

Opinion

The Temporal Dynamics of Multiple Stressor Effects: From Individuals to Ecosystems

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Multiple stressors, such as warming and invasions, often occur together and have nonadditive effects. Most studies to date assume that stressors operate in perfect synchrony, but this will rarely be the case in reality. Stressor sequence and overlap will have implications for ecological memory – the ability of past stressors to influence future responses. Moreover, stressors are usually defined in an anthropocentric context: what we consider a short-term stressor, such as a flood, will span multiple generations of microbes. We argue that to predict responses to multiple stressors from individuals to the whole ecosystem, it is necessary to consider metabolic rates, which determine the timescales at which individuals operate and therefore, ultimately, the ecological memory at different levels of ecological organization.

Temporal Dynamics of Single and Multiple Stressors in Natural Systems

Predicting how anthropogenic stressors, such as pollution events, warming, and novel pathogens, affect natural ecosystems is a major challenge for contemporary ecology. The presence, frequency, and magnitude of multiple stressors varies over time and space, however, with implications for their independent and combined effects on responses from individual behavior to entire ecosystem processes [1]. Here, we argue that the timing and duration of both the initial impacts of and recovery from stressors are particularly critical, and at least as important as the spatial component that has been the primary focus of most research to date. In particular, the temporal dynamics of multiple stressor events has been largely overlooked, yet time is critically important because stressors rarely, if ever, act in perfect synchrony, and the order and overlap duration will shape their combined impacts. Furthermore, stressors do not need to overlap in time to have cumulative effects, since the ‘legacy’ of previous stressors can alter the response of the ecosystem (and its component populations) to future stress.

Stressor–response relationships are not consistent through time [1]. Time can be important through both evolutionary **adaptation** (see [Glossary](#)) and **‘ecological memory’**. The former refers to the relatively well-known process of natural selection over multiple generations, where species’ adapt to function better in the face of environmental challenges [2,3]. Here, we focus on the latter phenomenon, defined as the ability of past stressors to influence the future ecological responses of a population, community, or ecosystem [4,5]. This can include **acclimation**, **parental effects**, and species sorting due to past stress, including lagged indirect legacy effects. For instance, a recent single-stressor study found that marine sticklebacks (*Gasterosteus aculeatus*) exhibit carry-over effects of a high CO₂ environment, causing offspring to perform poorly under conditions that differ from those experienced by their parents (even if these new conditions were actually less ‘stressful’) [6]. At the wider community level, another study has demonstrated how the impacts of a severe heatwave in 2017 on corals in the Great Barrier Reef were shaped by the effects of a heatwave in the preceding year [4] (i.e., multiple heatwave stressors separated in time but not space). Impacts can also manifest long after the stressor itself

Highlights

Multiple anthropogenic stressors rarely overlap in perfect synchrony in time, yet most research quantifying how they interact assumes that they do.

Stressor sequence and the degree of temporal overlap will have implications for ecological memory – the influence of past stressors on future ecological responses – from genes to ecosystems.

Adding to this complexity, organisms with different generation times will experience multiple stressors (and the degree to which they overlap in time) in different ways.

We propose that lifespan and associated metabolic rates can be used to define stressor type (continuous or discrete) and temporal overlap for different focal organisms.

Moving forward, we need to embrace the temporal complexity of multiple stressors and quantify how various realistic asynchronous scenarios will alter their cumulative impacts across different ecosystems.

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has disappeared, because of dispersal limitations or lagged effects due to species interactions (e.g., trophic cascades) [7]. For instance, lichen diversity remained unchanged 2.5 years after adjacent forest clearance, but declined after a further 14 years [8] due to dispersal limitations. Another example is the Nitrogen Cascade, whereby increased soil nitrogen content (from deposition) causes changes in plant composition, which then causes lagged changes in herbivore, and subsequently predator, communities [9]. These studies demonstrate that ecological memory can alter our ability to detect and predict multiple stressor impacts: even if a past stressor has long since disappeared, its legacy may still be playing out in a system facing new stressors.

