

# Rate of environmental change across scales in ecology

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## ABSTRACT

The rate of change (RoC) of environmental drivers matters: biotic and abiotic components respond differently when faced with a fast or slow change in their environment. This phenomenon occurs across spatial scales and thus levels of ecological organization. We investigated the RoC of environmental drivers in the ecological literature and examined publication trends across ecological levels, including prevalent types of evidence and drivers. Research interest in environmental driver RoC has increased over time (particularly in the last decade), however, the amount of research and type of studies were not equally distributed across levels of organization and different subfields of ecology use temporal terminology (e.g. ‘abrupt’ and ‘gradual’) differently, making it difficult to compare studies. At the level of individual organisms, evidence indicates that responses and underlying mechanisms are different when environmental driver treatments are applied at different rates, thus we propose including a time dimension into reaction norms. There is much less experimental evidence at higher levels of ecological organization (i.e. population, community, ecosystem), although theoretical work at the population level indicates the importance of RoC for evolutionary responses. We identified very few studies at the community and ecosystem levels, although existing evidence indicates that driver RoC is important at these scales and potentially could be particularly important for some processes, such as community stability and cascade effects. We recommend shifting from a categorical (e.g. abrupt *versus* gradual) to a quantitative and continuous (e.g. °C/h) RoC framework and explicit reporting of RoC parameters, including magnitude, duration and start and end points to ease cross-scale synthesis and alleviate ambiguity. Understanding how driver RoC affects individuals, populations, communities and ecosystems, and furthermore how these effects can feed back between levels is critical to making improved predictions about ecological responses to global change drivers. The application of a unified quantitative RoC framework for ecological studies investigating environmental driver RoC will both allow cross-scale synthesis to be accomplished more easily and has the potential for the generation of novel hypotheses.

*Key words:* global change, physiology, ecology, rate of change, time, abrupt, gradual

## CONTENTS

I. Introduction	1799
II. General trends and definitions	1799
(1) Literature synthesis	1799
(2) General publication trends	1800
(3) Problems with definitions of ‘abrupt’ and ‘gradual’	1801
(4) Range of RoC treatments and experimental duration	1801
III. Trends at each level of ecological organization	1802
(1) Individual level	1802
(a) General trends	1802
(b) Temperature RoC and plastic responses	1803

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(c) Phenotypic plasticity and RoC .....	1803
(2) Population level .....	1804
(3) Community level .....	1805
(4) Ecosystem level .....	1806
IV. Prospects and research priorities .....	1807
(1) Shifting the focus from categorical definitions to a continuous framework .....	1807
(2) Towards reproducibility: experimental design and reporting parameters .....	1807
(3) Cross-scale analysis as a common goal .....	1807
V. Conclusions .....	1808
VI. Acknowledgements .....	1808
VII. References .....	1808
VII. Supporting information .....	1811

## I. INTRODUCTION

It has long been established that organisms respond differently to ‘gradual’ and ‘abrupt’ treatments of equal intensity – the outcome depends on the rate of change (RoC) (e.g. Dallinger, 1887; Mast, 1910). The widespread myth of the frog boiled alive (i.e. that a frog thrown into boiling water will leap out, whereas a frog in gradually heated water will remain in the pot and meet its demise) attests to society’s recognition of the importance of RoC outside of the scientific arena and its ‘common sense’ nature. Although this topic was not a major focus of research in the 20th century, within the last decade it has generated a spike of interest in the scientific community (Siteur *et al.*, 2016; Ratajczak *et al.*, 2018). One reason for this may be the importance it could have for our ability to predict the impact of global change, particularly global warming (Luo & Reynolds, 1999; Hui *et al.*, 2002; Luo & Hui, 2009).

Existing studies indicate that for carbon storage processes (Luo & Reynolds, 1999; Hui *et al.*, 2002; Luo & Hui, 2009; Yuan *et al.*, 2017), mutualistic interactions (Klironomos *et al.*, 2005), fitness and thermal limits (Terblanche *et al.*, 2007; Hoffmann, Chown, & Clusella-Trullas, 2013), the effect of an environmental driver appears stronger when an abrupt treatment is applied. This illustrates the general need to address the relationship between organismal responses and the temporal dynamics of global change factors: abrupt treatments may overestimate ecological responses or instigate different response mechanisms than the ‘real world’ situation of a slower rate of environmental change.

Studying the effect of RoC of environmental drivers on organismal responses is crucial. Warming and CO<sub>2</sub> enrichment experiments typically apply abrupt treatments; therefore, models that use experimental data to predict future species distributions in climate change scenarios rely on reaction norms that are based on abrupt treatments (Dillon, Wang, & Huey, 2010). For a number of factors (both climate-related and otherwise), organisms and mechanisms, the RoC strongly influences the outcome, thus models based only on data from abrupt treatments may not be representative (Dillon *et al.*, 2010; Siteur *et al.*, 2016). In order to increase the predictive power of those models, it is important

to study the effect of driver RoC in addition to the effect of the magnitude of change.

The issue of RoC spans multiple spatial and ecological scales: changes in various environmental factors can elicit effects at the level of the individual organism as well as the population, community and ecosystem levels. Linkages between these sub-fields of ecology are impeded by differential and sometimes competing concepts of time and its derivative principles (Ryo *et al.*, 2019). Additionally, there is ambiguity surrounding the description of these changes in terms of what precisely constitutes abrupt or gradual change, making it difficult to make cross-scale linkages. Understanding the differential effects across spatial scales is particularly important to improve predictions about extinctions and changes in biodiversity and ecosystem functioning. Thus, there is a need for cross-scale unification of RoC-related research.

To address the issue of clarity of RoC-related terms, establish links among fields concerned with this theme and provide future perspectives, we conducted a literature search with *Web of Science* (WoS) from 1945 to August 2019 across fields of biology. In this review, we are concerned primarily with the temporal dynamics of the environmental driver, and not the response, because this is a common parameter that can be studied across ecological hierarchy and fields, allowing broader knowledge synthesis about global change (Ryo *et al.*, 2019). We considered the relationship between the RoC of environmental factors and biological responses across multiple levels of ecological organization. Our aims were to (i) summarize general publication trends across ecological levels, and (ii) highlight major challenges and opportunities related to the study of RoC.

