RELEVANCE IN ECOLOGY OF ENVIRONMENTAL DRIVER RATE OF CHANGE: A CROSS-SCALE APPROACH

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Aujourd'hui je ne crois plus à grand chose d'autres qu'aux lois naturelles,
celles de Darwin et de ses successeurs.
Ma formation a commencé le travail d'abattage des plus grands arbres et
l'expérience du choix, répétée de nombreuse fois, a achevé les derniers
chênes qui restaient encore debout.
J'ai planté à la place un taillis de croix qui sont le maillage de ma nouvelle
subjectivité: sélection naturelle, chimie, physiologie, loi sociale, psychologie.
Toutes sont construites selon les règles de la Science. Elles conservent juste
quelques courbures à cause du bois duquel elles sont faites, dernières traces
de mon romantisme, de ma religiosité et de mes anciennes croyances.
Cette forêt qui s'élevait là... Cette forêt que j'étais.
Aujourd'hui il n'y a de place pour Dieu que dans le besoin de réconfort et la
solitude.
C'est-à-dire lorsqu'un semblant d'unité m'est nécessaire. C'est d'ailleurs
souvent plus une excuse contre mes échecs qu'autre chose.
Finalement c'est le pardon que je cherche contre cette culpabilité sans objet
que je ne peux pas m'empêcher d'éprouver.
La dernière racine dans le sol qui lutte contre l'érosion.
C'est le pendant de la conscience de ces choix. Une certaine aridité.

— Liliana Pinek - Fragment Journal Intime

non-scientific addition that has no relation to the content of the doctoral thesis

(Translation: Today I no longer believe in much else than natural laws, those of Darwin and his successors.
With my training began the work of felling the tallest trees.
Having to pick drop and cut my choices many times, finished off the last oaks that were still standing.
I ravage the desert of stumps and forced a copse of crosses in the exposed and scarred clay... trapping sky, horizon, and perspectives in the mesh of my new subjectivity: natural selection, chemistry, physiology, social law, psychology.
All the crosses are built according to the rules of Science.
They just retained a few curves of the wood they were made of, the last traces of my romanticism, my religiosity and my old beliefs.
That forest that stood there... That forest that I was.
Today there is no place for Gods, except in the need for comfort and solitude. That is to say when a semblance of unity is necessary for me. It's often more of an excuse for my failures than anything else. In the end, it's forgiveness that I seek for this pointless guilt that I can't help but feel.
The last root in the soil that fights erosion.
It is the counterpart of the awareness of your choices. A certain aridity.)

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Thanks to my family for always having my back and making my mind.

Thank you to India to have been next to me in very dark moments in personal and professional life.

And I am sorry Nada I wasn’t there..

Ha! Yes, of course, Goji, my dearest soul, and companions, thank you for not bitting me too much when I couldn’t pet you.

DECLARATION

Herewith I certify that I have prepared and written my thesis independently and that I have not used any sources and aids other than those indicated by me.

Freie Universität Berlin, 2022

Liliana Pinek

I also declare that I have not submitted the dissertation in this or any other form to any other institution as a dissertation

ABSTRACT IN ENGLISH

In the context of accelerating changes and the massive challenges those changes represent for the ecosystems, temporal ecology has emerged. Some work already exists that describes the importance of temporalities from the point of view of communities (i.g., describing temporal dynamics of communities, the timing of biological events in phenology, co-occurrence and coupling study of synchrony). However, investigating the role of temporal dynamics of environmental drivers' importance for biological responses remains scarce. The dynamic of the temporal driver is the temporal context of the temporality of communities, and it defines their time environment. Chapter 1 classifies the varieties of the temporality of drivers, shows how those temporalities are relevant, and proposes a systematic framework for their study.

One particular aspect of the temporal dynamics of environmental drivers we focused on is the rate of change. This particular aspect has received growing attention in the last five years as it has been pointed out that it could be determinant in the passing of thresholds between stable states. We conducted a review and synthesis of the existing experimental and theoretical work on rates of change of environmental drivers across levels of complexity in biology (i.e. organism, population, community, ecosystem). We did not limit ourselves to ecology because we believe a reductionist approach is needed to understand how the rate of change impacts the ecosystem since the response originates at the individual level. Chapter 2 results from our work: rate of change matters for a variety of driver effects and shows no homogenous effects between magnitude for one diver, between drivers, and across levels of organizational complexity.

Finally, we put into practice the framework we develop in chapter 2 to study the rate of change in a series of three experiments. We wanted to demonstrate that rates of temperature change affect growth and show in practice how to study this effect. We used a fungal community collection of 30 strains. The rate of temperature affected fungal growth for moderate heat stress but did not affect thermal limits; hence, the temperature rate of change has a non-uniform effect on our tested system. We also showed a non-uniform effect across the strains, indicating strain-specific diversity in responses to temperature rate of changes. Finally, we showed that the rate of temperature change impacts competition outcomes. Our work demonstrates how the rate of change can be relevant in ecology and shows how it can be studied.

ABSTRACT IN GERMAN

Im Zusammenhang mit sich beschleunigenden Veränderungen und den massiven Herausforderungen, die diese Veränderungen für die Ökosysteme darstellen, ist die Zeitökologie entstanden. Es gibt bereits einige Arbeiten, die die Bedeutung von Zeit aus Sicht von Lebensgemeinschaften beschreiben (z. B. Beschreibung der zeitlichen Dynamik von Gemeinschaften, des Timings biologischer Ereignisse in der Phänologie, des gemeinsamen Auftretens und der Kopplungsstudie von Synchronie). Andererseits bleibt die Untersuchung der Rolle der zeitlichen Dynamik der Bedeutung von Umwelttreibern für biologische Reaktionen rar. Die Dynamik des zeitlichen Treibers ist der zeitliche Kontext der Zeitlichkeit von Gemeinschaften und definiert ihre Zeitumgebung. Kapitel 1 klassifiziert die Varietäten der Zeitlichkeit von Treibern, zeigt, wie diese Zeitlichkeiten relevant sind, und schlägt einen systematischen Rahmen für ihre Untersuchung vor.

Ein besonderer Aspekt der zeitlichen Dynamik der Treiber, auf den wir uns konzentriert haben, ist die Änderungsrate. Dieser besondere Aspekt hat in den letzten fünf Jahren verstärkte Aufmerksamkeit erfahren, da darauf hingewiesen wurde, dass er entscheidend für das Überschreiten von Schwellenwerten sein könnte. Wir haben eine Überprüfung und Synthese der bestehenden experimentellen und theoretischen Arbeiten zu Raten von Treiberänderungen über Komplexitätsebenen in der Biologie hinweg durchgeführt. Wir haben uns nicht auf die Ökologie beschränkt, weil wir glauben, dass ein reduktionistischer Ansatz erforderlich ist, um zu verstehen, wie sich die Änderungsrate auf das Ökosystem auswirkt, da die Reaktion auf der individuellen Ebene entsteht. Kapitel 2 ist das Ergebnis unserer Arbeit: Die Änderungsrate ist für eine Vielzahl von Treibereffekten von Bedeutung und hat keine homogenen Effekte zwischen der Größe für einen Taucher, zwischen Treibern und über Ebenen der organisatorischen Komplexität.

Schließlich setzen wir den in Kapitel 2 entwickelten Rahmen in die Praxis um, um die Änderungsrate in einer Reihe von drei Experimenten zu untersuchen. Wir wollten zeigen, dass Temperaturänderungsraten von Bedeutung sind, und in der Praxis zeigen, wie dieser Effekt untersucht werden kann. Wir verwendeten eine 30 Pilzstämmen. Die Temperaturrate spielte bei mäßiger Hitzebelastung eine Rolle, beeinflusste jedoch nicht die thermischen Grenzen. Wir zeigten auch einen Pilzstamm-spezifischen Effekt, was auf Diversität in der reaktionsbreite der Pilze hindeutet. Schließlich haben wir gezeigt, dass die Geschwindigkeit der Temperaturänderung die Konkurrenzfähigkeit der Pilzstämme beeinflussen kann. Unsere Arbeit zeigt, wie die Än-

derungsrate in der Ökologie relevant sein kann und wie sie untersucht werden kann.

CONTENTS

PUBLICATIONS AND CONTRIBUTIONS

CHAPTER 1: Basic Principles of Temporal Dynamics (Published; DOI: https://doi.org/10.1016/j.tree.2019.03.007). Masahiro Ryo, Carlos A. Aguilar-Trigueros, Liliana Pinek, Ludo A.H.Muller and Matthias C. Rillig.

Author contributions: All authors contributed to the conceptualization and writing of this review paper.

CHAPTER 2: Rate of change across scales in Ecology (Published; DOI: https://doi.org/10.1111/brv.12639). Liliana Pinek, India Mansour, Milica Lakovic, Masahiro Ryo, Matthias C. Rillig

Author contributions: All authors contributed to the conceptualization and writing of this review paper.

CHAPTER 3: Rate of temperature change influences fungal response to heat stress and competitive outcomes under heat stress conditions (in preparation) Liliana Pinek, Anika Lehman, Anna Grandchamp, India Mansour,Carlos A. Aguilar-Trigueros, Tessa Camenzind and Matthias C. Rillig

Author contributions: LP MCR designed the study, LP, AL, IM conducted laboratory work, AG LP analysed image in python, LP AL AG CAAT TC contributed to data analysis and interpretation, LP AL AG CAAT TC MCR contributed the manuscript.

ANNEXE A: Fungus–bacterium associations are widespread in fungal cultures isolated from a semi-arid natural grassland in Germany. (Published; DOI: https://doi.org/10.1093/femsec/fiab059) L.A.H. Muller, M.-B. Ballhausen, D.R. Andrade-Linares , L. Pinek, P. Golubeva and M.C. Rillig

Author contributions: all authors contributed to the writting, all authors contributed to sampling and isolation of the fungal colonies, the rest of the analysis was mainly performed by LM and MB.

1

GENERAL INTRODUCTION

In the early twentieth century, the field of biology was grappling with the concept of phenotypic plasticity (Sarkar, 1999). Diverse study types were employed to investigate how different magnitudes and timescales of environmental factors influence organismal responses to their environment (Fry, Hart, and Walker, 1946; Hathaway, 1921; Huntsman and Sparks, 1924; Loeb and Wasteneys, 1912). From this diversity of experimental designs, the field eventually focused on the magnitude of environmental factors, as illustrated by reaction norms. This streamlining of plasticity studies within a common framework led to an explosion of biological knowledge. However, some of these early studies reported that temporal factors influenced biological responses, which has been overlooked (cf. chapter 2). Environmental change, particularly climate change, is occurring much more quickly today than 100 years ago. It is critical to build models with strong predictive power to inform conservation and policy decisions to prevent biodiversity loss and maintain ecosystems in our changing world. Nevertheless, do we have sufficient predictive power with insufficient information about the temporal influence of global change factors on organismal and ecological responses?

1.1 PLASTICITY AND ECO-EVO

"You're all clear, kid. Now blow this thing and go home!" - Han Solo (Star Wars)

Up to the '50s, describing the phenotype under a range of environmental conditions was seen as no more than describing "reactions of the genotypical constituents" (Acqua, 1920). In other words, the phenotype was only the product of the genotypes. Later on, it was emphasized that the phenotype was an interaction between the genotype and the environment (e.g., Lewontin and Gould against sociobiology in the 70s). Nonetheless, for a long time, the opposition "Nature or Nurture" remained central in setting terms of debates in the scientific community and for some reasons persists up to today in the larger media and public opinion. This artificial opposition (and the associated antagonistic political views) were an obstacle to the synthesis of the field. Plasticity has since become a subject in itself as the interaction between environment and genotypes, with the affirmation that it is Nature AND Nurture.

Furthermore, the ecological (niche) and the evolutionary (phenotype) approach of plasticity have been unified in the literature corpus of Ecology and Evolution (Eco-Evo) studies and synthesis (Donohue, 2005; Moczek, 2015). The concept of plasticity has even been extended to the community level nowadays with the use of a reaction norm like measurement to predict community response to temperature change (Donhauser et al., 2020; Rinnan et al., 2009). The merge of the two subfields of biology (Ecology and Evolution) is a paradigm change and, as such, led to an explosion of studies.

Our work on RoC of drivers is entirely tributary to this legacy since our cross-scale approach and the dynamical perspective we chose could not be conceived outside of the Eco-Evo paradigm and without the plasticity defined as Nature and Nurture. Eco- Evo is profoundly a historical science that studies dynamics and hopes to make predictions. The idea of evolution "places all reality in a perpetual becoming" (i.e., "place toute réalité Dans un perpétuel devenir", Riper and Parodi, 1920). It changes our perspectives on our object from its stability to its "mobility, universal instability" ("la mobilité, l'instabilité Universelle") as said by Parodi about the introduction of the idea of evolution in social sciences (Riper and Parodi, 1920). The merge of Ecology and Evolution gives rise to a field that combines a static and dynamical description of ecosystems across the scale of organization and implicitly gives rise to a temporal scale. The next step was the constitution of temporal ecology. It is still an ongoing process to which our work is meant to contribute.

