Impact of an extreme climatic event on community assembly. *Proc. Natl. Acad. Sci.* **105**, 3410–3415 (2008).

41. Bergen, E. *et al.* The effect of summer drought on the predictability of local extinctions in a butterfly metapopulation. *Conserv. Biol.* cobi.13515 (2020).

42. Papakostas, S. *et al.* A proteomics approach reveals divergent molecular responses to salinity in populations of European whitefish (*Coregonus lavaretus*). *Mol. Ecol.* **21**, 3516–3530 (2012).

43. Thom, D. *et al.* The climate sensitivity of carbon, timber, and species richness covaries with forest age in boreal–temperate North America. *Glob. Chang. Biol.* **25**, 2446–2458 (2019).

44. Strayer, D. L. Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. *Freshw. Biol.* **55**, 152–174 (2010).

45. López-Maury, L., Marguerat, S. & Bähler, J. Tuning gene expression to changing environments: from rapid responses to evolutionary adaptation. *Nat. Rev. Genet.* **9**, 583–593 (2008).

46. Kokko, H. *et al.* Can evolution supply what ecology demands? *Trends Ecol. Evol.* **32**, 187–197 (2017).

47. Verhagen, I., Tomotani, B. M., Gienapp, P. & Visser, M. E. Temperature has a causal and plastic effect on timing of breeding in a small songbird. *J. Exp. Biol.* **223**, jeb218784 (2020).

48. Carpenter, S. R. *et al.* Early warnings of regime shifts: A whole-ecosystem experiment. *Science* **332**, 1079–1082 (2011).

49. Zitnik, M., Sosič, R., Feldman, M. W. & Leskovec, J. Evolution of resilience in protein interactomes across the tree of life. *Proc. Natl. Acad. Sci.* **116**, 4426–4433 (2019).

50. Tonteri, A., Vasemägi, A., Lumme, J. & Primmer, C. R. Beyond MHC: signals of elevated selection pressure on Atlantic salmon (*Salmo salar*) immune-relevant loci. *Mol. Ecol.* **19**, 1273–1282 (2010).

51. Steane, D. A. *et al.* Genome-wide scans detect adaptation to aridity in a widespread forest tree species. *Mol. Ecol.* **23**, 2500–2513 (2014).

52. Abed, R. M. M., Kohls, K. & de Beer, D. Effect of salinity changes on the bacterial diversity, photosynthesis and oxygen consumption of cyanobacterial mats from an intertidal flat of the Arabian Gulf. *Environ. Microbiol.* **9**, 1384–1392 (2007).

53. Leivesley, J. A. *et al.* Survival costs of reproduction are mediated by parasite infection in wild Soay sheep. *Ecol. Lett.* **22**, ele.13275 (2019).

54. Grant, P. R. *et al.* Evolution caused by extreme events. *Philos. Trans. R. Soc. B Biol. Sci.* **372**, 20160146 (2017).

55. Ellegren, H., Lindgren, G., Primmer, C. R. & Møller, A. P. Fitness loss and germline mutations in barn swallows breeding in Chernobyl. *Nature* **389**, 593–596 (1997).

56. Garpe, K., Yahya, S., Lindahl, U. & Öhman, M. Long-term effects of the 1998 coral bleaching event on reef fish assemblages. *Mar. Ecol. Prog. Ser.* **315**, 237–247 (2006).

57. Barnosky, A. D. *et al.* Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems. *Science* **355**, eaah4787 (2017).

58. Lyons, S. K. *et al.* Holocene shifts in the assembly of plant and animal communities implicate human impacts. *Nature* **529**, 80–83 (2016).

59. Papakostas, S. *et al.* Gene pleiotropy constrains gene expression changes in fish adapted to different thermal conditions. *Nat. Commun.* **5**, 4071 (2014).

60. Bustos-Korts, D. *et al.* Exome sequences and multi-environment field trials elucidate the genetic basis of adaptation in barley. *Plant J.* **99**, 1172–1191 (2019).

61. Franks, S. J. *et al.* The Resurrection Initiative: storing ancestral genotypes to capture evolution in action. *Bioscience* **58**, 870–873 (2008).