## II. GENERAL TRENDS AND DEFINITIONS

### (1) Literature synthesis

We performed an exploratory literature review in September 2019 using WoS. To identify research related to RoC of environmental driver, we used the search terms: [(abrupt\* or sudden or rapid or fast or “step increase\*” or step or “rate of change”) AND (gradual\* or progressive or slow\* or “step-

by-step” or “rate of change”) AND (“environmental change” or “climate change” or “global change” or “rate of change”)]. This search yielded 757 papers. The search was then restricted to the following WoS categories: Biology or Soil Science or Biodiversity Conservation or Ecology or Limnology or Evolutionary Biology or Paleontology or Physiology or Marine Freshwater Biology or Plant Sciences or Zoology or Forestry or Microbiology or Environmental Science, yielding 477 papers. Among these papers we selected those that were focused on RoC of the driver and excluded those concerned with RoC of the response, giving a total of 85. Eleven additional papers were identified from the reference lists of this body of literature, giving a final total of 96 papers (see online Supporting information, Table S1). One potential limitation of our methodology is that we only considered search terms related to speed (e.g. ‘fast’ and ‘slow’) but not terms related to driver variability. For example, some modelling studies use the term ‘fluctuation’ to describe changing environmental conditions; these studies may either maintain one mean for the driver variable over time or the mean may increase or decrease. In the latter case, these models would indeed describe RoC of the driver but would be missed by our search terms.

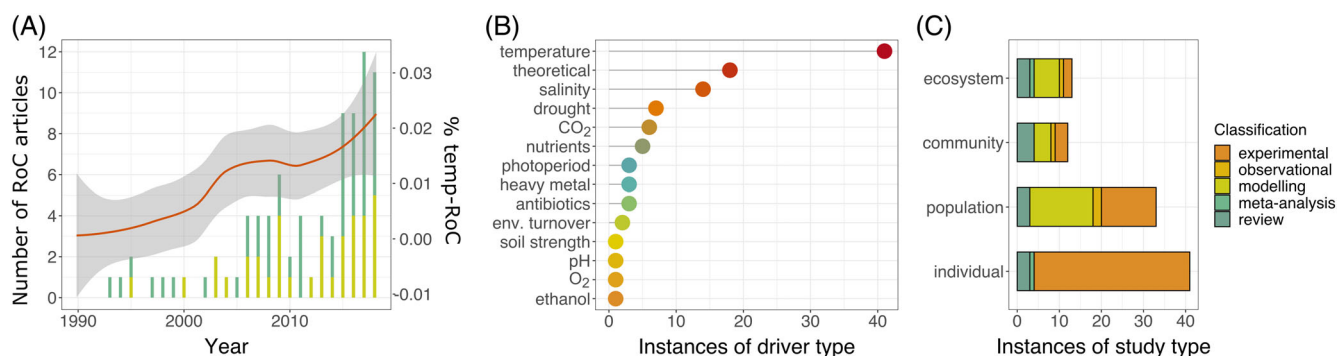
The literature was then categorized according to the type of driver considered, the type of study (e.g. experimental, review, etc.) and the level of ecological organization. Level of organization was assigned based upon the experimental unit for treatment application and the types of response variables measured (Table S1). For example, a treatment applied to a single individual or genotype would be classified at the individual level, while studies comparing populations or measuring population-level parameters (e.g. demography) would be classified at the population level. Studies

investigating community properties or metrics, such as species interactions and richness, were assigned to the community level and those considering ecosystem function or properties to the ecosystem level. Any study that investigated variables at multiple levels of organization (e.g. richness and carbon fluxes) was assigned to the highest applicable level of organization.

We then performed an additional analysis to distinguish whether the increased number of RoC papers over time resulted simply from an increasing amount of total research published or from an increasing proportion of research focused on RoC. We identified the subset of papers investigating the most studied environmental driver (temperature) in the driver RoC literature body and then normalized by the total number of papers about temperature in the same fields and years. To find the total number of papers about temperature in these fields and during this time period, we performed an additional search in WoS for the key term “temperature” for the categories cited above ( $N = 315,288$ ) and among our 96 papers ( $N = 41/96$ ). We then calculated the ratio of [RoC + temperature] papers to [total temperature] papers for each year, providing an approximation of the percentage of temperature-related research that included an RoC perspective.

## (2) General publication trends

There has been a notable increase in the number of papers on RoC over time, especially in the last 10 years (Fig. 1A). In the case of temperature-related studies, this pattern is not only due to a general increase in the number of papers published in this field and time period, but also to an increase in the percentage of papers with an RoC perspective



**Fig 1.** Synthesis of literature on rates of change (RoCs). (A) Number of publications on RoC from 1990 to 2018 (dark green: all papers from that year, light green: papers investigating temperature) and number of papers per year that studied the effects of RoC of temperature relative to the total number of papers found with the key word “temperature” [per cent of total studies (% temp-RoC), orange line]. The publication year range was limited to years for which we had a complete data set (i.e. ending in 2018). Note that limited data were available to produce the trendline because few studies per year met our inclusion criteria. (B) Number of instances of investigation of a particular driver in our set of 96 RoC papers, including modelling/review papers where the driver was unspecified (i.e. ‘theoretical’). Some papers investigated multiple drivers; the instance of each driver is shown here (total driver occurrences = 106; see Table S1); env. turnover, environmental turnover. (C) Instances of paper type (experimental, observational, modelling, review or meta-analysis) for each level of ecological organization in our set of 96 RoC papers (total instances of different study types = 99). Some studies were given multiple study-type classifications (e.g. modelling and observational); these papers were counted twice here, once for each category (see Table S1).

(Fig. 1A). This mainly results from an increased number of studies at the population level (27/32 published since 2009) and the ecosystem level (11/12 published since 2009). Studies investigating the effect of the driver RoC at an individual level have been published for a longer period of time and at a relatively constant rate during the last 10 years. Very few studies ( $N = 11$ ) have investigated RoC at the community level (Fig. 1A, C).

A variety of drivers ( $N = 14$ ) were investigated in our set of papers (Fig. 1B). Temperature was the most frequently studied, followed by unspecified drivers (i.e. modelling and some review papers) and salinity. Temperature and salinity are relatively easy to manipulate experimentally and are also both of major interest in terms of global climate change. Four drivers were each investigated only once: ethanol, oxygen and pH levels, and soil strength (Fig. 1B). Emerging contaminants and pollutants were under-represented; these could be interesting as their RoC will be affected by human activity and political decisions.

Experimental and modelling studies were the dominant study types in our data set, comprising 57 and 26% of total papers, respectively. Study types were not evenly applied across the different levels of ecological organization (Fig. 1C). Studies at the individual level were mainly experimental, while at the ecosystem level studies were primarily reviews and models. At the population level, there was a roughly even split of modelling and experimental work. Across all levels of organization there were very few observational studies ( $N = 4$ ) and meta-analyses ( $N = 2$ ) (Fig. 1C).