Despite multiple anthropogenic stressors being an increasingly common phenomenon, most research to date has focused on a single stressor, a single trophic level (but see [10,11]), and either the spatial component – comparing locations with and without a stressor – or simple ‘before’ and ‘after’ stress ecosystem states, ignoring temporal oscillations in magnitude and dissipation time (Figure 1). Recent reviews have discussed the complexity of temporal dynamics [1] and the importance of species’ traits in determining timescales [7,12], and time is now

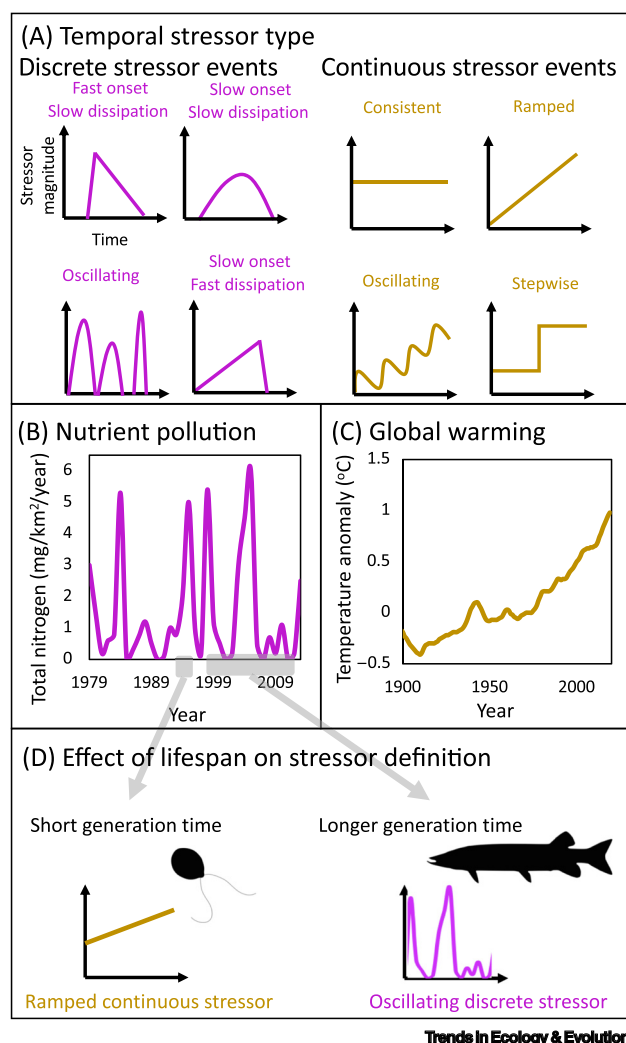


Figure 1. Importance of Timescales in Defining Stressors. (A) Classification of stressor type (adapted from [1]), expanded with real-world examples (B, C) and linked to generation time (D). (B) Nutrient pollution in coastal basins in Florida [35] is an oscillating discrete stressor (from an anthropocentric perspective), with peaks associated with agricultural activity. (C) Global warming is a ramped continuous stressor: average global annual air temperatures are getting higher each year (data from NASA; www.data.nasa.gov). (D) The same type of stressor as in (A) will be experienced differently by species depending on their generation time. Taking the example of nutrient pollution, a single-celled alga (generation time ≈ 1 day) experiences the pollution as a ramped continuous stressor, while a larger, longer-lived predatory fish (generation time ≈ 8 years) experiences the pollution as an oscillating stressor at absolute timescales closer to our own anthropocentric perception of time. All organism silhouettes are from open source software PhyloPic.org.

Glossary

Absolute time: time that exists independent of any events or processes.

Adaptation: the acquisition or recombination of traits that improve performance or survival over multiple generations.

Acclimation: physiological, morphological, or behavioral adjustments within a single organism that improve performance or survival under certain conditions.

Antagonistic interaction: the effect of two stressors is less than the sum of their parts.

Continuous stressor: a stressor present throughout the generation time of a focal organism.

Discrete stressor: a stressor present for part of the generation time of a focal organism.

Ecological memory: the ability of past conditions and experiences to influence the future ecological responses of a population, community, or ecosystem.

Generation time: the average time between two consecutive generations in the lineages of a population.