1.2 THE IMPORTANCE OF TEMPORAL DYNAMICS OF DRIVERS

"Scotty, I need warp speed in three minutes, or we're all dead." - Kirk (Star Trek)

Time is the name of many measurements of duration with varieties of functions. All these "time" concepts are related to temporal dynamics they allow to describe the functions associated with them. In physics, time has a unified unit, as absolute as possible, the atomic clock, but it is still diverse in its concepts (i.e., 5 Times: radiative, thermodynamic, microscopic, quantic, cosmologic;E. Klein, 1996). The social times describes temporal dynamics determined by social rituals and institution structures like calendars. It is rather diverse both in concepts and units. These social measures of duration allow synchronization, cooperation, and the emergence of societies in the human species (Fabiani, 2019). Psychological time is related to cognition and plasticity in the human species (E. Klein, 1996). It is intrinsically about the subjective measurement of duration, although there are some indications that psychological time relies on the biological clock (Kahawage et al., 2022; Wittmann, 1999). The biological clocks and the physiological time have their ticking systems, but it is less absolute than the atomic clock and varies with environmental cues. It also serves the purpose of synchronization of functions in the bodies of most organisms. What are the appropriate time concepts to understand temporal dynamics in ecosystems? What temporal models, categories, and tools do ecologists need to study temporal dynamics in ecology? In ecology, time concepts can be about particular temporal dynamics of environmental changes, for example, recurring temporal change (i.e., phenology). Ecological time is also about temporal dynamics inside communities and in response to the environment changing, as in the temporal niche concept that tries to capture the temporal structuring of biodiversity or the study of synchrony that studies the co-occurrence of different organisms. What remains largely unexplored in temporal ecology is the temporal dynamics of environmental drivers. Chapter 1 presents a work we contributed to that attempts to provide categorical unity for the field of temporal ecology in the study of dynamics of temporal drivers.

1.3 DRIVERS RATE OF CHANGE (ROC)

"Insufficient facts always invite danger." - Spock (Star Trek)

I once asked a child I was responsible for providing entertainment to, "What is Time ?". On the contrary to what you may think, my question was well received and seemed to do the job of entertaining my juvenile audience, as I had peace for the following hours. Finally, the child came back to me with this answer "It is speed". Speed is about how fast something moves or changes. Speed is a rate, a rate of change, and just like that, this child had struck that match in my brain, leading to a burning obsession that has consumed my life for the last five years. Intuitively time is a RoC, but how relevant is RoC in temporal ecology? While collective evidence from multiple ecological levels supports the importance of considering the RoC of environmental drivers, this point has been only studied independently at separate organizational scales. We collect and synthesize this information in chapter 2. Briefly, changes in environmental factors can elicit effects at the level of the individual organism, the population, community and ecosystem levels (n.d.(b); Levin, 1992; Raffa et al., n.d.). The effect of the driver's RoC spans multiple scales but is rooted in the individual level, where it elicits physiological responses. The consideration of differential effects across scales is critical in the context of climate change in order to improve predictions regarding such issues as extinction, changes in biodiversity, and ecosystem functioning (n.d.(b); Levin, 1992; Raffa et al., n.d.; Wu et al., 2006). Thus the study of driver RoC effects provides a mechanistic understanding of cross-scale temporal dynamics facing global change.

A well-known methodological challenge in experimental global change studies is the application of treatments that represent what occurs in natural systems. Illustrations of this issue in temporal ecology are experiments investigating temperature change that apply an abrupt temperature increase (i.e., instantaneous) compared to an ambient control. Temperature increases are not occurring abruptly most of the time, instead they occur at various RoCs (same for other drivers). Thus, it is essential to understand better the relation between driver RoC and biological responses. Some recent works have tried to address this problem by applying "gradual" as well as “abrupt" treatments. The problem with using the opposition "abrupt vs. gradual" is that it masks the diversity of what "gradual" can be. The opportunity with the multiple RoCs approach is to access nonlinear relationships for RoC and its effect.

1.4 "THE ANSWER TO THE GREAT QUESTION... OF LIFE, THE UNIVERSE AND EVERYTHING... IS. . . " TEMPERATURE.

N.B.: Just kidding, it’s 42.

(Douglas Adams,The Hitchhiker’s Guide to the Galaxy)

Temperature is a major driver across all science fields. Its effects and properties are studied in physics, chemistry, and ecology. I can only turn something to ash if I heat it up: temperature is the energy of transformation. It has noticeable effects for the human eyes and is part of most technological revolutions of human history, particularly the industrial revolution. Our entire societal model is based on the fact that heat is a transformational power. As a result, temperature effects on biological systems are most prominent in the literature. This is why it is a recurrent illustration of our concepts for drivers’ RoC effect (chapter 2) and the driver we choose for our experimental work (chapter 3).

The effect of temperature on organisms has been studied from different angles. On the one side was the ecological approach, trying to define species’ thermal niches and thus focusing more on thermal limits (i.e., when organisms stop performing and/ or die). On the other side was a more reductionist approach in the evolutionary science field that described the performance of a particular genotype under different temperature conditions to estimate the heritable part of the phenotype distribution. This field used the reaction norm and the particular example of the thermal performance curve to describe this variation practically. A reaction norm is a two-dimensional curve that describes how a particular phenotypical trait varies along a gradient of a specific environmental driver. A performance curve is a reaction norm of a rate process (e.g., growth), and the thermal performance curve is associated with temperature variation.

Our last chapter presents the experiments we set up to test our hypotheses. They are also meant to be examples of the guidelines we provided in chapter 2. We chose to work with temperature as a driver, and our biological object was a 30 strain fungal collection.

1.5 OUTLOOK OF THE THESIS

In this thesis, we will present a conceptual work defining the road for temporal ecology in the studies of drivers temporality effects (chapter 1), then focus on the importance of RoC of driver across scale in a synthesis and review work (chapter 2), and finally, present our experimental work on fungal strains and competitive fungal interactions under different RoC (chapter 3).

"All those moments will be lost in time, like tears in rain." (Roy Batty in Blade Runner), actually it's more like the rain got lost in my tears those last 6 years

1.5.1 *Chapter 1*

In our first chapter, we present a piece of theoretical work to which I contributed. This piece is meant to provide guidelines to study temporal dynamics in ecosystems. The focus in this work is the description of temporal dynamics of drivers like temperature, drought, light, and the kind of temporal forms they can take and can be studied under. The idea is that with this framework, the study of the temporal dynamics of the driver should be unified, and as a consequence, a synthesis of knowledge would be easier. This is crucial because understanding the temporal dynamic of ecosystems can simply not be a one-person job, so we need to collaborate and a common framework.

1.5.2 *Chapter 2*

Chapter 2 is entirely about how and why drivers' RoC is a very important aspect of environmental change at all levels of organization in Biology. We performed a review exercise and synthesized the knowledge we found on how driver RoC influences different biological responses to change at the organism level, population level, community, and ecosystem level. We also provided specific hypotheses and guidelines for its experimental study.

1.5.3 *Chapter 3*

Chapter 3 combines three experiments to study the effect of RoC on individual fungal strains and competitive interaction among them. In this study, we employed a study design with multiple rates of temperature change (i.e., how quickly the temperature increased from ambient to target/heat stress). Because we manipulated the driver's rate of change (RoC), we could apply the same treatment regime to both fungal individuals and fungal communities, thereby gaining information across scales of organization. Furthermore, we applied multiple (n = 3) rates of change. Using a gradient of RoC allows us to capture nonlinear trends and information about thresholds – information that cannot be attained with the 'abrupt' and 'gradual' framework. Finally, we attempt to resolve the analytical complications by applying both 'dose-based' and 'event-based' sample comparisons. The experimental design shown here could be applied to other organism groups and other scales of ecological organization.

Our results demonstrate the importance of temperature RoC for many different fungal strains. We show that different RoC leads to different responses at both the individual and community levels under two different levels of heat stress. We also found that fungal mycelial architecture and thermal limits were associated with responses to fast rates of change, implying that underlying selection may play a role. Our study also provides a widely applicable experimental design and two new analytical approaches that could be applied in (evo-)ecological studies to gain more profound knowledge about the importance of changing environmental drivers.

2

BASIC PRINCIPLES OF TEMPORAL DYNAMICS

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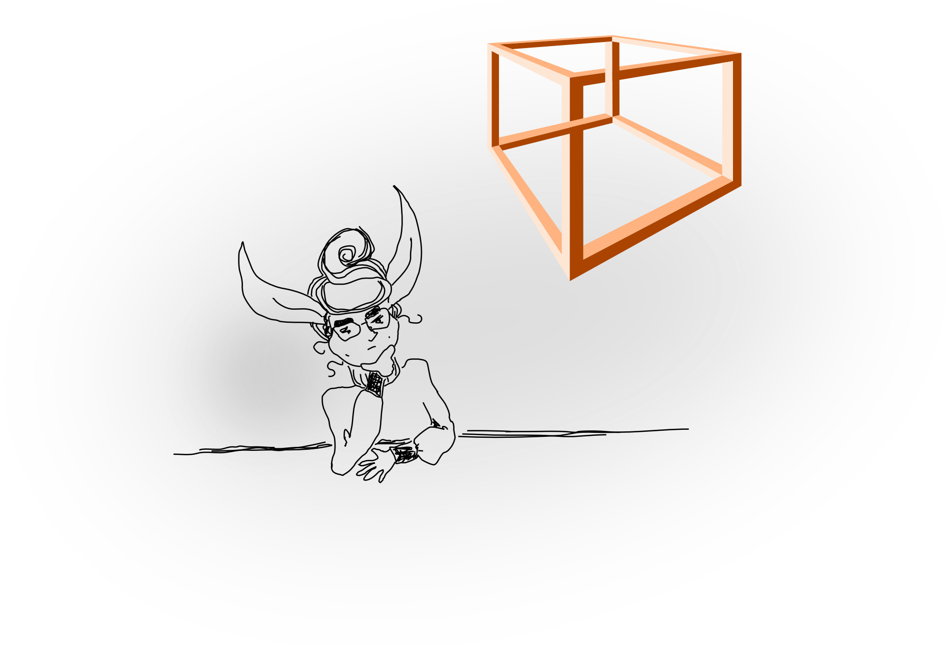

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Trends in Ecology & Evolution

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Review

Basic Principles of Temporal Dynamics

Masahiro Ryo,[1,2,*] Carlos A. Aguilar-Trigueros,[1,2] Liliana Pinek,[1,2] Ludo A.H. Muller,[1,2] and Matthias C. Rillig[1,2]

All ecological disciplines consider temporal dynamics, although relevant concepts have been developed almost independently. We here introduce basic principles of temporal dynamics in ecology. We figured out essential features that describe temporal dynamics by finding similarities among about 60 ecological concepts and theories. We found that considering the hierarchically nested structure of complexity in temporal patterns (i.e. hierarchical complexity) can well describe the fundamental nature of temporal dynamics by expressing which patterns are observed at each scale. Across all ecological levels, driver–response relationships can be temporally variant and dependent on both short- and long-term past conditions. The framework can help with designing experiments, improving predictive power of statistics, and enhancing communications among ecological disciplines.

Highlights

Temporal dynamics are inherently complex.

Concepts and techniques have flourished to understand ecological temporal dynamics in recent years.

A key finding of recent studies is that driver–response relationships are not necessarily constant through time, but rather, that they are conditioned by the recent and historical past.

Basic principles of temporal dynamics need to be summarized to increase the understanding and predictability of complex temporal dynamics in ecology and evolution.

The Need for Basic Principles of Temporal Dynamics

All ecological disciplines consider temporal dynamics with major paradigms shifting from one to another: **equilibrium** (see Glossary) to **nonequilibrium**, and **stationary** to **nonstationary** (Box 1). Understanding temporal dynamics is becoming more important in the Anthropocene. Several time-related concepts and statistics have emerged recently [1–4]. Nevertheless, ecology still lacks basic principles that underlie all studies relevant to temporal dynamics [5], and the exchange of knowledge about temporal dynamics among subdisciplines is limited [6,7].

Recently developed concepts include, for example, **temporal ecology** [5], abrupt shifts in ecological systems [8], **ecological memory** [3], **lag hypothesis** for community dynamics [9], and **asymptotic environmentally determined trajectories** [1]. These were proposed almost independently of each other. However, they all consider that driver–response relationships are not necessarily constant through time, but they depend on the recent and historical past. This perspective brings together various concepts to figure out the essence of temporal dynamics across ecological and temporal scales.

We here introduce basic principles of temporal dynamics in ecology. Our primary challenge was to figure out essential features that describe temporal dynamics by finding similarities among about 60 ecological concepts and theories. The examples are taken largely from population, community, and evolutionary ecology, but more examples can be found in Table S1 (see supplemental information online). We also summarize the value of the concept, ranging from improving study design to catalyzing knowledge integration among disconnected subdisciplines.

Hierarchical Complexity

We applied the concept of hierarchy [10–12] for describing temporal patterns (i.e., driver–response relationships in time series) to uncover universal features across the existing time-related concepts. The concept of hierarchy often considers a nested structure of hierarchical scales including absolute scale (seconds < minutes < hours) and relative scale (period

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Box 1. Paradigm Shifts in Understanding Temporal Phenomena

The studies about temporal dynamics relied historically on the equilibrium concept. The equilibrium concept posits that any ecological system will sooner or later return to a determined stable condition after any perturbations [68,69]. The notion of a balance traces back to the ancient Greeks [70,71]. The concept was reformed in the 17th century with more mechanistic views [72,73], and the 18th century gave rise to the concept of balance of nature [74]. This concept is widely supported by the existence of self-regulating mechanisms [18] (e.g., homeostasis of individual, population growth, negative feedback of community, and resistance-resilience and compensatory dynamics of ecosystems).

The equilibrium concept flourished, but at the same time, was also criticized [75–77]. Negative results reporting failure to provide equilibrium states were rarely seen, until Pickett [69] and others called for broad attention to this situation. The need to reconcile both equilibrium and nonequilibrium paradigms hatched the theory of multiple equilibria in the 1970s and 1980s [16,48,78]. An ecological system can shift its state from one state to another, when the degree of a perturbation exceeds an allowable capacity [16,79–81]. Together with the notion of these nonlinear dynamics, considering temporal dynamics also paved the way for ecology beyond the equilibrium concept. The nonequilibrium paradigm focuses explicitly on time series to better describe the temporal dynamics of ecological systems. It assumes that no stable condition exists, and the past experiences across various scales influence on the current state of a system [1,19,44,82]. Understanding such nonequilibrium dynamics has been at the center of modern ecology [82].

Collectively, this paradigm shift has given rise to a range of questions about temporal dynamics of ecological systems. These include how do temporal changes in environmental conditions determine system states, and how has the current state of the system been reached through time?