### (3) Problems with definitions of ‘abrupt’ and ‘gradual’

Definitions of driver temporal dynamics often contain ambiguities, particularly in the use of the terms ‘abrupt’ and ‘gradual’ in the biological literature. These terms are frequently applied using circular descriptive logic, that is an abrupt treatment is abrupt because it is strong and fast enough to expect a strong response, and this strong response justifies the use of ‘abrupt’ (found in 55% of experimental studies on temperature). Other authors have already drawn attention to issues with *a posteriori* categorization of drivers and circular logic of categorization (Bowler, 2005; Loeschke & Sørensen, 2005; Sinclair & Roberts, 2005). Clearly, the same environmental driver RoC could be described by both terms, depending on the response considered.

Furthermore, definitions of ‘abrupt’ and ‘gradual’ vary with scientific discipline. Evolutionary biologists tend to refer to global change as an abrupt change, whereas ecologists see it as gradual (Luo & Reynolds, 1999; Hui *et al.*, 2002; Kliromos *et al.*, 2005; Luo & Hui, 2009; Bell, 2010, 2013). In these fields, defining ‘abrupt and gradual’ depends on the exact aspect of climate change considered (i.e. the type of driver: events *versus* trends, *sensu* Jentsch, Kreyling, & Beierkuhnlein, 2007) and on the biological mechanism (e.g. evolution, phenology), organism (e.g. lifespan and generation time; Jentsch & White, 2019) and/or dynamics of

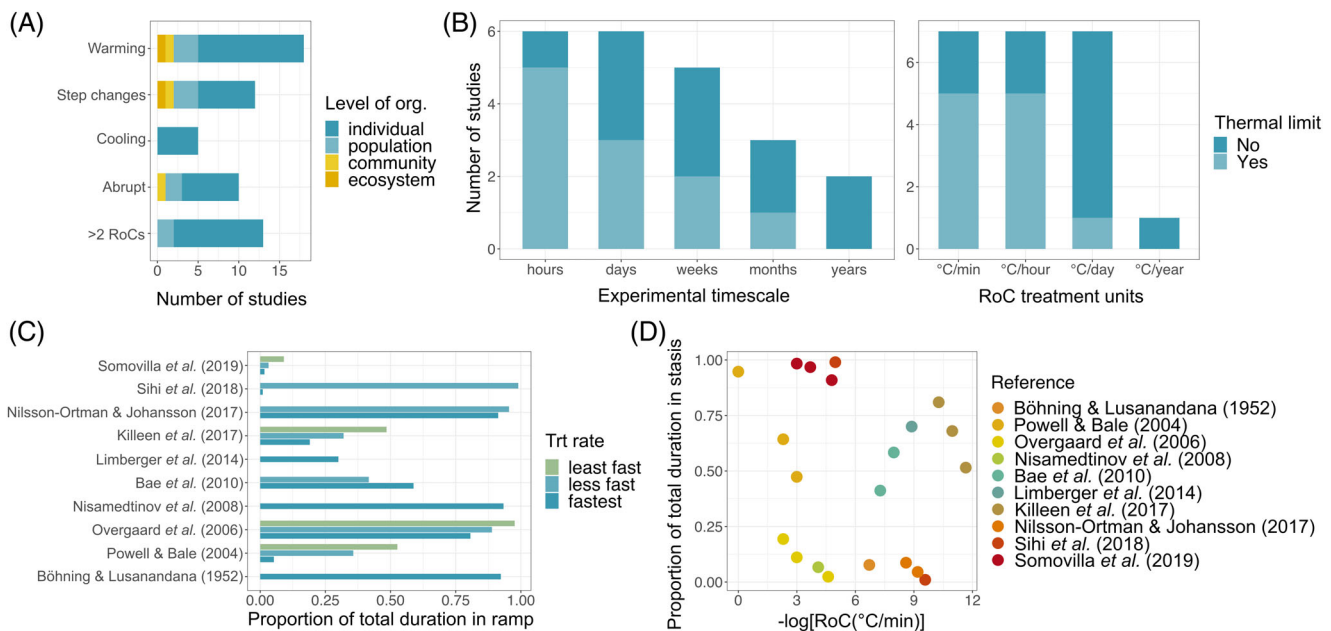
the system under study (e.g. aquatic *versus* terrestrial food webs; Nowlin, Vanni, & Yang, 2008). These cross-field differences make it difficult to synthesize evidence about driver RoCs at different scales and particularly at the ecosystem level. In order to study the relationship between the temporal dynamics of the driver and the response, we need to describe the temporal dynamics of the driver independently of the response of the organism or system.

### (4) Range of RoC treatments and experimental duration

The RoC is determined by two variables: the magnitude  $M$  of the treatment, and the period of time  $T$ , or ramp duration, over which it is applied ( $\text{RoC} = M/T$ ). The timescales of the experiments included in our literature review ranged from hours to years, with correspondingly broad treatment RoC units (Fig. 2B). In addition to the ramp duration, many experiments have an additional stasis period. Thus the duration of an experiment consists of a period when the environmental driver is dynamic (i.e. the ramp period) and a period in which it is static. Both components are important because they determine the amount of time available for a response to develop. The importance of duration is increasingly becoming recognized and discussed in various ecological contexts, including short-term intensified weather events due to climate change (Jentsch *et al.*, 2007) and ecological regime shifts (Ratajczak *et al.*, 2017).

To gain further insight into the range of RoC treatments and experimental durations, we extracted additional information from a subset of experimental studies investigating temperature change (of the 41 total studies investigating temperature, 22 of these were experimental studies; Fig. 2). We found that the temperature studies could be broadly divided into two groups: those seeking to determine thermal limits ( $N = 11/22$ ) or not ( $N = 11/22$ ; Fig. 2B). Warming treatments were three times more common than cooling treatments (Fig. 2A). Note that the temporal scale of change described as ‘gradual’ in the literature covered a very wide range, from 1°C per min to 1°C per year.

Studies investigating thermal limits constitute a distinct subset with a specific methodology. Thermal limits are defined by the minimum and maximum temperature at which an organism can survive. This is experimentally determined by a death or near-death event, thus the timelines of the organismal response, the experiment and the treatment are the same. Most thermal limit studies included at least three RoC treatments, and some had up to seven treatments. These studies tended to have relatively fast RoCs (minutes to days) and shorter overall experimental durations (8 of 11 were conducted over hours to days; Fig. 2B). Some theoretical studies on thermal limits discuss the importance of RoC in the responses of individual organisms and the relevance of RoC across different scales of ecological organisation (Beitinger, Bennett, & McCauley, 2000; Santos, Castañeda, & Rezende, 2012; Morley *et al.*, 2016).