Parental effects: the phenotype of an individual is affected by the phenotype or environment of its parents.

Synergistic interaction: the effect of two stressors is more than the sum of their parts.

recognized as being particularly critical for gauging climate change impacts, especially in terms of the progressive rises in average temperature that continue to ramp up under global warming [13]. This thinking has started to enter the wider realm of empirical multiple stressor ecology [14–18], including the introduction of an initial conceptual framework for the marine realm [15], but temporal dynamics in multiple stressor ecology are still largely ignored and have yet to be formalized more generally.

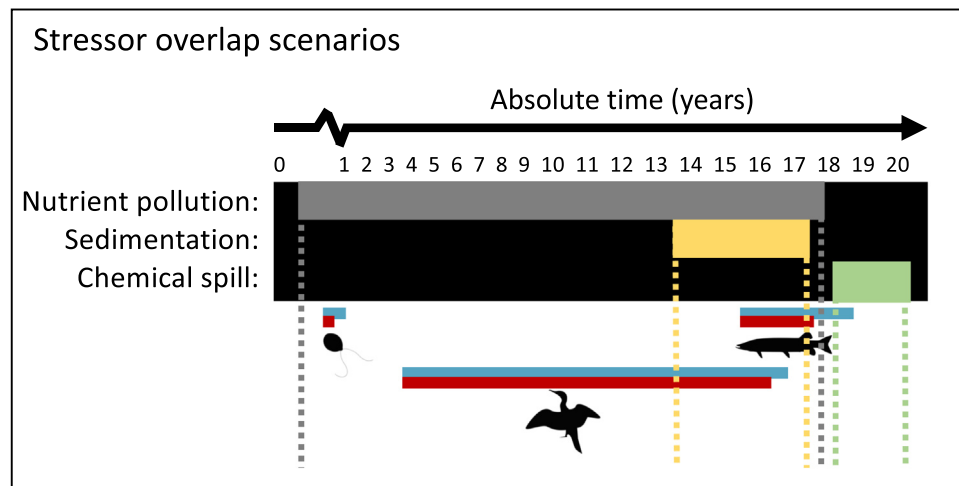
Stressor Timescales

As a first step towards filling these knowledge gaps, we need to embrace the temporal complexity of single stressors before we can start to address them in combination. Stressors are either discrete or continuous and their magnitude (strength of impact) can also vary over time (Figure 1A). For instance, agricultural nutrient pollution is often a **discrete stressor** that oscillates over time (e.g., seasonal spikes in run-off reflecting farming activity; Figure 1B). By contrast, global increases in average temperature are a more **continuous stressor**, increasing progressively in severity over time (i.e., a ramped stressor; Figure 1C). Since temperature sets the pace of life through its effects on metabolic rate, climatic warming can be considered as an umbrella or master stressor under which all other stressors, which are increasingly prevalent across the world, play out [19–22]. Multiple stressor impacts can be additive or more (or less) than the sum of their single effects (**synergistic** and **antagonistic interactions**, respectively). This creates huge challenges for both science and policy, as most of the past century of ecotoxicology and biomonitoring has focused on single stressors, and the much smaller subset of studies on two or more stressors has typically assumed additivity by default [23–25]. This is a gross oversimplification, as global meta-analyses and reviews have revealed that nonadditive effects are common [26,27] in both the aquatic [10,28–31] and terrestrial [32,33] realms, although we still do not fully understand how and why they arise [25]. Some initial evidence suggests that when stressors occur simultaneously, nonadditive effects are the rule rather than the exception [34]. Beyond this overly simplistic scenario of synchronous stressors, the current limited data and theory constrain our ability to predict (and mitigate) multiple stressor impacts over time [25].