A < period B). Yet, instead of scale, we consider a nested structure of hierarchical complexity: single-event level, multiple-events level, and the trajectory level. A single event is a subset of multiple events occurring within a given period of the entire trajectory (i.e., single event < multiple events < trajectory; Figure 1). We refer to an event as an irregular change in either endogenous or exogenous conditions of the system within a limited period, in which the occurrence period and some aspects of the change are definable given a certain rule (e.g., exceeding a defined threshold value).

Hierarchical complexity is a key to summarizing basic principles applicable across temporal and ecological scales. For example, we consider that pulse-shape events are considered to belong to the same category, irrespective of scale. If we had relied on scale, similar patterns at different scales could not be compared. Moreover, many generic terms describing temporal dynamics (e.g., pulse and press) cannot be attributed to any specific time scale.

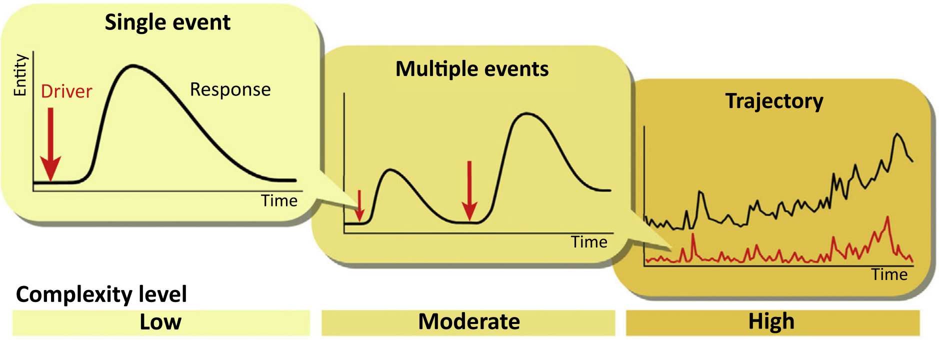

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Figure 1. Hierarchical Complexity. The idea deals with driver–response relationships in time-series across three levels of complexity. The levels are hierarchically nested, as single-event (i.e., one driver and one response) is a subset of multiple events that are a part of the trajectory. The key property is that driver–response relationships are not necessarily constant through time, but they can change over time due to recent and historical past experience. Hierarchical complexity can be observed at any scale. Temporal dynamics at each of the levels affect each other.

Glossary

Asymptotic environmentally determined trajectory: trajectory of a population process that is approached by other trajectories. For example, regardless of initial conditions, any trajectories converge eventually into a single trajectory that is determined by the surrounding environmental fluctuations. This concept can explain population and community dynamics in a nonstationary environment.

Carryover: interaction effects (additive or nonadditive) of multiple drivers that occur sequentially.

Ecological memory: capacity of past states or experiences to explain present or future responses of an ecological system. The length, temporal pattern, and strength of the memory are important components for quantification.

Equilibrium: state of stable conditions in which all forces cancel each other out and thus all factors remain temporally stable. The state goes back to the previous stable state or reaches another stable state after perturbations.

Lag hypotheses: The no-lag hypothesis, in community ecology, argues that a community composition is in equilibrium with the given environment at that location at a given time. On the contrary, the lag hypothesis argues that it is in nonequilibrium with the contemporary environment [9].

Nonequilibrium: state that does not reach an equilibrium (see Equilibrium).

Nonstationary: characteristic of time-series that is not stationary (see Stationary). Statistical parameters of time-series change over time.

Stationary: characteristic of time-series whose statistical parameters including mean, variance, and autocorrelation are temporally constant. Stationary and equilibrium are sometimes interchangeably used. However, stationary is a statistical term, while equilibrium is a term to represent the state of a system. A system can be considered at equilibrium under a stationary condition, but an equilibrium state does not necessarily satisfy stationarity.

Basic Principles of Temporal Dynamics

Basic principles of temporal dynamics are described at each level of complexity (Figure 2). Some ecological concepts can cover multiple levels (Table S1; see supplemental information online), but for simplicity, we sort them into one level in the following. When looking across scales, the proposed hierarchies can be further nested (e.g., a trajectory at a small scale could be a subset of a single event at a larger scale). This nestedness is a fundamental nature of temporal dynamics, and a level of complexity may depend on how closely the dynamics are observed (i.e., not the scale but the resolution). A level of complexity for an observed pattern can be reasonably assigned by clarifying which feature of the basic principles (discussed in detail below) is studied.

Temporal ecology: emerging field in ecology, which is focused on understanding how time influences ecological systems beyond the prevalent knowledge about temporal dynamics. Temporal ecology has been proposed to intertwine with spatial ecology, which is an integrative multidisciplinary field to address issues across spatial and ecological scales.

Single Event Level

Types

A single event characterizes both driver and response. For the sake of brevity, a driver and a response are represented by a single attribute each (e.g., temperature as driver and fitness as response), although multivariate attributes are possible [13].

Driver types are classified into pulse (transient), step (including press), or ramp [5,8,14]. After the emergence, a pulse returns to the previous condition after reaching a peak, a step ends up at a different magnitude, and a ramp makes a trend (upper left of Figure 2). No change (constant) can be additionally considered. Any pairings of driver and response types are possible (4 driver × 4 response types).

Characteristics

Driver and response are characterized by magnitude, duration, and rate of change (middle left of Figure 2; [15]). These characteristics allow various comparisons: norm versus extreme (any characteristic); low versus high (magnitude); transient versus persistent (duration); abrupt versus gradual (rate of change); fast versus slow (rate of change); acute versus chronic (rate of change and duration); and pulse versus press versus ramp (rate of change and duration).

Patterns

Threshold; Thresholds are attributable to the characteristics. A minimal exceedance threshold represents the value of a driver characteristic to trigger a response, while a maximal exceedance threshold represents the value at which the driver characteristic causes an irreversible response (cf. regime shift; lower left of Figure 2).

The equilibrium paradigm assumes no maximal threshold and transient responses [16,17]. Negative feedback is a key mechanism for equilibrium, irrespective of ecological scales [18]: for example, individual homeostasis, population density dependence, community compensatory dynamics, and ecosystem resilience. The nonequilibrium paradigm explicitly considers persistent responses beyond the maximal threshold, including mode switching of individual and regime shifts of ecosystems [16,17,19,20]. Regime shifts in an ecosystem can occur not only based on the magnitude of a driver [21], but also the rate of change of a driver [22], the duration of a pulsed driver, and their interactions [13].
Lag; Lags also cause nonlinear patterns; for example, lagged dynamics, legacy, antecedent effects, or ecological memory [3,23,24]. Lag patterns are quantifiable by latent duration (the interval between the occurrence timing of the driver and the emergence of the response) and time to peak (lower left of Figure 2).

In physiological ecology, lag patterns that have their origin early in development but that are first seen in juveniles or adults are known as latent effects [25]. In individual ecology, carryover

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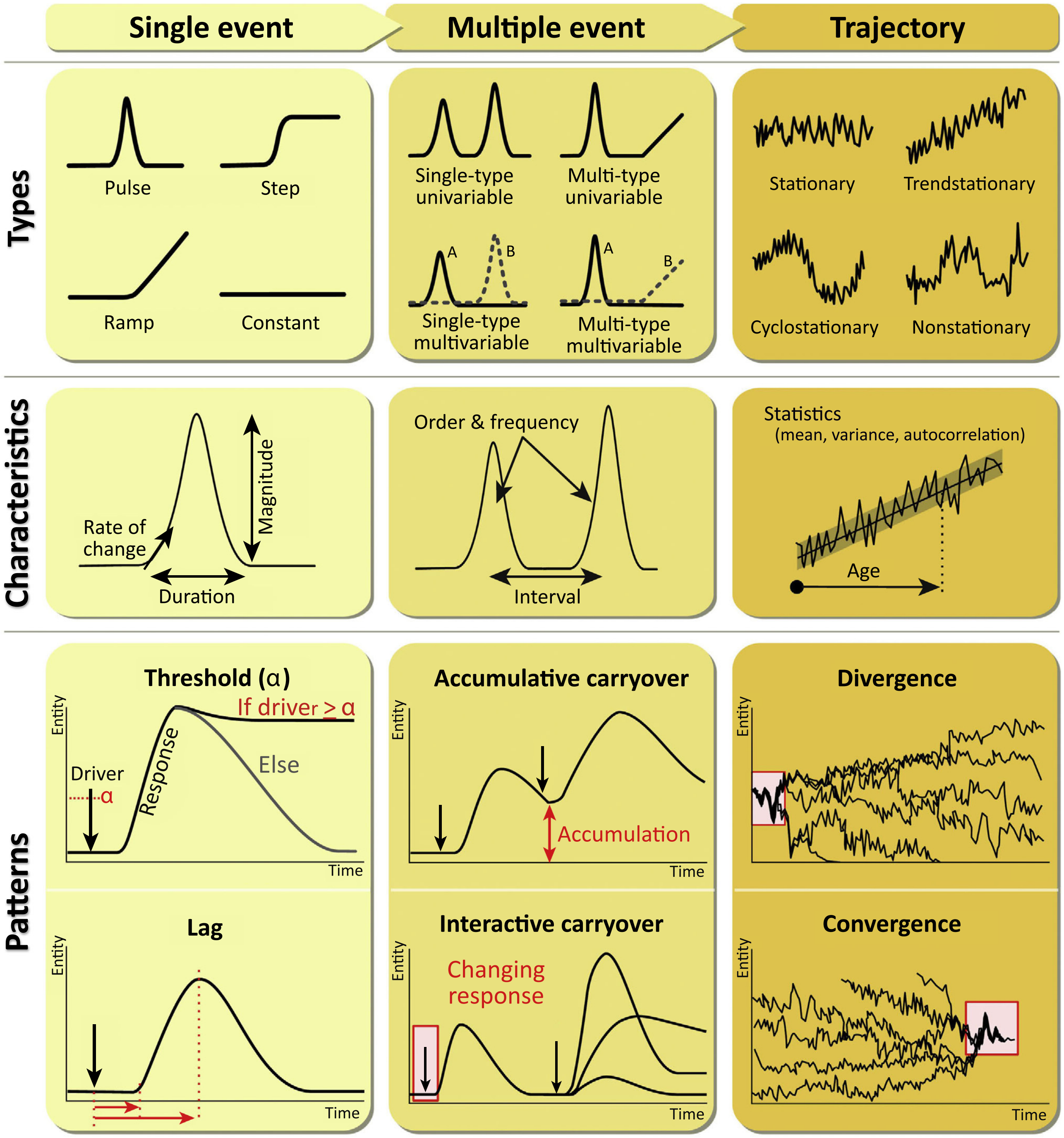

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Figure 2. Basic Principles of Temporal Dynamics. At each level of complexity, some unique properties are summarized. At single-event level, for instance, there are four different types of patterns, three quantifiable characteristics, and two important nonlinear patterns. For all drawings, the horizontal axis is time and the vertical axis can be any measurable quantity. Driver and response are categorized by their shape based on type (upper panels), and their characteristics are quantitatively measurable (middle panels). By considering the combination of driver and response, driver–response relationships may give rise to some level-dependent patterns (lower panels).

effects are referred when a nonlethal event during a previous season affects the current status of an individual ([26]; note that this definition differs from our definition of carryover which appears in the following section). Storage effects, linking population and community ecology, are a mechanism that explains species coexistence in a changing environment because each species can benefit from a transient opportunity for increasing fitness [27]. In community ecology, a 'ghost of competition past' is invoked when avoidance of competition in a current community is attributed to previous competition having led to niche separation [28]. In ecosystem ecology, 'afterlife effects' and 'legacy effects' describe the persistent impacts of a species and individual on abiotic or biotic processes of an ecosystem after their disappearance [29]. Their underlying common idea is that an event in the past partially explains the current behavior of the system [3,9].

Multiple Events Level

Types

Multiple events are combinations of two or more events. Depending on the number of drivers and responses and their respective event types, we consider the following four types: single-type univariable, multitype univariable, single-type multivariable, and multiple-type multivariable (upper middle of Figure 2). Single-type owns only one event type (e.g., repeated pulses), while multitype owns more types such as pulse and press. A variable with various temporal characteristics belongs to multitype univariable (e.g., hydrologic regimes in a river where the flow shows pulse-type floods and press-type droughts over time [15]). Multivariable, for example, studies multiple stressors.

Characteristics

The joint characteristics of the drivers and responses are definable: for example, the order, the interval period, and the frequency of occurrences (center of Figure 2). The order of occurrence can often cause significant consequences in ecology and evolution as historical contingency [30–34].

Patterns

Accumulative Carryover; **Carryover patterns**, the effect of a driver can change according to the previous events, are about lags but emerge at the multiple-events level. Accumulative carryover occurs when the effects of sequential events additively accumulate over time [8], because of a short interval between events (lower middle of Figure 2). Frequent disturbances are a cause of disequilibrium [9,17,35]. Accumulative carryover causes interesting dynamics in which a threshold is met by the accumulative effects of frequent, small disturbances.
Interactive Carryover; Interactive carryover occurs when the preceding driver changes an internal parameter or mechanism of a system, such that the system responds to a following driver differently from how it would have responded not having experienced the first driver. An antecedent driver may amplify some characteristics of the response of the system to the following driver (i.e., synergism) or weaken them (antagonism) (lower middle of Figure 2). While accumulative carryover results from a short interval between events (adding up), interactive carryover does not necessarily follow this and can happen due to a distant past memory.

Interactive carryover effects are often reported as physiological responses of organisms to sequential transient stresses as a defensive mechanism: for example, learning, imprinting, priming, and acquired resistance [36,37] (Table S1; see supplemental information online). Even organisms lacking a nervous system such as microbes and plants show interactive carryover [36–38]. The interactive carryover occurring at the individual level may influence population [38,39] and community dynamics [40].