**Fig 2.** Details of treatments in experimental studies investigating the effects of rate of change (RoC) of temperature ( $N = 22$ ). (A) Number of studies that included particular experimental design elements for each level of ecological organization. (B) Experimental timescale and RoC measurement units for two study types (i.e. whether a thermal limit was measured or not). (C, D) Ramp duration (C) and stasis period duration (D) in experiments without thermal limits. Treatments defined as ‘abrupt’ (by the original study) were excluded because frequently no RoC or duration data were provided. In C, the proportion of total experimental duration spent in the ramp period is plotted, each bar represents one treatment (Trt), and colours indicate relative rates of treatments. In D, the relationship is plotted between log-transformed RoC and the proportion of total experimental duration spent in the static period. One study out of 11 that did not use thermal limits (Donelson *et al.*, 2016) was excluded from C and D because ramp duration was not reported.

The studies not investigating thermal limits ( $N = 11/22$ ) generally had fewer overall treatments, a longer duration and slower RoCs (Fig. 2B). Of these, three recent works used a gradient approach, rather than categorical treatments. Very few studies provided information about the duration of the ramp phase of their ‘abrupt’ treatments; those that did sometimes had a duration equivalent to a ‘gradual’ treatment in other studies (minutes to days). The duration of the stasis period following an ‘abrupt’ treatment was sometimes equivalent to that of a gradual treatment in the same study, and was sometimes longer. Furthermore, the durations of the ramp and stasis periods in gradual treatments were not consistent (both within and among studies; Fig. 2C, D). There is clearly a need for clarity and precision in reporting, and ideally a more unified framework for the design of such experiments.

### III. TRENDS AT EACH LEVEL OF ECOLOGICAL ORGANIZATION

#### (1) Individual level

##### (a) General trends

Responses to different RoCs of an environmental factor have been best studied at the level of the individual organism

(Fig. 1C). Early last century, Mast (1910) showed different responses of amoebae subjected to different rates of increasing light intensity. When the light treatment was ‘abrupt’, amoebae stopped moving; however, this response reduced with more ‘gradual’ treatments, and sometimes disappeared. Similar patterns were seen for responses to salinity changes in fish, at both the level of muscle tissue and whole-organism physiological stress responses (Sherman & Cameron, 1934; Wells & Ledingham, 1940). The absorption of water by plant roots also depends on the RoC of the temperature of the rhizosphere (Böhning & Lusanandana, 1952). These pioneering studies showed that organisms can have different physiological and behavioural responses to changes in environmental factors based on both intensity and RoC.

Although temperature is the best-studied environmental factor, there is evidence that RoC is important for other drivers. For example, plants alter their gene expression in response to increased salinity; these responses include osmotic shock responses (characterized by rapid changes in gene expression related to turgor maintenance and water balance) and salt stress responses (characterized by genes related to reducing  $\text{Na}^+$  toxicity). The RoC of salinity impacts gene expression in diverse plant species: a rapid RoC leads to strong shock and stress responses, whereas a more gradual RoC leads to a small initial shock response followed by a strong stress response (Shavrukov, 2013). RoC also affects responses to light: rapid changes in diurnal light

cycles trigger hormonal and behavioural responses in Siberian hamsters (*Phodopus sungorus*), impacting reproduction (Gorman, Freeman, & Zucker, 1997). Differences in soil heavy metal RoCs preclude comparisons about impacts on microbial communities: toxicology studies are frequently short term and ‘abrupt’ with the entire dose applied at once whereas environmental-monitoring studies involve a gradual increase in levels of heavy metals over time (Giller, Witter, & Mcgrath, 1998). Such toxicology studies often report a reduction in microbial respiration rates in response to addition of a toxicant whereas monitoring studies report contrasting basal respiration rates in treatment *versus* control plots and attribute the differences to changes in community structure rather than physiology. Giller *et al.* (1998) make the important distinction that these approaches result in the study of adapting *versus* adapted communities, respectively; an important consideration when treatment application occurs over multiple generations of the study organism. Overall, RoC studies tend to show that combinations of different underlying mechanisms contribute to the observed responses.

#### (b) Temperature RoC and plastic responses

Thermal limits have been widely investigated, mostly for ectothermic marine and terrestrial organisms (Hathaway, 1928; Evans, 1948; Böhning & Lusanandana, 1952; Beiting *et al.*, 2000; Terblanche *et al.*, 2009; reviewed by Clusella-Trullas & Chown, 2014). The RoC of temperature can result in either an increase or a decrease in thermal tolerance (Hutchison, 1961; Terblanche *et al.*, 2007). There are three terms commonly used to describe the relationship between rate and intensity of changes in temperature and thermal tolerance: thermal shock, acclimation and hardening. Thermal shock is a rapid response to short-term thermal injury, which involves the synthesis of protective heat shock proteins; whereas acclimation occurs over a longer time period, and involves a variety of mechanisms (e.g. physiological and behavioural) leading to increased organismal endurance. Hardening is used ambiguously in the literature but typically refers to an intermediate response between thermal shock and acclimation (Bowler, 2005; Loeschcke & Sørensen, 2005; Sinclair & Roberts, 2005). Its ambiguity results from the difficulty of describing the temporal dynamics using categorical logic (i.e. as abrupt *versus* gradual) and without clearly distinguishing the RoC of the driver and the response (Bowler, 2005; Loeschcke & Sørensen, 2005; Sinclair & Roberts, 2005).

Abrupt thermal changes are generally associated with thermal shock responses. For such rapid rates of temperature change, a positive correlation between RoC and thermal tolerance has been reported (Beiting *et al.*, 2000; Mora & Maya, 2006). This positive correlation exists because there is a threshold (of temperature or stress) at which the thermal shock response is initiated; before this threshold, the organism is under heat stress without protection, when the RoC is more rapid, the threshold is reached more quickly. By

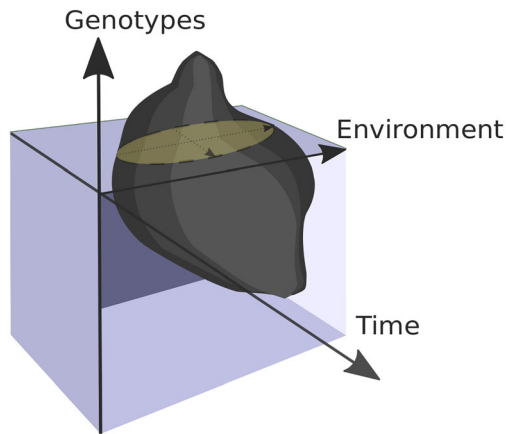
contrast, lower ‘gradual’ rates of temperature change (Hutchison, 1961; Beiting *et al.*, 2000) allow time for plastic responses to develop and therefore for thermal tolerance to increase by acclimation: here the correlation between the rate of temperature change and thermal tolerance is negative. Thus, the relationship between the RoC of temperature and the organismal response (e.g. survival, thermal tolerance or fitness) is not linear, due to the different underlying physiological mechanisms that may be involved (Colinet & Hoffmann, 2012; Hoffmann *et al.*, 2013). Different RoCs can trigger contrasting responses (e.g. tolerance *versus* sensitivity) of an organism because of distinct underlying kinetics between physiological mechanisms and RoC of temperature (Colinet & Hoffmann, 2012; Hoffmann *et al.*, 2013). Gene expression patterns may also differ with different temperature RoCs (Colinet & Hoffmann, 2012; Hoffmann *et al.*, 2013).