Organism-Level Timescales: Individuals as Foundational Units

Discrete and continuous stressors are usually defined in an anthropocentric context: what we might consider a discrete stressor, such as a flooding event, might be present for the entire **generation time** of a shorter-lived species (Figure 1D). We argue that it is more meaningful to think in terms of the timescales at which focal organisms operate rather than **absolute time** *per se*. In particular, the distribution of generation times of different species in a community is critical in determining the ecological memory of the ecosystem as a whole. This is because generation time sets the characteristic timescale at which individuals experience, and respond to, environmental perturbations (Figure 2). Organisms operating at different timescales will do so in different ways to a given set of stressors over a particular absolute timescale [36]. Therefore, the taxonomic composition of species with different generation times in an ecosystem should arguably shape overall ecological memory. To get to grips with this, we must first be able to predict the generation times of different species and how these species respond differentially to a particular sequence of stressor events. To this end, Ecological Metabolic Theories (EMTs), drawn from both the Dynamic Energy Budget and the Metabolic Theory of Ecology (MTE) frameworks [37,38], provide a good starting point.

At the most fundamental level, EMTs describe how rates of metabolic processes in cells predict how individual organisms take up resources from the environment, convert them into other forms for growth and reproduction, and excrete the altered forms. This sets the stage for the prediction of rates and, at higher levels of biological organization, biomass and diversity. Importantly, at the



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Figure 2. The Relationship between Stressor Overlap and Organismal Timescales. (A) An example of ‘common syndromes’ of multiple agricultural stressors in freshwater ecosystems overlapping in absolute time, and how organisms of different generation times experience them. Normal generation time is shown as blue bars, while red bars represent reduced generation time caused by higher metabolic rates under warmer conditions due to global climate change (an umbrella ‘master stressor’). In this example, a single generation of single-celled algae (e.g., *Chlamydomonas* spp.; generation time ≈ 1 day) experiences only one stressor (nutrient pollution in gray) in addition to warming, while a larger, endothermic, longer-lived predatory bird (e.g., cormorant, *Phalacrocorax carbo*; generation time ≈ 20 years) experiences two further stressors (nutrient pollution in gray and sedimentation from bank erosion in yellow). A fish species (e.g., northern pike, *Esox lucius*) with generation time (≈ 8 years) intermediate between the alga and the bird experiences three stressors in addition to warming (nutrient pollution in gray, sedimentation from soil erosion in yellow, and a chemical spill in green), but the proportionate exposure to each differs from that of the bird. Warming as our ‘master stressor’ reduces generation time and alters how individuals experience stressor events over the two decades shown in the figure; for instance, the individual pike’s generation time is reduced such that it does not experience the chemical spill (in green) in a warmer world.

population level, EMTs can predict our key trait of interest: generation time. The simplest such prediction comes from the MTE, that across species,

$$G = G_0 m^{1-\alpha} e^{E/kT}, \quad [1]$$

where G is the generation time, m is the species’ average body mass, α is the (scaling) constant of the whole-organism metabolic rate, E is an activation energy, k is Boltzmann’s constant (8.62×10^{-5} eV/K), T is the temperature in kelvin, and G_0 is a size- and temperature-independent constant that captures variation from other sources such as trophic level [37,39–41]. According to the MTE, variation in generation times across species is largely determined by their body sizes and (physiologically) operational temperatures. In multicellular eukaryotes, typically $\alpha \approx 0.75$ and $E \approx 0.65$ [37], with significant and systematic deviations from these values for unicellular eukaryotes and prokaryotes that drive ecosystem processes lower in the food web [42,43]. Equation 1 stems from a well-known general inverse relationship between generation time and mass-specific metabolic rate [44,45].

Metabolic rate and the life-history traits it drives (and in particular, generation time) therefore holds great potential to help us predict which stressors are relevant for a given organism, as well as the rate and magnitude of its response. With EMT as a foundation, a stressor’s impact can potentially be quantified based on a focal species’ generation times, inferred from its average adult body size and thermal physiology (Figure 2). Metabolic rate and generation time are the fundamental reasons why a small single-celled alga and a large fish experience and respond to stressors in

vastly different timescales (Figure 1D) and through different mechanisms. For example, a recent study showed that size can explain considerable variation in the rate of thermal acclimation across a diverse range of taxa, with smaller organisms apparently acclimating faster, but to a lesser extent, than larger ones [46]. In terms of evolutionary (as opposed to just ecological) responses, the relationship between generation time and metabolic rate can also play a significant role, with faster adaptation expected for smaller organisms [47]. Furthermore, the critical timescale that one should consider to understand or quantify the overlap between multiple stressors for a given organism should be predictable from relatively simple measures of metabolic rate, via body mass and temperature (Figure 2). As a general rule, smaller, short-lived individuals in a warmer environment would be likely to experience fewer events and perceive them as rather constant or ramping, while larger, long-lived organisms in a colder environment would be likely to experience more events and perceive them as pulses (Figure 1).