Trajectory Level

Type

Trajectory level represents the long-term variability of a system, including a large number of events: for example, life history strategy, community assembly, and succession. Trajectory types can be classified based on statistical properties [8,41] (4 driver × 4 response types): Stationary, trend stationary, cyclostationary, and nonstationary (upper right of Figure 2). Stationary assumes time-invariant mean and covariance, which may additionally follow a trend (i.e., trend stationary) or cyclic pattern (cyclostationary; e.g. seasonality in temperature). Nonstationary dynamics change mean, variance, and/or autocorrelation in time [42]. Regime shifts are an example of such [43]. Yet, nonstationary is far less studied than stationary but being recognized as an important feature [1,44,45].

Characteristics

Statistical properties characterize trajectory patterns, including mean, variance, and autocorrelation [5,8]. A variance is often used to evaluate the severity of a single event (norm or extreme).

Age, the time since the system emerged, is another key characteristic (middle right of Figure 2). Several properties of single and multiple events may depend on the system age (e.g., emergence or terminal phases). Ecosystems change in functional performance depending on the successional stage of the community (e.g., young and old forests differing in resource use efficiency [46]). Many systems are the most sensitive to perturbations throughout the lifetime when they are emerged.

Ecologists' interpretations of the same driver also vary according to system age: for example, at the population level, the effect of individual arrival is called founder effects at the establishment phase of a local population [47] and called rescue effects at the terminal phase. At the community level, species arrival is studied as priority effects if a local community is sparse [34] and studied as species invasion if the community was already established. Considering age clarifies many ecological contexts.

Patterns

Divergence; Small differences may completely change the dynamics of a system and thus the future trajectory [48] (lower right of Figure 2), known as butterfly effects in chaos theory [49]. Divergence patterns have been often studied in the context of genetics and evolution as historical contingency [33]. Examples are maternal effects at the individual level, where the maternal genotype or phenotype influences the offspring phenotype [50]. Founder effects occur at the population level, where the establishment of a new population by a small number of individuals from a larger population determines the genetic variation within the established patch [51]. Priority effects are at the community level, where the first arrival of a species influences establishment success of the later-arriving species [34]. In evolution, adaptive radiation explains a process in which organisms diversify from an ancestral species to a variety of forms at an exceptionally high speed when species arrive in a novel environment. Contrary to adaptive radiation, phylogenetic niche conservatism is the result of processes that inhibit trait divergence in related lineages [52,53].

Convergence; The idea opposite to divergence is convergence, where the recent past conditions might be more influential for the current dynamics of a system, and therefore they are eventually independent of initial conditions (lower right of Figure 2; [1]). Convergence is implicitly assumed in most ecological studies that correlate drivers and responses as a snapshot, as this assumption requires only current or recent past information and allows neglecting the influence of long-distant past. Divergence and convergence jointly determine the dynamics of a system [31].

Interactions across Levels

Recognizing the inter-relatedness of single events, multiple events, and trajectory levels is inevitable to understand temporal dynamics. For example, the effect of a physiological stress on growth of an organism is studied mostly at the single event level, but results may greatly differ depending on both recent and distant-past experiences [54]. This is a retrospective recognition of the inter-relatedness. In this case, one can study the possibility that lag and threshold patterns depend on what the system has experienced previously and the age. On the contrary, as a prospective recognition, one can study the effects of a stressor at the infancy stage on the following trajectory dynamics.

A review emphasizes the need of modeling species and community responses to climatic and ecological changes by taking paleo-information (i.e., trajectory) into account [55]. On the contrary, a single driver may determine multiple-event level consequences (e.g., warming determines the degree of priority effects [56]), and multiple events determine trajectory dynamics (e.g., historical human activity influences arctic vegetation dynamics over millennia [57]). Yet, the inter-relatedness of hierarchical complexity is understudied.

Short- and Long-Term Benefits of Applying This Framework

Short-Term Gain: Study Design and Improving Predictive Power

The components we summarize in Figure 2 can be used as a comprehensive checklist for designing and evaluating studies (Box 2). Referring to these components helps with planning a time-related study systematically: which levels of the complexity are targeted; are cross-level interactions tested; which aspects of temporal patterns are quantified (e.g., magnitude and interval); and what patterns may emerge (e.g., lag and threshold). As a reference, we highlight some established experimental designs and statistical analyses in Figure S1 (see supplemental information online). We also consider that the predictive ability to model the effects of past conditions on ecological variables could be substantially improved by designing studies and analyzing data using our approach [3,58].

The basic principles we offer can promote the use of existing time-series data to better understand temporal dynamics [5,8]. Although many observations in ecology are either nonreplicated or infrequently repeated [59], some databases and techniques are already available: for example, the Long Term Ecological Research Network (https://lternet.edu/), the National Ecological Observatory Network (https://www.neonscience.org/), Ameriflux (http://ameriflux.lbl.gov/), the global species time-series database [60], and analysis of environmental DNA [61].

Short- to Medium-Term Gains: For Identifying Gaps and Transferring Concepts

Similar concepts may have different names and are applied in different fields. Identifying such conceptual linkages can help transfer concepts from one ecological level to another. For instance:

- Priority effects (i.e. system components arriving in different order) at the community level [34] are conceptually similar to founder effect at the population level [47]. By transferring the equivalent idea to the ecosystem level, we can ask if it plays a role which component of a nutrient cycle establishes first (during a new colonization) for developing biogeochemical dynamics.
- Priming effects (i.e., an initial stimulus prepares a system for a subsequent more deleterious stressor; not the priming effect which refers to strong short-term changes in organic matter decomposition in soil science [62]), originally defined at the individual level [37] and then

Box 2. The Concept as a Checklist to Contextualize Study Designs

We here demonstrate how the concept of the basic principles (see Figure 2 in main text) can be used as a checklist to systematically categorize time-related studies, by introducing some examples: a laboratory experiment, statistical modeling framework, and meta-analysis.

(A) **Experiment:** The experimental study [54] investigated the effects of past inundation or drought events on the subsequent growth responses of plant species to the same, opposite or more favorable conditions (cf. priming effects explain that an initial stimulus prepares a system for subsequent more deleterious stressor; cross-protection, which is priming with different types of stresses). They found that the past inundation was more beneficial for species from wet habitats than for others, while species from dry habitats acquired the strongest drought tolerance after a drought event. Therefore, this study was about carryover effects at the multiple-events level, for which effect sizes were partially explained by the historical past at the trajectory level, as summarized in Table I (A).

(B) **Modeling framework:** The statistical modeling framework proposed in [3] takes recent past fluctuations into account for explaining the current status of any ecological system (e.g., stomatal conductance, soil respiration, ecosystem productivity, and tree growth). They demonstrated that models with the recent past effects included explained an additional 18–28% of response variation compared to models without them. This study was about explaining the variance of a trajectory by including lag effects at the single-event level and both accumulative and interactive carryover effects at multiple-events level, seen in Table I (B).

(C) **Meta-analysis:** The meta-analysis [58] revealed that survival of primed microbes was about tenfold higher compared with that in nonprimed microbes based on the findings from over 250 trials. This study is a meta-analysis about a specific type of interactive carryover effects across microbes [i.e., priming; Table I (C)].

We demonstrated that such categorization in the standardized rule makes comparison across studies easier. For instance, the examples A and C share a similar focus based on the categorization, and similarity was more difficult to notice before categorization. In addition, the checklist (Table I) allows researchers to identify which aspects of temporal dynamics are investigated, and more importantly, which of them have not been investigated. This systematic assessment helps with finding novel and unexplored aspects of temporal dynamics.

Table I. The Proposed Concept as a Checklist for Evaluating Study Designs.

	(A) Experiment			**(B) Modeling framework**			**(C) Meta-analysis**		
	Single	**Multiple**	Trajectory	Single	Multiple	**Trajectory**	Single	**Multiple**	Trajectory
Types		Multitype univariable				Applicable to any types		Multitype univariable	
Characteristics		The order of occurrence	Different means			Quantifiable		The order of occurrence	
Patterns		Carryover observed		Lag modeled	Carryover modeled	Convergence assumed		Carryover evaluated	

The most relevant levels are in bold type.

argued to be applicable at the community level [40], can also be considered at population and ecosystem levels. For instance, does a prior milder stress provide greater resistance or resilience in an ecosystem process rate?

Long-Term Gains: Toward Knowledge Integration across Ecological Fields

The idea of hierarchical complexity opens the door to comparing among organisms with completely different lifespans, such as microbes and macrobes (i.e., irrespective of biological hierarchy and temporal scale). Hierarchical scale captures the multiscale nature of temporal dynamics by expressing what happen across scales (e.g., forest fires can last from hours to years, from a hundred meters to hundreds of kilometers) [5,59,63–65]. By contrast, hierarchical complexity describes the fundamental nature of temporal dynamics by expressing which patterns are observed at each scale.

The concept of hierarchical complexity realizes the value of organizing disconnected fields of research, including improving communication among scientists in disparate fields. Nearly 60 concepts we collected (Table S1; see supplemental information online) can be used to make inroads towards unifying terminology:

- Using the same concept regardless of scale. For example, resilience is an ecosystem concept, but could it also be applied to individuals, where it is currently not used but instead described in terms of recovery, even though resistance is used equivalently at both levels.
- Creating a hierarchy of concepts. At a broader level, we also found that many concepts can be organized in a hierarchical fashion. Such hierarchies could be used to unify different

concepts. For example, the concept of carryover effects in population ecology, in itself, has been broadly defined to occur ' . . . in any situation in which an individual's previous history and experience explains their current performance in a given situation.' [66]. Thus, this concept encompasses a range of dynamics.

Concluding Remarks

We propose hierarchical complexity as a fundamental concept that describes temporal patterns of driver–response relationship, based on the collection of nearly 60 terms and concepts across subfields in ecology and evolution (Table S1; see supplemental information online). We think that using this concept will advance ecology and evolution in two main ways. First, it provides a common language for better communication among ecologists studying analogous concepts in different subfields. Second, it stresses the need to consider past events for adequately considering the current and future state of ecological phenomena. Across all ecological levels, from individual to ecosystem, the ecological driver–response relationships can be temporally variant and dependent on both short- and long-term past conditions.

Finally, we pose an open question: can hierarchical complexity be a nucleus for the development of a temporal ecology [5] (see Outstanding Questions)? Such a field would be analogous to spatial ecology, for example, where local and regional-scale processes would be the equivalent of short-term (multiple-event) and long-term past (trajectory). While spatial ecology has flourished as a field to study the spatial nature of ecological phenomena, no equivalent exists for the study of the temporal nature of ecological phenomena. There are books on spatial ecology [67] but not on temporal ecology. In addition, we found 300 000 versus 10 000 Google search hits of the terms 'spatial ecology' and 'temporal ecology', respectively (on March 7, 2019). This situation is paradoxical, given that there is no shortage of terms and concepts related to time in ecology and evolution. We think the time is ripe for the development of such a field.

Outstanding Questions

Can the concept can be a nucleus for the development of a temporal ecology in analogy to spatial ecology, for example, where local and regional-scale processes would be the equivalent of short-term and long-term past events? Temporal dynamics have been far less studied than spatial dynamics, even though there is no shortage of terms and concepts related to time in ecology and evolution.

The current states of ecological systems are often explained without the past information because acquiring time-series data takes time and is limited by logistic constraints. Thus, the temporal transition from the past is largely neglected. To what extent is it important to include past information to explain the current state of ecological systems? What is the relative importance of the short-term past vs. the long-term past?

Can basic principles of the idea of hierarchical complexity be used in ecological conservation and management? For example, can an ecosystem be 'trained' with repetitive milder perturbations to be more resistant and resilient?

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Supplemental Information

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RATE OF CHANGE ACROSS SCALES IN ECOLOGY

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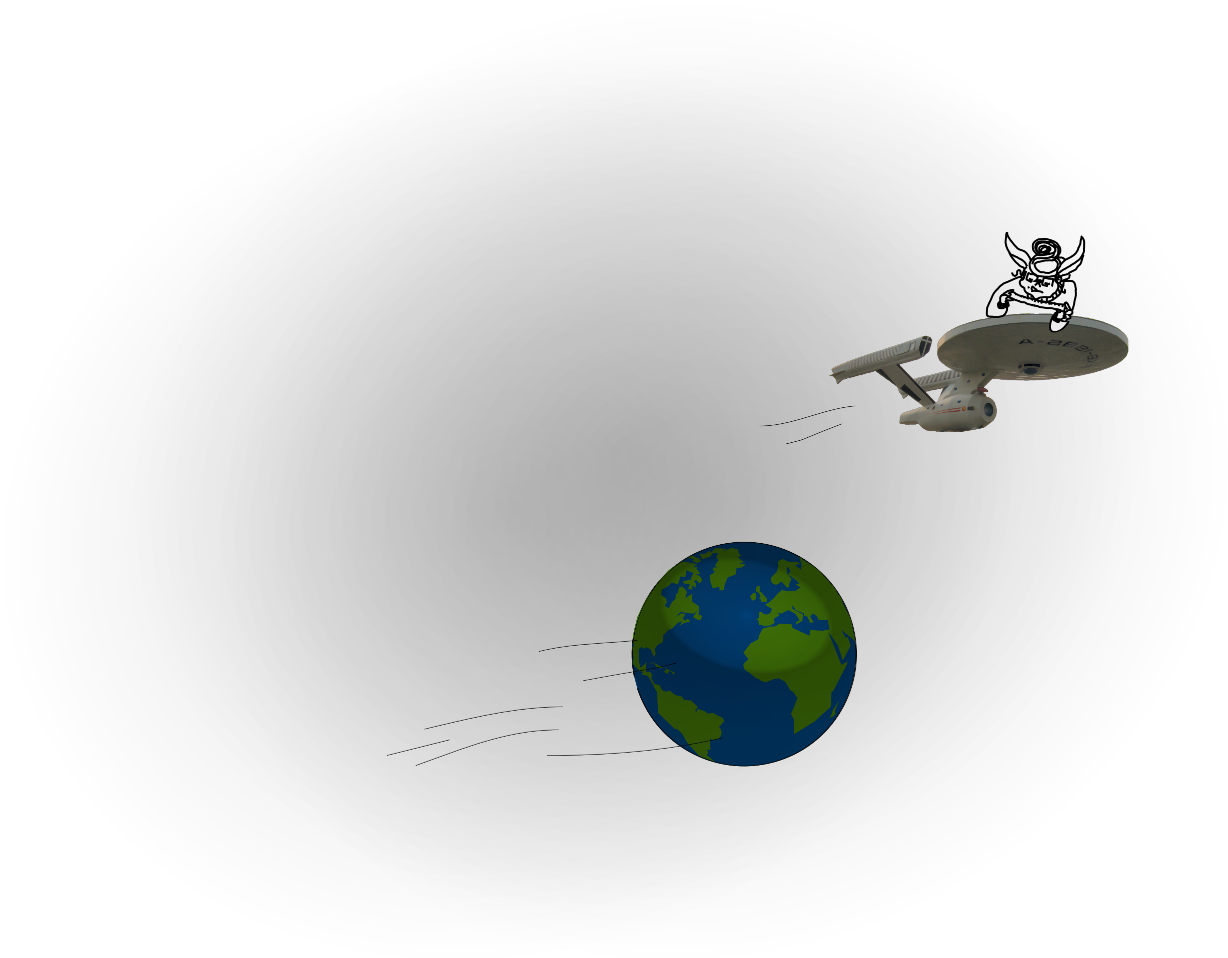
"So ! How fast is fast ?"
- Lilianus cuniculus