62. Goldenberg, S. Z. *et al.* Increasing conservation translocation success by building social functionality in released populations. *Glob. Ecol. Conserv.* **18**, e00604 (2019).

63. Rick, K. *et al.* Population genomics of *Bettongia lesueur*: admixing increases genetic diversity with no evidence of outbreeding depression. *Genes (Basel).* **10**, 851 (2019).

64. Krause, S. M. B. *et al.* Environmental legacy contributes to the resilience of methane consumption in a laboratory microcosm system. *Sci. Rep.* **8**, 8862 (2018).

65. Holeski, L. M., Jander, G. & Agrawal, A. A. Transgenerational defense induction and epigenetic inheritance in plants. *Trends Ecol. Evol.* **27**, 618–626 (2012).

66. de Mazancourt, C., Johnson, E. & Barraclough, T. G. Biodiversity inhibits species' evolutionary responses to changing environments. *Ecol. Lett.* **11**, 380–388 (2008).

67. Simberloff, D. *et al.* Impacts of biological invasions: what's what and the way forward. *Trends Ecol. Evol.* **28**, 58–66 (2013).

68. Bell, G. Evolutionary rescue and the limits of adaptation. *Philos. Trans. R. Soc. B Biol. Sci.* **368**, 20120080 (2013).

69. Copernicus Land Monitoring Service, E. E. A. CORINE land cover. (2018). Available at: https://land.copernicus.eu/pan-european/corine-land-cover.

70. US Geological Survey datasets (2020). Available at: https://www.usgs.gov/products/data-and-tools/science-datasets

71. Fick, S. E. & Hijmans, R. J. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* **37**, 4302–4315 (2017).

72. Bethesda (MD): National Library of Medicine (US) & National Center for Biotechnology Information. National Center for Biotechnology Information (NCBI)[Internet]. (1988). Available at: https://www.ncbi.nlm.nih.gov

73. Ashburner, M. *et al.* Gene Ontology: tool for the unification of biology. *Nat. Genet.* **25**, 25–29 (2000).

74. Primmer, C. R., Papakostas, S., Leder, E. H., Davis, M. J. & Ragan, M. A. Annotated genes and nonannotated genomes: cross-species use of Gene Ontology in ecology and evolution research. *Mol. Ecol.* **22**, 3216–3241 (2013).

75. Global Biodiversity Information Facility (2020). Available at: https://www.gbif.org.

76. Kattge, J. *et al.* TRY - a global database of plant traits. *Glob. Chang. Biol.* **17**, 2905–2935 (2011).

77. Madin, J. S. *et al.* The Coral Trait Database, a curated database of trait information for coral species from the global oceans. *Sci. Data* **3**, 160017 (2016).

78. Dornelas, M. *et al.* BioTIME: A database of biodiversity time series for the Anthropocene. *Glob. Ecol. Biogeogr.* **27**, 760–786 (2018).

79. Ovaskainen, O. *et al.* Chronicles of nature calendar, a long-term and large-scale multitaxon database on phenology. *Sci. Data* **7**, 47 (2020).

80. Miller, J. *et al.* From taxonomic literature to cybertaxonomic content. *BMC Biol.* **10**, 87 (2012).

81. Park, I. W. & Mazer, S. J. Overlooked climate parameters best predict flowering onset: Assessing phenological models using the elastic net. *Glob. Chang. Biol.* **24**, 5972–5984 (2018).

82. Ovaskainen, O. & Abrego, N. *Joint species distribution modeling with applications in R*. (Cambridge University Press, 2020).

83. DeAngelis, D. L. & Grimm, V. Individual-based models in ecology after four decades. *F1000Prime Rep.* **6**, 39 (2014).

84. Kotta, J. *et al.* Integrating experimental and distribution data to predict future species patterns. *Sci. Rep.* **9**, 1821 (2019).

85. Hartmann, M., Hosack, G. R., Hillary, R. M. & Vanhatalo, J. Gaussian process framework for temporal dependence and discrepancy functions in Ricker-type population growth models. *Ann. Appl. Stat.* **11**, 1375–1402 (2017).

86. Schmidt, M. & Lipson, H. Distilling free-form natural laws from experimental data. *Science* **324**, 81–85 (2009).

87. Weise, H. *et al.* Resilience trinity: safeguarding ecosystem functioning and services across three different time horizons and decision contexts. *Oikos* **129**, 445–456 (2020).