From Individuals to Ecosystems

Ultimately, all ecosystems comprise individuals nested within species' populations, which are themselves nested within food webs, and the combination of the metabolic activity and the dynamics of these populations shapes responses at the higher organizational levels. The simplest way to go from individuals, through populations, to ecosystem-level responses to stressors is to assume that the ecosystem response is a weighted sum of the individual populations' responses to one or more stressors [43,48]. For example, Smith *et al.* [43] weight the responses of different functional groups of species according to their biomass to predict that warming will permanently elevate ecosystem-level respiration. Such approaches, which allow simple linear up-scaling from individuals to ecosystems, can easily accommodate multiple stressors provided the (multivariate) physiological response of the component species' populations can be quantified. However, this simple upscaling approach necessarily assumes that species' biomasses are constant relative to the timescale of the stressor's influence (such that it changes species' physiological rates but not their abundances). This approach can be extended via trait-driver theory, which allows species' traits (e.g., body size) that determine population responses to (multiple) stressors to dynamically modify population biomasses in the system [49,50]. However, this approach is currently limited in that it cannot accommodate realistic trophic and nontrophic interactions between species' populations. To truly go from the multistressor responses of individual organisms to entire communities and ecosystems, the complexity of time-varying, nonlinear species interactions (i.e., food-web mediated) needs to be considered (Box 1).

Box 1. Species Interactions and Temporal Stressors

In addition to considering how multiple drivers operate in the temporal dimension, we also need to understand the importance of indirect cascading effects due to species interactions (i.e., food-web mediated; Figure I). Nonlinearities and cascading effects can generate unpredictable fluctuations in the sizes of interacting populations and, therefore, the propagation of stressor-induced perturbations across the food web (e.g., from primary producers to top consumers). Furthermore, the effects of stressors often attenuate or change directionally as they move through the food web because of systematic differences in timescales or interacting species. For example, in aquatic systems where the primary producers are (small-bodied and fast-lived) algae, one may observe very rapid responses at the base of the web, with time-lagged and more aggregated effects at the higher trophic levels (which are larger-bodied and longer-lived; Figure I). The body-mass structure of the web drives these dynamics via metabolic rates and generation times (Figure I), but also its effects on trophic status and abundance.

As an example, if we know the absolute timescale at which a stressor affects the base of the food web, we can start to put bounds on how long it will take to 'ripple' upwards to the top (to account for the temporal dimension of indirect effects) and disentangle this from more direct effects (Figure IB). Of course, food webs are not simply unidirectional networks: consumers can also exert top-down control. Stressors can modulate these cascading effects, as seen with pesticides, nutrients, acidification, and climate change, for instance; as yet, how multiple stressors play out over time across the food web remains poorly understood.