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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

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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_2 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

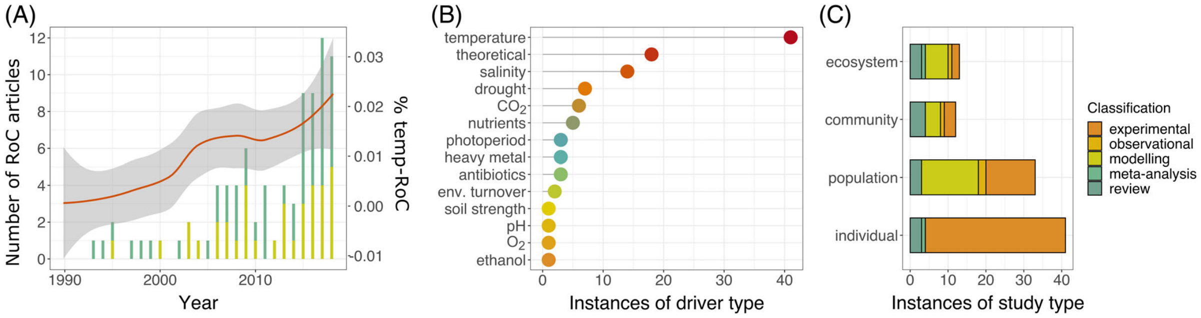

Fig 1. Synthesis of literature on rates of change (RoCs). (A) Number of publications on RoC from 1990 to 2018 (dark green: all papers from that year, light green: papers investigating temperature) and number of papers per year that studied the effects of RoC of temperature relative to the total number 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 occurences = 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; Loeschcke & 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; Klironomos *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).

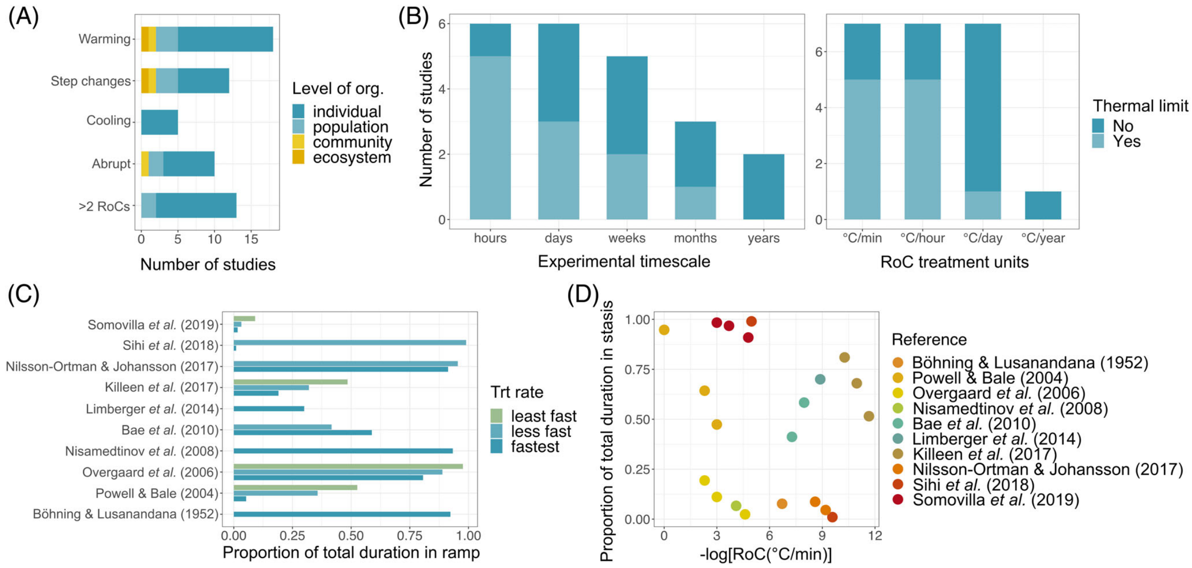

Fig 2. Details of treatments in experimental studies investigating the effects of rate of change (RoC) of temperature ($N = 22$). (A) Number of studies that included particular experimental design elements for each level of ecological organization. (B) Experimental timescale and RoC measurement units 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 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; Beitinger *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 (Beitinger *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; Beitinger *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 a 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

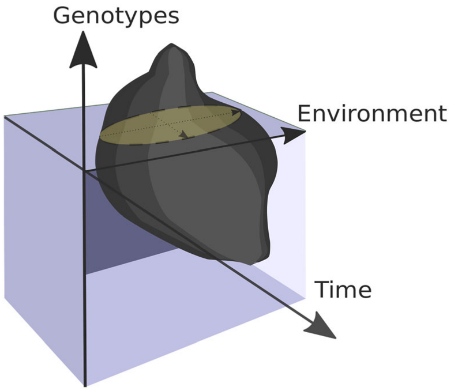

Fig 3. Phenotypic plasticity is the interactions over time of a genotype with its environment to produce a particular phenotype at a given point in time. Experiments frequently consider only the phenotype of the organism at the point of study and under one temporal treatment regime, ignoring the effects 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 × environment interactions over time for a single genotype. The black volume is the phenotype space possible for all genotypes in a population × environment × 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

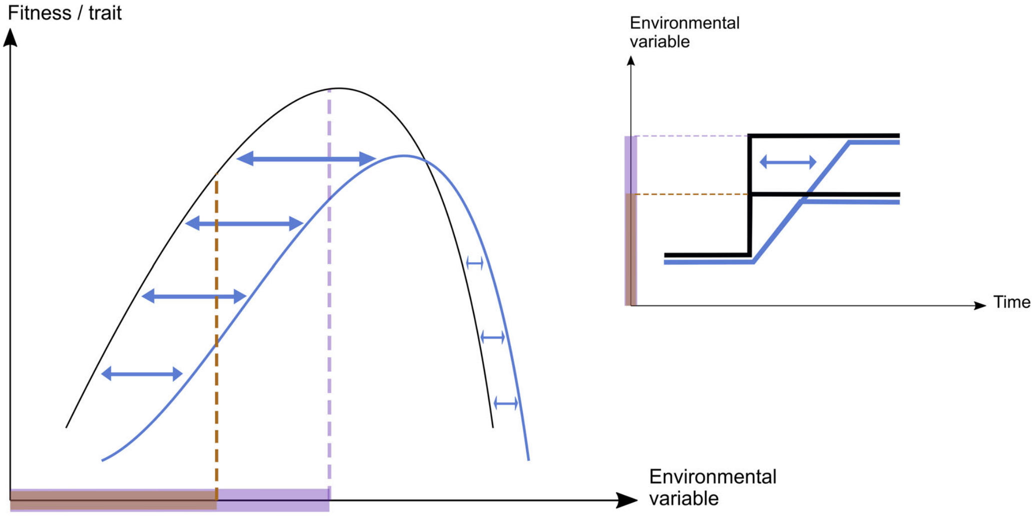

Fig 4. A theoretical reaction norm and its temporal aspect. Representation of two reaction norms for the same genotype with the same environmental variable applied at two different rates of change (RoCs). The inset panel shows the two treatment application regimes (red and lilac bars). The intensity 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_2 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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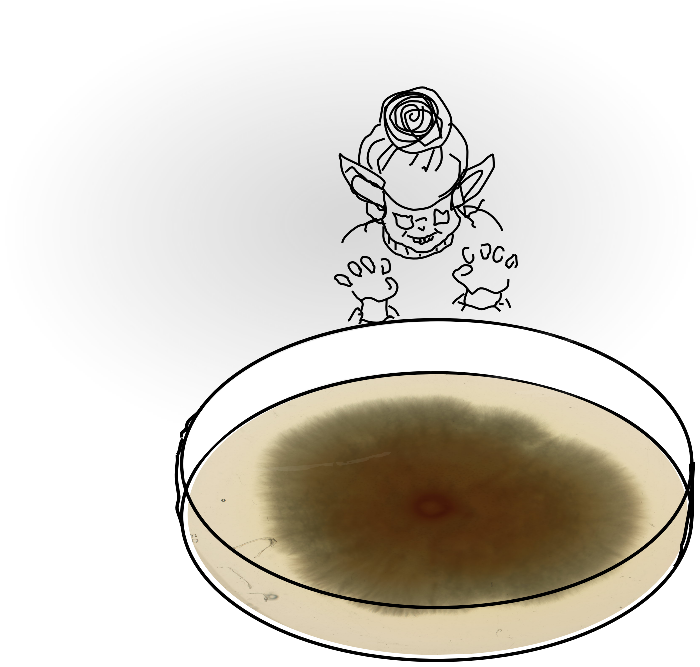
4

RATE OF TEMPERATURE CHANGE INFLUENCES FUNGAL RESPONSES

in preparation

"You WILL talk !
Fungus..."
- Lilianus cuniculus



4.1 INTRODUCTION

Climate change is a critical challenge humanity is facing today. A focus of research and related policy has been the magnitude of temperature change, illustrated by targets such as "+1.5", which have been capturing a lot of attention.. However, even considering only temperature, climate change is about more than its magnitude. Lately, the temporal dynamics of climate change drivers has received attention in the ecology community (Ryo et al., 2019) and, in particular, the rate of change (RoC) of a driver (Siteur et al., 2016). In most experiments that test the response of ecosystems to global change drivers, an abrupt rate of change is applied (Luo and Hui, 2009). Abrupt in the sense that the treatment is applied in a single, near-instantaneous step (given methodological limitations) and the RoC of the change is simply ignored (Pinek et al., 2020). The question is then, can we predict an ecosystem's response to a four-degree-celsius magnitude of change over several years, using abrupt change data? Although studies investigating RoC are much more rare than studies looking at magnitude, there are data suggesting that rate of driver change influences community composition (Klironomos et al., 2005) and the reliability of estimation of the heritability of thermal performances (Terblanche et al., 2007). In most systems, basic knowledge of the temporal relationship between environmental drivers and ecological responses is missing (Dillon et al., 2016). To make better predictions, we need to describe the impact of driver RoC on their effects on biological systems. One approach to addressing this complex question is to start at a lower level of organization (individual responses) and go up on the complexity scale: a bottom up approach that provides mechanistic insights.

The underlying mechanisms of perception and response to an environmental driver vary (sometimes strongly) depending on the RoC at which that driver is applied (reviewed in Pinek et al., 2020). This variation can impact biological outcomes, like in the case of an organism's response to a temperature change, where several mechanisms come into play but that exhibit different temporality (Hoffmann, Chown, and Clusella-Trullas, 2013); e.g, stress responses develop rapidly, while acclimation responses take longer to develop. The order in which responses develop and how they interact also determines the response of the organism (or population, community or ecosystem) under study. For example, under a very slow rate of change, acclimation potential could be a more important mechanism behind the response to an environmental driver than stress responses (Beitinger and Bennett, 2000). This temporal complexity has not yet been studied in microbial individuals, and furthermore it generally remains uncertain how the effect of RoC can transmit to levels of ecological organization above the individual for most organisms (Pinek et al., 2020).

Fungi serve essential functions in communities, especially in soil where they function as decomposers, play a role in establishing and maintaining soil structure, form mutualist relations and also act as pathogens (Moore, Robson, and Trinci, 2020; Zanne et al., 2020). Fungi are known to be temperature sensitive. Temperature stress can affect fungal activity and thereby ecosystem functioning – for example, the virulence of fungal pathogens (Shapiro and Cowen, 2012) and fungal organic matter decomposition (A'Bear et al., 2014) are altered under elevated temperatures. Fungal physiology and life history are also affected by temperature stress. Phenotypic changes (e.g. colony morphology, production of stress response proteins) and strongly reduced growth rates have been observed for some fungal strains, as well as changes in reproductive sporulation activity (Brown, Cowen, and Pietro, n.d.).

To our knowledge, studies of temperature change effects on soil fungi have only applied abrupt treatments, and thus, the effects of temperature RoC on this group of soil biota are unknown. In fungal ecology, little is known about how soil fungi react to temperature change through time. Experimental data on strain-specific responses to diurnal or seasonal change associated with their relative temperature change patterns are scarce (but see for example Kronholm and Ketola, 2018). However, these studies tend to report plastic responses related to temperature change (e.g., Hernandez and Allen, 2013 for diurnal rhythms in the growth rate of arbuscular mycorrhizal fungi linked to temperature variation). Additionally, some authors directly showed thermal acclimation in saprobic fungi (Crowther and Bradford, 2013). It has been shown for other organisms that when acclimation abilities exist, the effect of temperature on an organism's physiology and functions is reduced at lower rates of change (Hoffmann, Chown, and Clusella-Trullas, 2013). A better understanding of how soil fungi react to temperature RoC would allow us to better model and predict how soil fungal community structure and function could be impacted by temperature change.