#### (c) Phenotypic plasticity and RoC

Phenotypic plasticity describes the relationship between organismal responses and a dynamic environmental driver; plasticity is the interactions between a genotype and the environment over time (Fig. 3). However, time is not an explicit component of the classical representations of phenotypic plasticity, that is performance curves or reaction norms (Schlichting & Pigliucci, 1998), which show only the phenotypic variation expressed by the same genotype in different environments, that is the phenotypic plasticity associated with a genotype for one trait. Because the reaction norm (represented by the black line in Fig. 4), does not explicitly consider time as a variable, it fails to give a proper description of the interaction between a genotype and its (dynamic) environment (see blue line and arrows in Fig. 4). Each reaction norm curve is also only valid for one particular set of starting conditions (e.g. mean value of the environmental variable and/or standard growth conditions). The shape of the reaction norm curve would be expected to vary with different starting-point conditions as well as with RoC (Fig. 4).

Considering phenotypic plasticity as a function of time reveals it as a multi-dimensional response of the organism, where the response curve is also a function of the RoC of the environmental driver. For example, in the case of salt tolerance, it has been shown that responses to salinity shock and stress involve different mechanisms in response to different rates of salinity change (Shavrukov, 2013). Similar mechanistic differences have been found for organismal responses to cold temperatures with different RoCs (Overgaard *et al.*, 2007; Teets & Denlinger, 2013). This indicates that for the same environmental driver, different organismal responses (with different underlying mechanisms) are possible. Typically, fitness outcomes are better when RoCs are slow enough to trigger acclimation-like processes. A review investigating phenotypic plasticity in extreme environments (Chevin & Hoffmann, 2017) suggests that there may be a relationship between the fitness benefits of plasticity and RoCs of the drivers: plasticity can be maladaptive when environmental





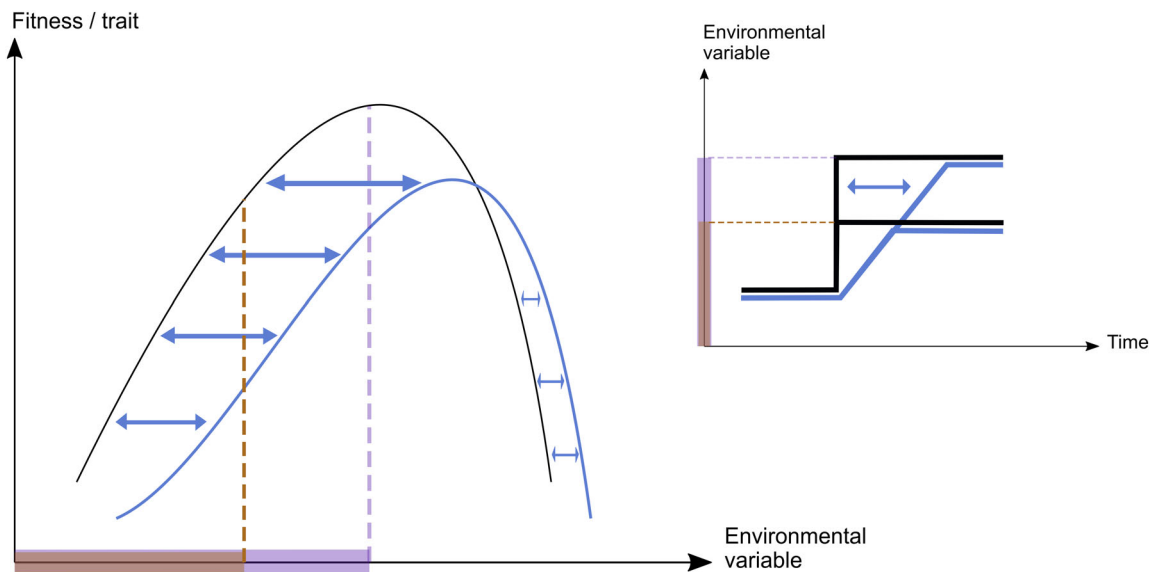
**Fig 3.** Phenotypic plasticity is the interactions over time of a genotype with its environment to produce a particular phenotype at a given point in time. Experiments frequently consider only the phenotype of the organism at the point of study and under one temporal treatment regime, ignoring the effects of time. Integrating rate of change (RoC) into experimental designs allows the phenotype to be placed into a dynamic context including its development, life history and interactions with the environment over time. The yellow area represents all potential phenotypes that could result from genotype  $\times$  environment interactions over time for a single genotype. The black volume is the phenotype space possible for all genotypes in a population  $\times$  environment  $\times$  time. This conceptual representation is valid at any temporal scale within the life cycle of the organism (excluding maternal effects and evolution). Redrawn from Debat (2000) with author agreement.

conditions become extreme, and the speed and fluctuations of these changes could influence tolerance.

Thus, a single reaction norm across a gradient of different driver ‘doses’ is insufficient to describe organismal responses in varying temporal contexts (i.e. the way that organisms actually face these drivers in the ‘real world’). Traits that are measured as responses of the organism are in reality the result of multiple processes (e.g. growth rate, mortality, behaviour, respiration). The underlying processes have their own temporal dynamics, so studying how they relate to driver RoCs could reveal elements of interactive cross-talk between them (i.e. how they interact and influence each other inside and outside the organism, in the extended phenotype perspective (Dawkins, 1982). The incorporation of time into studies on plastic responses could be guided by the following key question: what is the influence of RoC on organismal responses to environmental change?