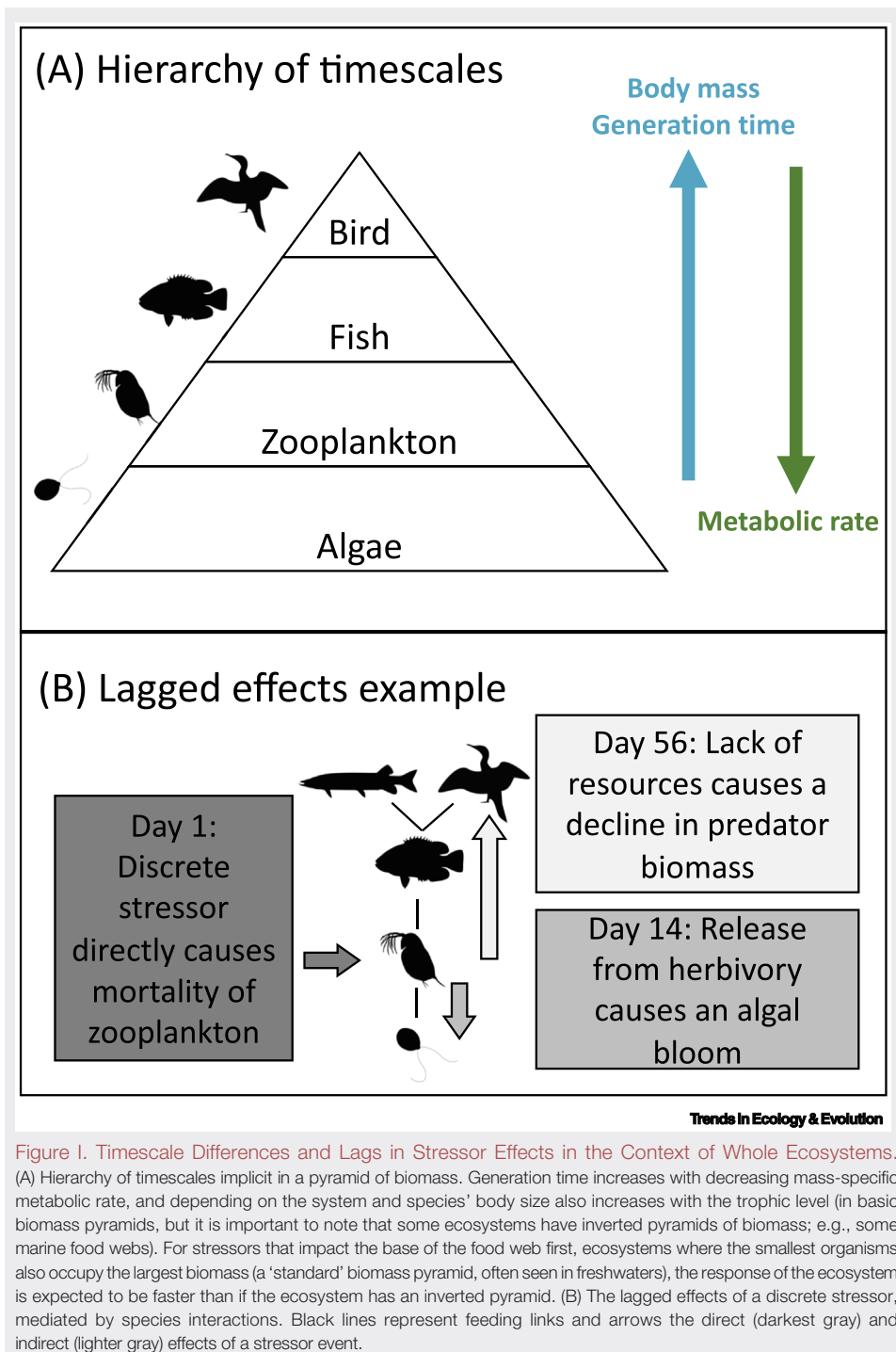


Figure 1. Timescale Differences and Lags in Stressor Effects in the Context of Whole Ecosystems. (A) Hierarchy of timescales implicit in a pyramid of biomass. Generation time increases with decreasing mass-specific metabolic rate, and depending on the system and species' body size also increases with the trophic level (in basic biomass pyramids, but it is important to note that some ecosystems have inverted pyramids of biomass; e.g., some marine food webs). For stressors that impact the base of the food web first, ecosystems where the smallest organisms also occupy the largest biomass (a 'standard' biomass pyramid, often seen in freshwaters), the response of the ecosystem is expected to be faster than if the ecosystem has an inverted pyramid. (B) The lagged effects of a discrete stressor, mediated by species interactions. Black lines represent feeding links and arrows the direct (darkest gray) and indirect (lighter gray) effects of a stressor event.