Our goal in this study was to investigate the effect of different RoC at a given increase in temperature on fungal growth (individual level) and fungal competition (community level). Three different RoC scenarios were applied to all experiments: 1) abrupt, in which fungal strains are exposed to a sudden temperature increase (representing the classical experimental treatment), 2) gradual-fast, in which temperature increases over the course of a day (simulating daily temperature change in nature) and 3) gradual-slow, in which temperature rises over a week simulating seasonal change. We also explored different heat stress levels (intermediate and strong). We formulated three hypotheses: 1) slower RoC will reduce the negative impact on growth of intermediate (31°C) and high heat stress (36°C); 2) slower RoC can increase thermal growth limits; 3) RoC modifies competitive outcomes in fungal interactions. To test hypothesis 1, we challenged 29 saprobic fungal strains with rising temperature from 25°C to 31°C (intermediate heat stress) and 36°C (strong heat stress) and three RoC scenarios (abrupt, gradual fast and gradual slow). For the second hypothesis, we looked for evidence of an increase in the thermal limit for 10 fungi with thermal growth limits > 35°C under gradual RoC treatments (experiment 2). To test hypothesis 3, competition outcomes for 8 fungal strains in pairwise interaction were evaluated under the three different RoC scenarios with the temperature change of 25°C to 31°C (experiment 3). Finally, in order to link potential mechanisms, we correlated the observed RoC effects with morphological and physiological traits.

4.2 MATERIALS AND METHODS

4.2.1 *Fungal collection*

The fungal collection strains were originally isolated from soil samples of a dry grassland ('Oderhänge Mallnow' Lebus, Germany; 52°13'N, 14° 13'E) as described in Andrade-Linares, Veresoglou, and Rillig, 2016. Briefly, soil samples were washed and diluted to reduce spore loading while improving fungal hyphae availability attached to soil particles. Various media and antibiotics were used to target isolation of Ascomycota (18), Basidiomycota (4), and Mucoromycota (3) strains (SI -1.1 for list with RLCS number, taxon name, accession number). For our experiments, we started new stock cultures from the lab culture collection on potato dextrose agar (PDA; Carl Roth GmbH) and stored these for 3 months at 12 °C. Before every experiment, new cultures were made from these stock cultures. These new cultures were grown on PDA at 25°C for 1 to 2 weeks (depending on the growth rate of the strain) to produce sufficient amounts of active fungal material.

4.2.2 *Temperature rate of change treatments*

Based on a preliminary experiment to determine fungal thermal growth limits, we set two target temperatures in our experiment: 31°C, representing an intermediate stress level (experiment 1 and 3) and 36°C, representing a strong heat stress level (experiment 2). At 31°C, all strains grew but their growth was impaired and at 36°C, a temperature that for most strains reached or exceeded their thermal limit (i.e. no growth was observed) (SI - 1.1 to 1.3). For the temperature controls we chose 25°C, the standard culture temperature for our fungal isolates (assumed to be near maximum performance temperature; Dix and Webster, 1995).

To study the effect of RoC, both experiment 1 (target temperature 31°C) and experiment 2 (target temperature 36°C) consisted of two phases: a ramping phase, during which temperature is increasing until it reaches a target temperature, followed by a stasis phase with constant temperature (Figure 1a). Specifically, we applied the temperature increase from a starting temperature of 25°C to the experiment-specific target temperature (31 or 36 °C) following three RoC treatments: 1) abrupt (Ab): ramping time of 0 days (samples were immediately heated up to the target temperature); 2) gradual-fast (Gf): samples were continuously heated up to the target temperature over the course of 1 day (to mimic rising temperature from night to day time), 3) gradual-slow (Gs): samples were continuously heated up to the target temperature over the course of 6 days (to simulate a seasonal rise in temperature, Figure 1). In order to apply the same amount of thermal energy (i.e. temperature dose, SI - 1.4) to each sample, we adjusted the duration of the stasis phase depending on the RoC treatment (i.e. the number of days after reaching the target temperature, see Figure 1 and further details below). This temperature dose is calculated as the product of the rate of change of temperature x the rate of change in time (thus temperature dose is measured in °C.days units). Control samples were maintained constantly at 25°C throughout the entire experiment (9 days). Our treatment regime has an inherent challenge: comparing fungal growth among samples across treatments with the same growth period after the target temperature is reached, means that they have received different temperature doses; while comparing samples when they reach the same temperature dose, means that they have had a different growth period after target temperature is reached. In order to address this challenge, we collected and compared fungal growth data at different time points in our experiment following "dose-based" and "event-based" sampling approaches (Figure 1b,c). In the "dose-based" approach (Ballhausen, Hewitt, and Rillig, 2020), we compared fungal growth data at days when they had reached the same temperature dose across all the three RoC levels but, as a result, had different total growth periods: 6 days after reaching the target temperature for Ab and Gf treatment and 3 days after reaching target temperature for Gs treatments (see further details on the calculation in the supplementary material). In contrast, in the "event-based" approach, we compared fungal growth data among samples after 1 day and 3 days of growth in the stasis phase (but as a result have received different temperature doses).

4.2.3 *Experimental design*

For all experiments, fungal inoculum was grown on potato-dextrose agar (PDA) in 9 cm petri dishes at 25°C for 1 to 2 weeks (see above). Addition of an agar plug with fungal tissue (Ø 5 mm) from the inocula to the experimental PDA petri plates (referred to as the experimental units) marked day 1 of the experiment. All petri dishes were sealed with parafilm after inoculation. Within each experiment we prepared 9 fungal replicates for each of the three temperature treatments and the 25°C control. The control incubators were maintained at 25°C for the entire experiment (9 days). The Gf, Gs and Ab treatments followed the temperature regimes illustrated in Figure 1. These were set up in three incubators (of the same treatment) to avoid pseudoreplication. Experimental durations were different depending on temperature treatment; each treatment lasted until the temperature dose was achieved. In experiment 1, we tested individual fungal strains under the Gf, Gs and Ab treatments and control conditions with a target temperature of 31°C. In experiment 2, we tested individual fungal strains under the Gf, Gs and Ab treatments and control conditions with a target temperature of 36°C. The overall experimental durations for each treatment were 6d for Ab, 7d for Gf and 9d for Gs. Each experiment consisted of 29 fungal strains x 4 temperature treatments (i.e. 25°C control, Ab, Gf and Gs) x 9 replicates, yielding 1044 plates per experiment. In experiment 3, we set up pairwise competition scenarios. A subset of seven fungal strains were selected following preliminary data on competitive ability from which we chose two of strongest (RLCS01) and the weakest (RLCS29) competitor and additional four strains representing a range of competitive abilities (SI -1.1). We set up all 54 possible combinations of fungal pairs and applied a similar design as explained above: three RoC levels (Gf, Gs and Ab treatments) and control conditions with a target temperature of 31 °C (temperature dose = 36°C-days). In addition to interspecific competition pairs we also produced intraspecific pairs (in which each fungal strain faced itself) as interaction controls. In order to synchronize the timing of fungal interactions across the temperature treatments (with their different ramping and stasis durations), we positioned the fungal tissue agar plugs adjacent to one another so that the interaction would start immediately.

4.2.4 *Image collection*

During the course of each experiment, we regularly collected images of experimental units for downstream image analysis. With an Epson Perfection V700 Photo Scanner (300 dpi, 16-bit, color), we scanned the bottom of each petri dish. The translucent PDA provided clear sight without interference of any condensed droplets. Scanned images of all experimental units were collected every two days for the entire duration of the experiment and on the final day for each treatment, when not an even-numbered day.

4.2.5 *Fungal mycelial area - experiments 1 2*

Given the amount of scanned images generated (4437 in experiment 1 + 4437 experiment 2 = 8874 scanned images in total), we measured the fungal surface area using a partially automated numerical approach, based on different python modules (matplotlib by Hunter, 2007 (2007), numpy by Harris et al., 2020 (2020), PIL by Umesh, 2012 (2012), and CV by Bradski, 2000 (2000)). Briefly, this script was built to differentiate pixels associated with the fungal mycelium from the pixels associated with the Petri dish, agar and background outside the petri dish (SI - 1.5).

4.2.6 *Fungal competitive ability - experiment 3*

The program was not capable of distinguishing between mycelium from differing fungal strains, thus the fungal mycelial area of each competing fungal strain was measured by hand for experiment 3. Using ImageJ we measured the relative surface occupied by each fungal strain (two per plate) and categorized the shape of the line of interaction, i.e. an imaginary line laid between the competing colonies. We scored the outcome of each interaction by using three qualitative categories: clear win/loss, intermediate win/loss, tie (criteria listed in SI 1.6). Each partner was categorized into one of five groups: 'winner' or 'loser' (clear or intermediate), or 'tied'. We also noted cases of distance inhibition. The competitive outcomes were scored for every measurement date, i.e. every two days during the duration of the experiment (thus the growth period was the same, but the temperature dose differed by treatment). Competitive outcomes were also scored on the final date of the experiment, when the 36°C-day temperature dose was achieved (i.e. same temperature dose but different growth period). Consistent with the choice to implement the dose- and event-based approaches previously described, the latter set of data are presented here. The competition outcomes (particularly the form of the interaction line) remains the same once the target temperature is achieved in all treatments, regardless of duration.

4.2.7 *Statistics*

All statistical analyses were done in R v. 4.0.4 (R Core Team 2020) using the packages emmeans, ggfortify and ggplot (Lenth, 2021, Tang, Horikoshi, and Li, 2016, and Wickham, 2016).

To compare the different time points in the dose and event based approach with each other we always used transformed data, standardized by control values at the same time point. For our analyses of experiments 1 and 2, we used the natural log response ratios (LRR) of the area occupied by a fungal mycelium and the associated control on the same day. For each data point, the response ratio was generated by dividing by the mean of the control data from the same strain on the same experimental day. We used the LRR, instead of raw surface area values, because they allow comparisons between fungal strains that have inherently faster or slower growth rates. Additionally, this metric also allows us to compare colony areas at different time points across treatments by excluding the variation due to the extra time to grow.

Response Ratio of replicate i of fungus a under treatment x at time t = ln (Area of replicate i of fungus a under treatment x at time t / average(Area of all replicates i of fungus a under control treatment at time t))

We tested the effect of the RoC treatments on the LRRs by linear, mixed-effects model (lmer() function, lmeTest package (Kuznetsova, Brockhoff, and Christensen, 2017). First, we ran a model for dose-based comparisons (i.e. endpoint comparison):

Model 1: LRR   treatment + (1 | isolate) + (1 | isolate:treatment))

For the event based approach, we used two time points during the stasis period (+1 and +3 after target temperature was reached) to compare the RoC effect on the LRR over time

Model 2: LRR   Time in stasis * Treatment + (1 | fungal isolate) + (1 | Treatment:fungal isolate)) + (1 | Time in stasis:fungal isolate))

Model 2′: LRR   Time in stasis * Treatment+fungal isolate

We tested the model residuals for normality and homogeneity and implemented type III sums of squares to account for imbalances in the data set. We performed post-hoc Tukey tests using the emmeans() and pwpm() functions from the emmeans package (Lenth) to test the degree of evidence for effects of specific RoC treatments. In order to study the effect of RoC on individual fungal strains, we ran this model with fungal isolate as a fixed factor and investigated RoC effects on the individual strains.

In order to characterize strain responses to RoC of temperature, we ran a PCA of the model parameters extracted from model 2′ (experiment 1) and used a mathematical clustering approach to classify the observed responses. We grouped the different behaviors of the strains. The variables used to describe the behavior of individual strains were the estimated effect (emeans) and effect sizes difference (Cohens SD) between RoC treatments for each strain based on the post-hoc anova analysis. This was realized with the kmeans() function from the basic R “stats” package. To look for correlations of fungal traits with the contrasting behavior types associated with fungal response clusters, we performed a PCA analysis including traits previously described for this fungal collection (Liang et al., 2019; Zheng et al., 2020), by applying the prcomp() function. The PCA visualizations were realized with the ggfortify package and autoplot() function (Tang, Horikoshi, and Li, 2016). The traits included were mycelium structure traits, thermal upper limit, spore size and enzymatic activity traits.

For experiment 2, we chose to only apply model 2′. We also assessed possible changes in thermal limits: for fungal strains with a thermal limit of 36°C or higher (n = 10), we visually assessed the data to check if any strains grew at temperatures above the previously established thermal limits under the RoC treatments.

For experiment 3 we calculated competition scores for each fungal strain and under every treatment, with the following formula : competition score = 2*(W-L)+(W1/2-L1/2)

with W (win), L (loss), T (tie) , W1/2 (intermediate win) and L1/2 (intermediate loss) (SI-19). The competition scores were then used to generate a competitive ranking for each treatment group. To statistically test for changes in competitive outcomes based on RoC treatments, we performed a Chi square test. First, we tested for differences across treatment groups. Then we checked if certain groups of fungi drove differences between treatment groups. Because there were few data points for each fungal strain, we first classified the eight strains into groups based on competitive ability at 25°C (data from an earlier experiment, personal communication from Anika Lehman). The groups were 'extremes competitors' (strains with very high or very low competitive abilities) and 'intermediate competitors'. The competition scores for strains in each group were aggregated, and the frequency of outcomes were compared across treatment groups using the Chi-squared test performed using chisq.test() (Pearson's khi test).

To avoid potential pseudoreplication, we distributed replicates of all treatment combinations to three different incubators in every experiment (12 incubators were used for each experiment). We did not find any evidence for an incubator effect, thus we excluded this factor from downstream models.