## (2) Population level

We found 32 papers relating to driver RoCs at the population level, of which 13 were experimental (12 involving temperature), three were reviews, 14 were modelling studies, one was observational, and one included both modelling and observational data. Most were published in the last 10 years ( $N = 26$ ). Population size, gene flow, genetic diversity, as well as species-specific traits (level of specialization) are all important determinants of evolutionary trajectories in populations experiencing environmental change and in particular where



**Fig 4.** A theoretical reaction norm and its temporal aspect. Representation of two reaction norms for the same genotype with the same environmental variable applied at two different rates of change (RoCs). The inset panel shows the two treatment application regimes (red and lilac bars). The intensity of the treatment is shown in both parts of this figure by the dashed lines; the two treatments are applied at different rates: fast (black line) and slow (blue line; difference between treatments indicated by the blue arrows; time difference and response difference for the inset panel and reaction norm plot, respectively). The reaction norm plot shows that the measured trait or fitness outcomes for these fast and slow treatments along a gradient of intensities of the environmental variable are different, resulting in unique reaction norms depending on the treatment RoC.

there are higher RoCs in environmental variables [reviewed in Hoffmann & Sgrò, 2011 and Bellard *et al.*, 2012]. Studies of evolution always necessarily involve a time component, and this work has been reviewed elsewhere (Bell, 2010; Chevin, Lande, & Mace, 2010; Bell, 2013). We present below some key findings regarding RoCs to place the population level into a cross-scale framework, with a focus on evolutionary responses.

For a long time, ecology and evolution have been treated as separate, with gradualist views dominating under the assumption that natural selection tends to be weak on ecological timescales and that evolutionary changes occur slowly over long periods of time (Bell, 2010, 2013). However, over recent decades, the field of evolutionary ecology has allowed deeper insights into eco-evolutionary dynamics and feedbacks (Hendry, 2016), one of which is to bring the rate of environmental change within and between generations into focus (e.g. Hao *et al.*, 2015). Research has shown that whether a population adapts (e.g. evolutionary rescue) or goes extinct depends on the mode of action of a particular environmental driver on organismal physiology (Gorter *et al.*, 2016), RoC of the driver (Collins & De Meaux, 2009; Morley & Turner, 2017; Somovilla, Manrubia, & Lázaro, 2019), population size (Samani & Bell, 2010; Gonzalez & Bell, 2013) standing genetic variation (Bradshaw, 1991) and gene flow (Perron, Gonzalez, & Buckling, 2008). Knowledge on population-level effects of driver RoCs is derived to a much greater extent from theoretical contributions (56% of studies are models and reviews) than individual-level effects where experimental studies prevail (Fig. 1C). This may be a legacy of the field of evolutionary biology, which historically relied on theoretical conceptualization and model development due to the prevalence of gradualist views that it would not be possible to observe evolution over the relatively short timescales within which experiments are conducted. However, a growing number of studies are adopting an experimental approach to investigate the effects of RoCs on fitness landscapes (Gorter *et al.*, 2018), evolutionary trajectories (Lindsey *et al.*, 2013), adaptations (Gorter *et al.*, 2017) and evolutionary rescue (Bell & Gonzalez, 2011; Killeen *et al.*, 2017). Several authors identify the necessity to evaluate and parameterize the relationship between the genetic adaptive responses of populations and the RoC of the environmental drivers for the advancement of eco-evolutionary models (Visser, 2008; Kearney & Porter, 2009; Chevin *et al.*, 2010; Hoffmann & Sgrò, 2011; Bellard *et al.*, 2012). Therefore, a combination of experimental and theoretical methodologies will allow the linking of organism-level responses to driver RoCs and hence to a better understanding of their intergenerational consequences and population-level effects.

### (3) Community level

At higher levels of ecological organization, far fewer studies have investigated the effects of driver RoC. We found only 11 studies investigating the importance of RoC at the scale of the community (Fig. 1C), of which four were reviews, four

were modelling studies and three were experimental studies that reported contradictory results on the role of RoCs at the community level. Klironomos *et al.* (2005) compared two atmospheric CO<sub>2</sub> treatments of the same magnitude but at two different rates (a rapid increase on day 1 followed by a constant elevation or a stepwise increase over 21 plant generations). They reported a strong effect of the rapid-RoC treatment on the plant-associated arbuscular mycorrhizal fungal community (a decrease in richness) whereas the community receiving the slow-RoC treatment did not differ from controls. Limberger, Low-Décarie, & Fussmann (2014), in a study on microalgae in a microcosm, found that the final temperature was a better predictor of richness than the RoC, but that both rate and final temperature were important predictors of community evenness. Peck *et al.* (2009) applied a trait-based approach to investigate how body size and temperature RoC influence upper thermal limits. Based on their results, they hypothesized that slower RoCs of temperature (i.e. over weeks to months) would produce a community disequilibrium that advantaged juveniles and predators, as body size is negatively correlated with upper thermal limits and active species survive better at higher temperatures. Insufficient data exist to extrapolate and generalize from these few studies regarding the importance of driver RoCs at the community level.

Nonetheless, the existing experimental and theoretical work suggests that the RoC of environmental variables likely influences community-level responses. In most of these studies, slower RoCs tended to alleviate negative treatment effects, for example, on competitive interactions (Fortelius *et al.*, 2015a, 2015b), mutualistic interactions (Klironomos *et al.*, 2005) and biodiversity (De Blasio *et al.*, 2015) (although see Limberger *et al.*, 2014). Future studies should focus on the effects of RoCs in community ecology.

It should be noted that two substantial bodies of literature relating to temporal dynamics at the community level were excluded from our literature review by our criteria. The first involves investigations of perturbation/disturbance, including pulse treatments, because our focus was on environmental change as a process, rather than an event. The second is literature relating to resistance/resilience, because these terms relate to responses of the community rather than to the environmental driver. However, many researchers investigating these dynamics have considered the temporal nature of environmental disturbances, with some addressing the importance of RoCs [e.g. see Ingrisch & Bahn, 2018 for a discussion of 'resilience' and the need for a unified quantitative framework]. Carpenter *et al.* (2001) state that whether a system is deemed 'resilient' is dependent on the temporal scale considered, and that the timescale will determine whether system components are considered to be fast, slow, or so slow that they can be modelled as 'fixed' parameters. Some recent contributions to the perturbation/disturbance literature emphasize the importance of environmental driver characteristics on ecological outcomes, for example, disturbance duration on shifts to an alternative state (Ratajczak *et al.*, 2017). Jentsch & White (2019) discuss 'pulsed-ness' as a



continuous variable (like RoC, based on magnitude and duration), and that the manifestation of pulse events is variable and dependent upon the traits and phenology of the organism(s) under study.