88. Bernstein, A. All creatures great and small. *BMJ* **365**, l2385 (2019).

89. Allada, R. & Siegel, J. M. Unearthing the phylogenetic roots of sleep. *Curr. Biol.* **18**, R670–R679 (2008).

90. Vyazovskiy, V. V, Walton, M. E., Peirson, S. N. & Bannerman, D. M. Sleep homeostasis, habits and habituation. *Curr. Opin. Neurobiol.* **44**, 202–211 (2017).

91. Mason, I. C., Qian, J., Adler, G. K. & Scheer, F. A. J. L. Impact of circadian disruption on glucose metabolism: implications for type 2 diabetes. *Diabetologia* **63**, 462–472 (2020).

92. Maley, C. C. *et al.* Genetic clonal diversity predicts progression to esophageal adenocarcinoma. *Nat. Genet.* **38**, 468–473 (2006).

93. Alexandrov, L. B., Nik-Zainal, S., Siu, H. C., Leung, S. Y. & Stratton, M. R. A mutational signature in gastric cancer suggests therapeutic strategies. *Nat. Commun.* **6**, 8683 (2015).

94. Visconti, A. *et al.* Interplay between the human gut microbiome and host metabolism. *Nat. Commun.* **10**, 4505 (2019).

95. Tamburini, S., Shen, N., Wu, H. C. & Clemente, J. C. The microbiome in early life: implications for health outcomes. *Nat. Med.* **22**, 713–722 (2016).

96. Langdon, A., Crook, N. & Dantas, G. The effects of antibiotics on the microbiome throughout development and alternative approaches for therapeutic modulation. *Genome Med.* **8**, 39 (2016).

97. Spittlehouse, D. L. & Stewart, R. B. Adaptation to climate change in forest management. *J. Ecosyst. Manage.* **4**, 1-11 (2004).

98. Reyer, C. P. O. *et al.* Are forest disturbances amplifying or canceling out climate change-induced productivity changes in European forests? *Environ. Res. Lett.* **12**, 034027 (2017).

99. Swinfield, T. *et al.* Imaging spectroscopy reveals the effects of topography and logging on the leaf chemistry of tropical forest canopy trees. *Glob. Chang. Biol.* **26**, 989–1002 (2020).

100. Food and Agriculture Organization of the United Nations (FAO). *Assessing forest degradation: towards the development of globally applicable guidelines*. (2011).

101. Hänninen, H. *Boreal and temperate trees in a changing climate*. (Springer Netherlands, 2016). doi:10.1007/978-94-017-7549-6

102. Roberts, M. *et al.* The effect of forest management options on forest resilience to pathogens. *Front. For. Glob. Chang.* **3**, 7 (2020).

103. Messier, C. *et al.* The functional complex network approach to foster forest resilience to global changes. *For. Ecosyst.* **6**, 21 (2019).

104. Tricker, P. J., ElHabti, A., Schmidt, J. & Fleury, D. The physiological and genetic basis of combined drought and heat tolerance in wheat. *J. Exp. Bot.* **69**, 3195–3210 (2018).

105. Zhu, J.-K. Abiotic stress signaling and responses in plants. *Cell* **167**, 313–324 (2016).

106. Chang, Y. *et al.* Epigenetic regulation in plant abiotic stress responses. *J. Integr. Plant Biol.* jipb.12901 (2019). doi:10.1111/jipb.12901

107. Friedrich, T., Faivre, L., Bäurle, I. & Schubert, D. Chromatin-based mechanisms of temperature memory in plants. *Plant. Cell Environ.* **42**, 762–770 (2019).

108. Tao, F. *et al.* Contribution of crop model structure, parameters and climate projections to uncertainty in climate change impact assessments. *Glob. Chang. Biol.* **24**, 1291–1307 (2018).

109. Cardoso, P. & Leather, S. R. Predicting a global insect apocalypse. *Insect Conserv. Divers.* **12**, 263–267 (2019).

110. Wilkinson, M. D. *et al.* The FAIR guiding principles for scientific data management and stewardship. *Sci. Data* **3**, 160018 (2016).