4.3 RESULTS

4.3.1 *Experiment 1: RoC effects on fungal responses to intermediate heat stress*

In experiment 1, where we investigated the effects of intermediate heat stress, we measured the fungal growth response to three different temperature RoC treatments. Fungi grown under the Gs treatment, with the slowest temperature increase, performed similarly to those grown under control conditions (Figure 2 ; SI 3.1 to 3.4 and 4.1). Isolates grown under the Ab or Gf treatments showed a relative reduction in the area occupied by the fungal mycelium (Figure 2, SI 3″ and 4). This pattern was consistent across our two investigated approaches (dose-based and event-based approach; Figure 1 and Figure

2 ; SI 3.1 to 3.4 and 4.1). In the event-based approach, fungal surface area diverged from the control over time in all treatments, however the fungi grown under the Gs diverged more slowly (Figure 2 b ; SI 3.1 and 4.1).

Additionally, there is less interstrain variability in response ratios under control and Gs as for Ab and Gf (Figure 2 a ; SI 3.1, 3.4 and 4.1). When looking at the overall data of log response ratios through the time of the entire experiment (i.e. all data point disregarding dose based or event based comparaison see SI 3.1), Ab and Gf maintained a rather flat distribution of the log response ratios from 0 to - 4 indicating more variability in the response ratio across fungal strains under those RoC treatments that are maintained through the entire experiment time. Under Gs the distribution of the log response ratio across species transitions from a unimodal distribution centered around 0 (same as control distribution) into a bimodal distribution with one peak centered around 1.0 and another centered around - 0.5 (SI 3.1). This is because some strains started to exhibit negative responses to the temperature change; these are the same strains which were affected strongly by the heat stress in Ab and Gf (SI 3.1, 3.4 ,4.1 and 4.4).

Overall there is diversity among strains in the strength of the temperature change effect (31°C) and the RoC effects (Figure 3 ; SI 3.4, 4.1 and 4.4), which is more visible under Ab and Gf treatment even when taking exposure time or stasis phase time into account (Figure 2 ; SI 3.4 and 4). The diversity of RoC effect in fungal isolates and related trait variability

The fungal responses to temperature increases and RoC of different isolates could be grouped into four clusters, explaining most of the fungal response ratio variation (86.2%). Cluster 0 is composed of 8 strains with no effect of temperature or RoC. Cluster t-r includes 11 strains with reduced response to our temperature stress treatments in general (i.e. small differences to the control) and heterogeneous responses to RoC, but in general in this cluster Gs and control are same and Ab and Gf are same (Figure 3 ; SI 4.2 and 4.4). In cluster T-r (3 strains) fungi have a strong negative response to temperature (Figure 3 ; SI 4.2 and 4.4) but very small to no effect of RoC treatment compared to the temperature effect (i.e. the effect sizes Gf and Gs to Ab are smaller or very close to the value of their respective standard error, but it is the opposite for effect size of Gf and Gs compare to control, cf. SI 4.3 4.4). In cluster T-R (4 strains), strains have strong responses to both temperature and RoC [The slower the RoC, the closer to the control (Figure 3 ; SI 4.2 and 4.4)]. Cluster t-r , T-r and T-R together represent the majority of the strains and are driving the overall RoC effect we observed at the scale of the whole fungal set (Figure 2).

Two sets of fungal morphological and physiological traits were correlated with the parameters distinguishing the four clusters (the event-based RoC model2′ parameters): the thermal limits and traits related to mycelial architecture (Figure 4). Fungi in cluster 2, for which there was little to no response to the RoC treatments, had higher thermal limits and lower biomass density. Fungi in clusters 3 and 4, which had the biggest responses to the temperature treatments (and RoC in cluster 4) had lower thermal limits, higher biomass density and less mycelial complexity (i.e. fractal dimension and lacunarity) (Figure 4).

4.3.2 *Experiment 2: RoC effects on fungal growth at strong heat stress and on thermal growth limits*

For 10 fungal strains (with a thermal limit at or above 35°C), we investigated if slower RoC treatments would allow for a higher upper thermal limit in the strong heat stress treatment. We did not find evidence for any change in thermal limits: the thermal limits of each fungal strain was identical across treatments and controls. For the strains that did grow (i.e. those with thermal limits above 36°C, n = 5/29) we observed similar effects of RoC treatments as in experiment 1, i.e. buffering effect of Gs in most strains (SI 5).

4.3.3 *Experiment 3: RoC effects on competitive abilities*

In experiment 3, we tested seven isolates with strong, weak and intermediate competitive ability. There were differences in the competitive rankings between treatments (Figure 5 ; SI - 6.1). First, we found strong evidence for differences between treatment groups (P = 0.0001). Based on the results of the chi-square test, the competitive outcomes in the control group were the least likely to come from a random distribution (i.e. frequencies of competitive outcome in control are the least likely to come from a random distribution that would include all treatment: the control treatment has the strongest statistical difference to the other condition) and they were characterized by relatively more clear wins/losses than intermediate wins/losses and a low frequency of detected ties. On the other hand, competitive outcomes in the Gs treatment were the most likely to come from a random distribution (i.e. Gs is the closest to a mean distribution of competition outcome of the treatment) and was characterized by relatively more intermediate wins/losses and ties. Then we tested if there were differences driven by fungi with differing competitive abilities: we compared extreme competitors (strong and weak, n = 3) and intermediate competitors (n = 4). We found no evidence for differences in competitive outcomes in interactions involving extreme competitors (p= 0.517) while we did find evidence for differences in interactions involving intermediate competitors (p= 0.009). Interestingly we observed a difference in distance inhibition, particularly for two fungal strains (Figure 5 b, SI- 6.2) in the RoC treatments: there was no distance inhibition in the control, strong distance inhibition in the Ab treatment, and intermediate inhibition in the Gf and Gs treatments.

4.4 DISCUSSION

The series of experiments that we conducted show that temperature RoC influences fungal responses at both, the individual and community levels. Our first hypothesis was that slower temperature RoC reduces the negative impact of temperature stress on fungal growth compared to faster RoCs. In support of this hypothesis, we found that our slowest RoC (Gs) buffered against temperature-induced negative effects on fungal growth at 31°C, and we further observed the same buffering effect at 36°C for the 5 fungi that were able to grow at this temperature. Temperature RoC has been reported to influence the response to warming in terms of the behavior in amoebae (Mast, n.d.), fish (Wells and Ledingham, 1940) and plants (Böhning and Lusanandana, 1952); reviewed by Pinek et al., 2020. We here show the importance of RoC for filamentous fungi, key soil organisms, in their response to heat stress.

Although RoC affects fungal growth under elevated temperature, it may be less important for plastic adaptation of thermal limits. Our hypothesis that RoC shifts the thermal limit was not verified by our experiment: we did not observe increased thermal limits for any of the 10 fungal strains with thermal limits at 35°C or above. It is possible that for fungi the thermal limit is a hard threshold, whereas the thermal effect on growth is a more continuous effect. Upper thermal limits are generally less flexible than other temperature related traits: the evolution of thermal limits is highly constrained and evolutionary models point in the direction of a universal biological limitation of higher thermal limitations of life (Bennett et al., 2021). Our results indicate that when determining thermal limits for fungi the RoC may be irrelevant. This finding is in contradiction with Beitinger and Bennett and Hoffmann, Chown, and Clusella-Trullas (2013); both studies have documented thermal limits being changed by the RoC in fish and insects, respectively. A deeper investigation on how thermal limits across groups are or are not responsive to RoC could reveal underlying evolutionary constraints or larger trade-offs.

The diversity of responses to RoC of temperature in our set of fungi could be divided into four clusters, each associated with an archetypal response to temperature and RoC: strong effect of temperature but not of RoC (cluster T-r), no effect of temperature or RoC (cluster 0), strong effects of both (cluster T-R) and medium/weak effect of both (cluster t-r). We investigated the correlation between temperature RoC responses and a set of 8 morphological and physiological fungal traits previously recorded for our set of fungi (Lehmann et al., 2020; Zheng et al., 2020). We found that the diversity of RoC temperature responses across species is correlated to thermal limits of the species but in a non-uniform pattern (Figure 4). That is, RoC effects are stronger among species whose upper thermal limit is closer to the target temperature in our RoC treatment but does not affect the thermal limits itself (Figure 4). This confirms our hypothesis in (Pinek et al.) that the temporal aspect of the performance curve should be developed, in particular to the RoC dimension. A uniform relation to a driver's temporal changes can clearly not be expected along the gradient of temperature change magnitude as we show here and others have also shown (Fey et al., 2021; Kronholm and Ketola, 2018). Performance curves need to be corrected to systematically take into account the temporality of drivers and plastic responses (Fey et al., 2021).

We also found a correlation between the cluster of strains with the strongest response to RoC (cluster T-R) and strongest response to our temperature change (cluster T-r and T-R) with structural traits of the mycelium. The strains in these clusters have a dense (biomass density) and complex mycelium (fractal dimension and lacunarity, Plotnick et al., 1996). This could be related to differences in information transmission in more dense/complex mycelial networks (i.e. because they have a complex mycelia, they have better information transmission and this makes them more responsive to RoC). The interaction between spatiality (i.e. spatial characteristics) and temporality is crucial to understand how fungi react to environmental changes that are not just one event, because fungi are not only microbes but also organisms with a more macroscopic manifestation (Wesener and Tietjen, 2019). Thus the speed of the information transfer can not be assumed to be immediate and the pattern found in our PCA analysis could indicate that this plays a role in fungal responses to temperature, or perhaps generally to environmental change.

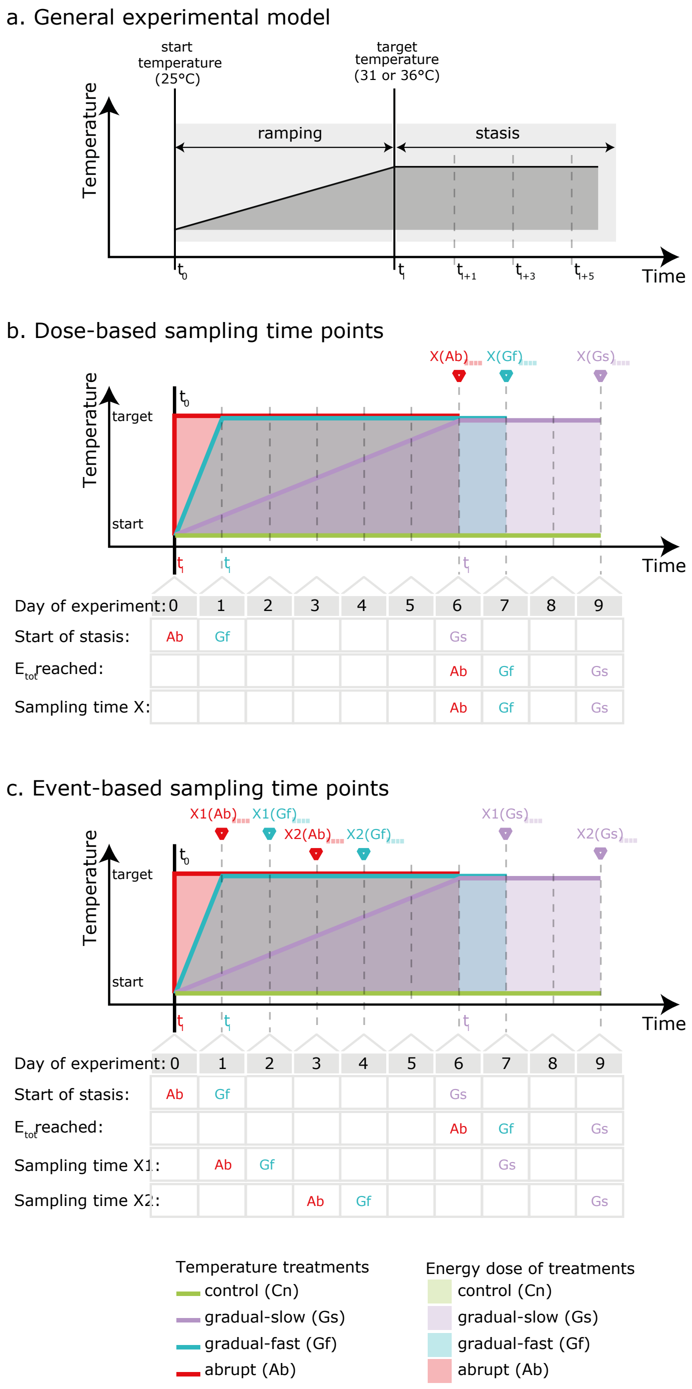
Temperature has been shown to play a role in interspecific interactions such as predation (El-Danasoury et al., 2017), mutualism (Zhou et al., 2017) and symbiosis (Higashi, Barton, and Oliver, 2020). Hoffacker et al. (2018) also showed that temperature has an effect on competitive abilities in salamanders and, among filamentous fungi, temperature has been shown to be important for competition in fungi and even can reverse competitive outcomes (Crowther, Boddy, and Jones, 2012). We build on such results here, and show for the first time that not only the magnitude of temperature, but also the rate of temperature change can influence competitive interactions. We found that RoC (when temperature was changed from 25 to 31°C) modified competitive outcomes, particularly for intermediate competitors. Any increased temperature treatment (regardless of RoC) also triggered distance inhibition mechanisms for two species (i.e. interference competition, see SI - 6′ for an example) that were not detectable under control/ ambient conditions. This indicates that defense compounds (e.g. volatiles) were produced only under elevated temperature, although it appeared as if under Gf and Gs the distance inhibition is differently triggered (less inhibition interaction than in Ab). Overall, our findings indicate clearly that not only the magnitude, but also the rate of temperature change affects interspecies interactions.