The history of environmental RoCs is also likely to be relevant for predictions of community stability in the face of a particular driver; this has been shown to be relevant for populations facing an abrupt change (Gonzalez & Bell, 2013). For example, environmental flows (e.g. river discharge, bioturbation, etc.) may cause rapid and extreme changes in both the physico-chemical and biotic conditions of a microbial community. This phenomenon is termed microbial community coalescence (Rillig *et al.*, 2015) and occurs at varying frequencies in terrestrial (Rillig *et al.*, 2016) and aquatic (Mansour *et al.*, 2018) environments. By forcing two previously distinct microbial communities into the same physical space, this environmental mixing represents a rapid change in both biotic and abiotic conditions, and community assembly processes are then driven by their interactions with one another and with the environment. In this case, the same RoC of environmental drivers may be 'perceived' very differently by the distinct communities with differing historical ranges of driver RoC: what is 'abrupt' for one community could be 'gradual' for another. Such differences in the historical range of environmental-driver RoCs could impact the functional and species diversity of the new community through environmental filtering and evolutionary processes. For example, a community previously exposed to a wide range of driver RoCs might contain members with higher plasticity variability (Fig. 3). These historical impacts of driver RoCs on coalescing communities could impact coalescence outcomes, both through community responses to mixing-related changes in the environment and through impacts on competitive abilities. However, when the RoC is rapid enough to be abrupt for both communities, we might expect the historical RoC range to have minimal influence.

When trying to understand the stability of a community in the face of a change, the historical ranges of RoCs and durations of change can be accounted for in experimental design and/or used to formulate mechanistic hypotheses. For example, the potential range of environmental RoCs that would be perceived as 'abrupt' (and by which community members) could be defined *a priori*. We make the assumption that the RoCs become particularly critical when these ranges are not the same within a community (e.g. in the case of community coalescence). We also hypothesize that outside of the historical RoC range, RoC-related plasticity variability appears and becomes critical in interspecific relationships. Finally, when the RoC is extremely rapid, it is likely that any plasticity related to RoC becomes irrelevant and resistance to stress and the evolutionary capacities of the populations become more significant.

#### (4) Ecosystem level

We found a few studies at the ecosystem scale. Only 12 out of 96 articles involved this scale of organization (Fig. 1C), of

which only two were experimental (one demonstrating the importance of the rate of warming on greenhouse gas production and decomposition; Sihi *et al.*, 2018). Most investigations at the ecosystem level were modelling studies or reviews addressing certain aspects of RoCs [e.g. the effects of abrupt environmental changes on ecosystems (Siteur *et al.*, 2016; Ratajczak *et al.*, 2018)]. The reviews and meta-analysis did not specifically address driver RoC, due to an insufficient number of available studies, but did conclude that RoCs are likely to be important. Ratajczak *et al.* (2018) reviewed abrupt changes in responses of ecosystems and identified driver RoC as an important factor. Jiang *et al.* (2016) reviewed coastal ecotone modelling in the context of global change and identified driver RoC as an important variable missing from current models and important to improve their predictive power. The meta-analysis (Yuan *et al.*, 2017) examined the effects of global change factors on nutrient cycles and demonstrated that experimental and observational data from environmental gradients produced contrasting predictions. They briefly argued that driver RoC plays a central role in those differences but did not develop this idea further. The few existing experimental and modelling papers mainly concern the carbon cycle, and indicate that carbon storage processes are contrastingly affected by gradual treatments (Luo & Reynolds, 1999; Hui *et al.*, 2002; Luo & Hui, 2009). In general, the effects of climate change-related variables are stronger for abrupt rather than gradual treatments, likely because the latter exclude cascade effects at the ecosystem scale as well as relationships between individual components of the ecosystem and driver RoCs.

The lack of data on the effects of RoC at the ecosystem scale has led to calls for more research from various fields. Several authors, in the context of alternative stable states and tipping points, have argued that the rate of an environmental change can be as important as the magnitude of change (Scheffer *et al.*, 2008). Using a mathematical model, Ashwin *et al.* (2012) proposed that an abrupt RoC (which the response system cannot track) can trigger a sudden shift in state, even if the magnitude of the environmental change is not strong. There is no empirical evidence with which to test this prediction, and its validity remains to be investigated (Siteur *et al.*, 2016). As suggested by Loreau (2010), linking community ecology and ecosystem ecology research will require better links between holistic and mechanistic approaches. It is our opinion that studying ecosystem stability and community synchrony (Wang *et al.*, 2019) in relation to driver RoCs will be important for making such links, because driver RoC effects span all scales of organisation in ecology and clearly relate to physiological mechanisms at the individual level (see Section III.1).

Cascade effects related to RoCs of environmental drivers will probably emerge in coupled systems. For example, global warming is predicted to advance the tree line in many locations (Harsch *et al.*, 2009). Thus, headwater streams at high altitudes could receive increased amounts of leaf litter, increasing the total amount of allochthonous carbon input. At the same time, communities of lotic leaf litter decomposers

are predicted to change as a result of temperature increases (Bärlocher *et al.*, 2008). Even if the rate of temperature change is spatially homogenous across the landscape in which these interactions occur, each part of the ecosystem (trees and decomposers) may not ‘perceive’ this RoC in the same manner: it could be a rapid RoC for trees and a slow RoC for the microbial community. This is an important aspect of food-web theory, in which different trophic levels may react to changes differently leading to decoupling of interactions. Such differential responses associated with this RoC in temperature could create, in our example, decoupling between the seasonal cycle of autumnal senescence and subsequent litter input to a stream and decomposition. Changes in both the total amount of litter entering the stream as well as upstream processing of litter (Vannote *et al.*, 1980) could impact downstream lotic communities dependent on the upstream transformation of carbon sources.

#### IV. PROSPECTS AND RESEARCH PRIORITIES

In the general context of driver RoCs, there have been relatively few studies conducted at the community and ecosystem levels of organization, particularly those involving empirical work (Fig. 1C). We recommend placing more emphasis on research at the community and ecosystem levels.

Studies of RoCs could provide an important opportunity to unify the perspectives of ecologists working at different scales (e.g. population, community, and ecosystem ecologists) and would be particularly important in the context of current and potential future effects of global change. Achieving a unified perspective will require changes in the way that RoC studies are conducted. Below we offer recommendations for future research.