Despite these complexities, even in the currently nascent state of the theoretical development of the field, we can start to make empirically relevant predictions about the combined effects of multiple stressors by qualitatively mapping stressor temporal dynamics onto the variation in organisms' generation times within a community or ecosystem. We can hypothesize that every

community has a characteristic absolute timescale depending on the relative proportions of organisms with different generation times within it, and how these organisms interact with each other (Box 1 and Figure 1A). For instance, if we take a stressor perceived as discrete in an anthropogenic context (e.g., a pollution event) and compare the response in a ‘slow’ community comprising large, long-lived organisms (i.e., a forest of trees) versus a ‘fast’ community dominated by smaller, short-lived organisms (i.e., oceanic phytoplankton), even with a ‘zeroth-order’ model for the community response as a biomass-weighted sum of species’ population responses one would expect fundamentally different community-level ecological memory. The slow community will experience a discrete stressor and the fast community a continuous stressor (Figure 2). However, most communities comprise both large long-lived and small short-lived organisms experiencing the stressors at different absolute timescales while interacting with one another, adding further complexity to multiple stressor ecology. As a first step towards this goal, we can at least start to group systems into broad typologies based on their size structure and hence metabolic capacity and the temporal envelopes of response, as in our two (extreme exemplar) cases earlier.

How to precisely quantify this community structure and how it maps onto ecosystem processes remains an open question, but considerable progress has been made in the past two decades or so and we now have a set of fairly simple rules that can be used to help narrow the field. For instance, aquatic systems have strongly size-structured food webs, with energy flowing from small, abundant, and diverse but short-lived organisms at the base (e.g., algae) to those that are increasingly larger, rarer, and less diverse but longer-lived at the top of the web (e.g., predatory fishes; Box 1). At each ‘trophic-level’ step there is an approximate order of magnitude drop in biomass transfer (Box 1) and similar degrees of change in terms of the other traits listed above – and many of these have well-described allometric scaling relationships that can be used here to predict broad shifts in communities and how these map onto temporal shifts in stressors. One approach could involve the resolution of community size spectra using a combination of molecular techniques (e.g., next-generation sequencing and metabarcoding of environmental DNA or bulk-sample DNA) to obtain detailed taxonomic information, and machine learning using images to gain complementary community body-mass distributions [51]. This could then be used to calculate the relative proportions of generation times distributed within the community, so that ecologists can decide when in absolute time to most accurately measure a community response to multiple stressor events.

Moving forward, we will need to focus future research effort into unraveling how temporally realistic stressors – occurring at different time points, with different degrees of overlap in absolute time – alter the response of organisms across the full scale of generation times, so we can start to resolve communities into ‘temporal types’ to start testing these predictions with both data and models.

Concluding Remarks

Multiple stressor ecology has taken off in the past few years [23,25,52,53], but there is still a huge chasm to be bridged between theory and reality. In particular, ecologists need to bring greater temporal realism to multiple stressor research to address some of the biggest challenges facing our rapidly changing world [25]. Here, we have shown the need to move beyond current overly simplistic scenarios of perfectly overlapping stressors: future research needs to consider stressor sequences, the degree of stressor overlap, and how these change for organisms of different generation times in ‘fast’ versus ‘slow’ communities (see Outstanding Questions). Most of our current knowledge on multiple stressor interactions is based on unrealistic synchronous scenarios. We argue that ecological responses will change dramatically under realistic asynchronous scenarios

Outstanding Questions

How do the order, frequency, and duration of multiple stressors affect their cumulative ecological impact on species’ populations?

Does previous exposure to a particular stressor promote or erode resilience to future stressors (through ecological memory) and does this response depend on stressor similarity?

Do temporally asynchronous multiple stressor events have outcomes (e.g., dominance of nonadditive effects) comparable with those of stressors acting in perfect synchrony?

If we rescale responses in terms of generation time (rather than absolute time), do we see a consistent response across species of different lifespans?

How do we scale up population-level responses to temporally variable stressors of organisms operating at different timescales to entire ecosystems?

due to ecological memory, with implications for the prevalence of additive versus nonadditive effects and, by extension, the management and conservation of natural ecosystems.

Acknowledgments

All authors are supported by Natural Environment Research Council (NERC) grants NE/M020843/1 and NE/S000348/1. M.C.J. is also supported by NERC grant NE/V001396/1.

Declaration of Interests

No interests are declared.

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