##### (1) Shifting the focus from categorical definitions to a continuous framework

We recommend moving away from the use of ‘common sense’ terms such as ‘abrupt’ and ‘gradual’ to using instead a quantitative framework to describe driver RoCs. As discussed in Section II, ‘abrupt’ and ‘gradual’ are neither well-defined nor equivalent across the subfields of ecology. Furthermore, the framework of ‘abrupt *versus* gradual’ encourages investigators to apply only two treatments. Such studies would be justified if it is known that the relationship between a driver RoC and the response (e.g. biomass, thermal limit, diversity) is linear. However, evidence from some studies on temperature changes show that this is not always the case (e.g. Mora & Maya, 2006; Overgaard *et al.*, 2006). When linearity cannot be assumed, a gradient of driver RoCs is required to understand the range of responses of the unit of study (e.g. organism, community). In addition to using more than two RoC treatments, the application of a continuous quantitative driver RoC framework makes studies more intercomparable and simplifies common discussion across

fields. Reporting a quantitative description of the RoC of any driver will facilitate synthesis and climate change predictions, especially at the ecosystem level.

##### (2) Towards reproducibility: experimental design and reporting parameters

Our literature search revealed large differences in the design of RoC experiments. The proportion of the experiment spent in the ramp *versus* stasis period differs widely among experiments (Fig. 2C) and there was no relationship between the magnitude of the RoC treatment and the duration of the stasis period across experiments (Fig. 2D) in the subset of temperature studies that we investigated. Furthermore, several studies failed to report ramp duration of their ‘abrupt’ treatments. These differences make it difficult to reproduce or compare studies. We recommend explicit reporting of all aspects of every RoC treatment, including the total magnitude of change, the overall duration, the duration of the ramp period and, if included, the duration and conditions of the stasis period. The RoC should be reported as the magnitude of change divided by the ramp period. Reporting any technical limitations (e.g. range of error, increments of step changes) would aid in comparisons between studies. It is also critical that these variables are considered explicitly when designing a study to answer a particular research question (e.g. how does stasis duration influence the development of the target response variable?).

##### (3) Cross-scale analysis as a common goal

Consideration of differential effects across ecological scales is particularly important in the context of global change in order to improve predictions regarding extinction, changes in biodiversity and ecosystem functioning (Levin, 1992; Raffa *et al.*, 2008; Cross *et al.*, 2015). There is some evidence that driver RoC exerts an influence across multiple scales of ecological organization; for example, interactions between plasticity and evolutionary mechanisms can be modulated by the RoC of the driver (Section III.2). Many research opportunities exist when considering driver RoC effects in multiscale systems; below we highlight several areas in which we believe that research would be particularly useful.

Plastic responses at the organismal level affect higher levels of ecological organization. Although there is evidence that RoCs of environmental drivers influence plasticity, there is not yet a unified theoretical framework that quantifies this temporal aspect of plasticity. This RoC-related aspect of plasticity both interacts with evolutionary dynamics and modulates community interactions (competition and predation through phenology). Yet the question of the importance of individual-level responses on cross-scale dynamics remains. For example, RoCs might exert a strong effect at the individual scale, while at the community level a buffering mechanism (e.g. ecological homeostasis, stability, and resilience) might alleviate this effect (Ghedini & Connell, 2016).

At higher levels of organisation, coupling and cascade effects are two cross-scale processes that could be affected by driver RoC. As an example, consider nitrogen levels as an environmental driver. There will be a certain level of variation in RoC in nitrogen input because this rate varies naturally through the seasons (Rysgaard, Christensen, & Nielsen, 1995; Hellemann *et al.*, 2017). Hellemann *et al.* (2017) consider an oligotrophic estuary receiving an anthropogenically increased nitrogen flux. The altered driver (nitrogen flux) RoC could exceed the rate at which the estuarine denitrification community can process the nitrogen influx, with consequences for downstream marine ecosystems. We can build on this by taking into account evolutionary possibilities or lower-scale responses in relation to nitrogen flux. Considering community, population and individual responses to the RoC of nitrogen flux could allow us to construct mechanistic hypotheses. For example, through the lens of a RoC framework, we might generate testable hypotheses such as: does the same anthropogenic nitrogen quantity applied at an input rate within the naturally occurring variation allow the estuary denitrification community to adapt and lead to a reduction in input into the ocean, or does the same quantity and even the same rate of upstream nitrogen flux, when applied at different time to naturally occurring peaks, have different effects because the community is adapted to a different rate at a different time point?

During the last 20 years there has been a shift toward a more dynamic perception of ecology, as evidenced by the increasing popularity of the alternative-stable-state concept over the equilibrium concept (Holling, 1998; Carmel *et al.*, 2013). Ashwin *et al.* (2012) suggested that an abrupt rate of environmental change can cause tipping (i.e. a transition from one state to another alternative stable state), even though the magnitude of the change does not reach a tipping point. They illustrated their mathematical model using a climate system, and their theory was then adapted by ecologists to explain novel temporal dynamics of ecosystems (Siteur *et al.*, 2016).

Despite this shift from static to dynamic descriptions of ecosystems, investigators do not commonly use a dynamic temporal framework in experimental design. The use of RoCs, like flux, is a sensible way to approach the kinetics of dynamic processes (e.g. enzymatic activity, evolutionary rates), but it also represents a technical challenge to analyse. It is still challenging to separate the effects of RoCs from the effects of the magnitude and duration of the change, because they are interrelated. It also requires repeated and non-destructive time-series measurements. Nonetheless, to respond to the challenges posed by global change, it is critical that we collect more experimental data relating to dynamic processes at multiple levels of ecological organization.

## V. CONCLUSIONS

- (1) We argue for the use of rates of change (RoC) instead of an ‘abrupt *versus* gradual’ framework, because there

is no universal and independent division between ‘abrupt’ and ‘gradual’ RoCs that applies at every spatial scale and among systems. In addition, the use of RoCs will allow more precise experimental or observational descriptions of aspects related to the magnitude and the duration of driver changes.

- (2) Phenotypic plasticity has been widely studied for a variety of factors, organisms and traits. While time is often not explicitly incorporated into these studies, the RoC has been shown to be relevant. It is therefore important to integrate time more broadly into the study of phenotypic plasticity. This could be accomplished through the integration of time as an additional aspect of reaction norms. One should include the broad diversity of potential mechanisms, which means taking into account the time scale of those mechanisms.
- (3) RoC studies can be carried out in two ways: (i) testing the effects of different rates of change on the same ecological component, and (ii) testing a single rate of change on different ecological components. These types of studies would both illuminate the importance of RoCs in ecology and also allow us to understand cross-scale effects of RoCs.
- (4) At higher organizational levels it will be important to investigate the effects of RoCs on interaction networks as dynamic processes. Such investigations may reveal decoupling, which would have implications for species co-occurrence patterns and ecosystem functions.

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## VIII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Table S1.** List of studies reviewed, including categorizations and responses measured (where applicable). Some studies included multiple driver and/or response variables; each variable is listed in a unique column (e.g. Driver 1, Response 2). Env. turnover, environmental turnover; na, not applicable.

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