The experimental design (i.e. placing the fungal plugs adjacent to one another) mimicked what would occur if the fungal strains were interacting during temperature change. The most clear win/loss outcomes (75%, Figure 5) occurred in the Gf treatment, whereas in the Gs treatment there were more intermediate win/loss situations and ties. Our slowest RoC (Gs) engendered a situation where more strains could maintain sufficient surface occupation against their competitor than under other RoC scenarios. This has implications for the relative strength of inter- vs. intra-specific competition in a community setting. Under slower RoC regimes, more 'players' are maintained in the game (reduced levels of competitive exclusion compared to abrupt regimes), thus interspecific competition strength would be higher. However, under faster RoC scenarios, competitive exclusion shortly after the stress event is expected, which would reduce diversity and likely increase the degree of intraspecific competition in the remaining species. Thus, under faster RoC scenarios it may be that intraspecific diversity becomes key to predict ecosystem outcomes, and in particular cryptic plasticity (i.e. latent, not visible plasticity in "normal" conditions of selection) that is known to be revealed by high stress situations (Levis and Pfennig, 2019). Likely, these temperature RoC effects on intra- and interspecific competition influence biodiversity and macroevolutionary trajectories (Fortelius et al., 2015). A similar phenomenon has been observed for plants, where environmental variability in general can buffer competitive abilities, leading to high competition strength and the persistence of higher biodiversity levels (Chesson and Yang, 2019; Toljander et al., 2006). Temperature RoC could also influence the functioning of soil communities: it has been shown for soil fungi that soil aggregation can be modified by increased temperatures (20° to 25°C) and that the rate of change of temperature can also increase or decrease this function (Liang et al., 2019).

We observed a broader diversity of responses under faster RoCs (Ab and Gf) compared to slower ones (Gs) for both the individual level (growth response ratios) and competition outcomes. Fungal responses under faster RoCs are less predictable and deviate stronger from control conditions. These variability patterns at individual and interaction levels could have implications at higher ecological levels. Changes in community structure resulting from the response of individual fungal strains to temperature change could alter the magnitude of the response of other fungal strains in the community (e.g. because of changes in facilitative or competitive interactions). This could have the potential of pushing the system out of equilibrium and to a tipping point situation by changing the balance of the network of interactions (Synodinos et al., 2021).

With our set of three large experiments, we demonstrated that RoC can modulate both the individual response to temperature and the outcome of competitive interactions under temperature change. Our results, thus, highlight the limitation in current predictions of biodiversity responses to climate change that are largely based upon experimental data based on studies in which only abrupt treatments have been applied, and which therefore do not take rate of change into account. This has important implications for biotic responses to global change factors, and may indicate that our current state of knowledge does not accurately represent potential outcomes to increased temperature stress.

4.5 FIGURES



a. General experimental model

b. Dose-based sampling time points

Day of experiment:	0	1	2	3	4	5	6	7	8	9
Start of stasis:	Ab	Gf					Gs			
E_{tot} reached:							Ab	Gf		Gs
Sampling time X:							Ab	Gf		Gs

c. Event-based sampling time points

Day of experiment:	0	1	2	3	4	5	6	7	8	9
Start of stasis:	Ab	Gf					Gs			
E_{tot} reached:							Ab	Gf		Gs
Sampling time X1:		Ab	Gf					Gs		
Sampling time X2:				Ab	Gf					Gs

Figure 1 - Concepts and terminology of the experimental design.
Panel a displays the temporal structure of our temperature RoC treatment. The treatment starts at a temperature of 25°C which is then increased by x °C (+6°C to reach 31°C (experiment 1 and 3) or +11°C to reach 36°C (experiment 2)) during the ramping phase. This defines the RoC as x°C/duration of the ramping time. Then follows a period with a stable temperature (31° or 36°), the stasis phase. The temperature dose is the total amount of thermal energy invested in the system over time, shown in dark grey shading in panel A. In order to compare the RoC effect, we investigated two approaches: The dose-based approach (panel b) compares the fungal responses to the different RoC treatments at equivalent energy doses. Depending on the RoC treatment (control, Ab, Gf, Gs) different time points throughout the stasis phase were compared (i.e. Ab = day 6 is compared with Gf = day 7 and Gs and control = day 9).The event-based comparison is a kinetic approach (panel c). Here, specific fixed time points (start of stasis phase +1, +3) are chosen after the system has reached the target temperature (31° or 36°) independent of total energy doses. Since these two approaches compare different time points of measurements (panel d), each treatment measurement is compared to the control at the same time point using log response ratios as effect sizes for all analyses (for more information see the statistics section).

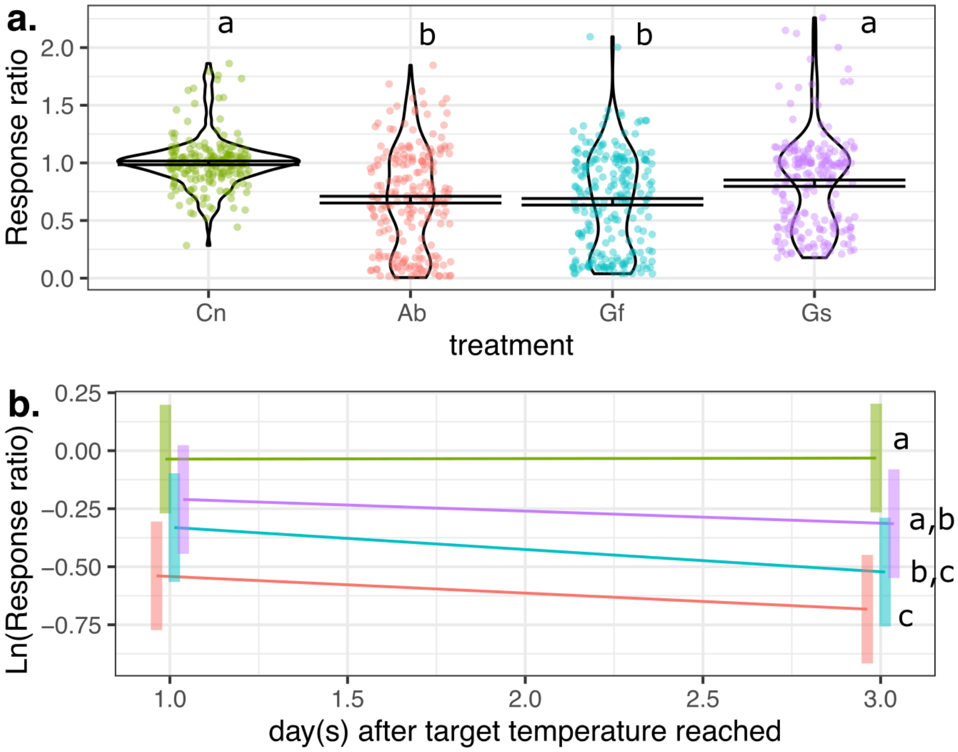


Figure 2. Experiment 1 (25°C to 31°C). Fungal growth responses to different temperature rate of change (RoC). RoC treatments are color-coded with abrupt (Ab) in red, gradual-fast (Gf) in blue and gradual-slow (Gs) in purple. The color code for the treatments is the same in (a) and (b). Control (Cn) conditions are in green. Letters indicate statistically different groups ($P<0.05$). **(a) Dose based:** response ratio distributions for the RoC scenarios following the dose-based analysis. All endpoints for each treatment and for all fungi are included here. n(Cn)=204, n(Ab)=221 n(Gf)=224, n(Gs)=219. **(b) Event based:** The vertical bars show 95% confidence intervals of ln transformed fungal surface occupation ratios for each treatment at one day and three days after the target temperature was reached; confidence intervals are based on the estimated marginal means and the central value is the estimated marginal mean; lines connecting the bars show the direction of change over time. n(Cn)=463, n(Ab)=465, n(Gf)=463, n(Gs)=440

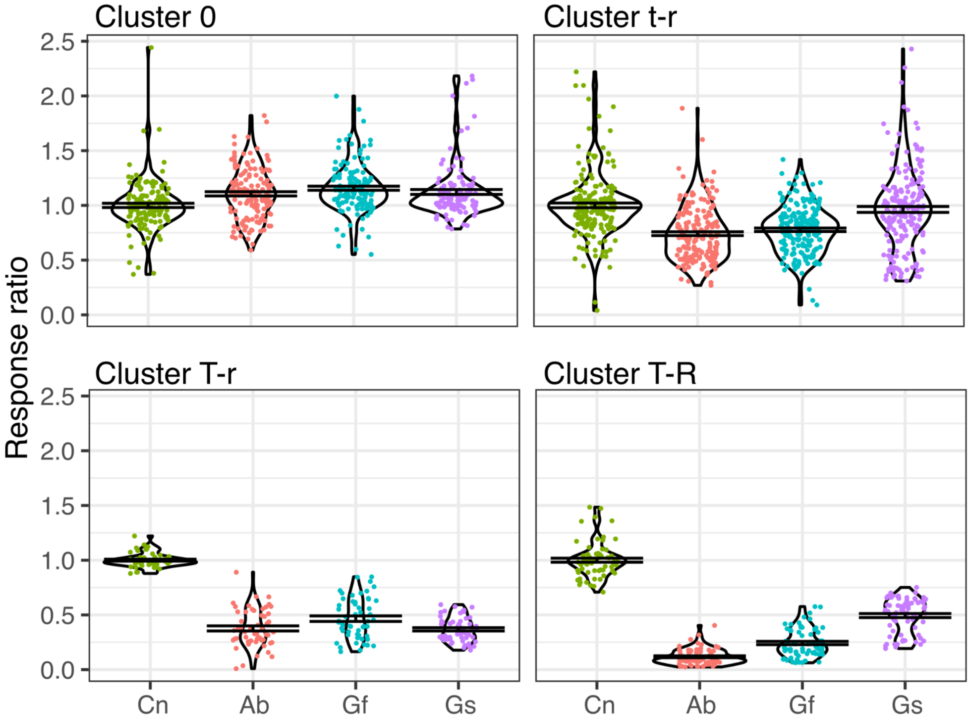


Figure 3. Fungal response ratio distributions in the different clusters for RoC treatments (experiment 1)**.** Violin plots show the distributions of response ratios across strain for treatment and in each cluster. Cluster O consists of 8 strains, Cluster t-r of 11 strains, cluster T-r of 3 strains and Cluster of T-R 4 strains. The time point comparaison used is event-based and we are showing the +3 days data (n(Cn +3 days)=229, n(Ab +3 days)=234, n(Gf +3 days)=230, n(Gs +3 days)=219). The horizontal lines are the 95% CIs for the mean response ratios. The clusters are different behavior patterns exhibited by the tested fungal strains under the RoC treatments. They were established based on parameters of model 2' which is an event-based approach model including both +1 day and +3 days data points. See SI 4.4 for strain specific responses to the trans-treatment pattern.

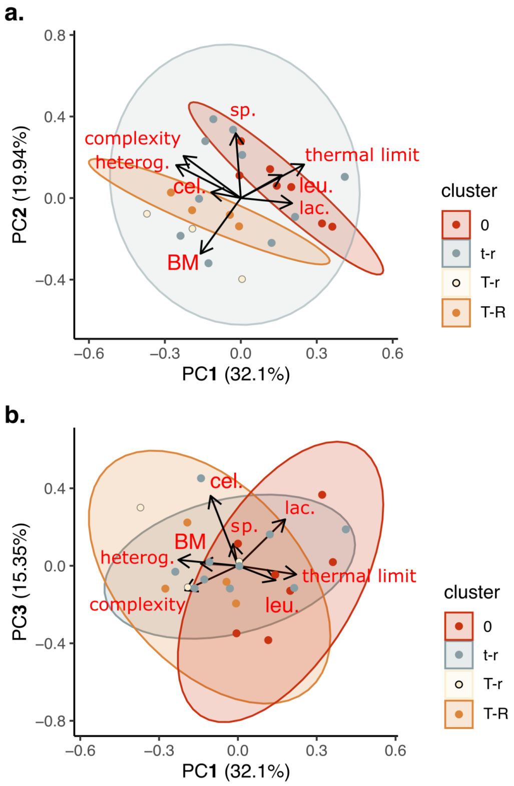
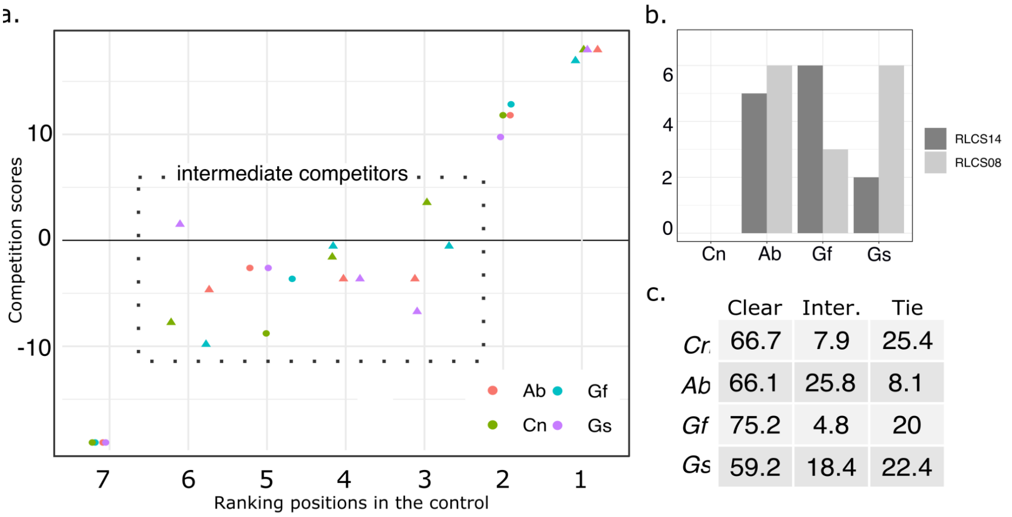


Figure 4. Relationship between morphological and physiological traits and fungal responses to RoC treatments (Model 2' parameters outcomes and Clusters of global patterns based on those parameters).
(a) Projection of the ordinated 4 behavior clusters onto 8 trait variables representing enzymatic, mycelium architecture and thermal limits of the investigated fungal strains. The PC axis 1 and 2 explain approximately 32 and 20% of variance, respectively **(b)** Similar projection but for PC axis 1 and 3, explaining 32 and 15% of the variance. sp.: spore size, BM: biomasse density, thermal limits: upper thermal limits, lac: laccase (lignin degradation), cel. : cellobiohydrolase (cellulose degradation), leu.: leucine aminopeptidase.



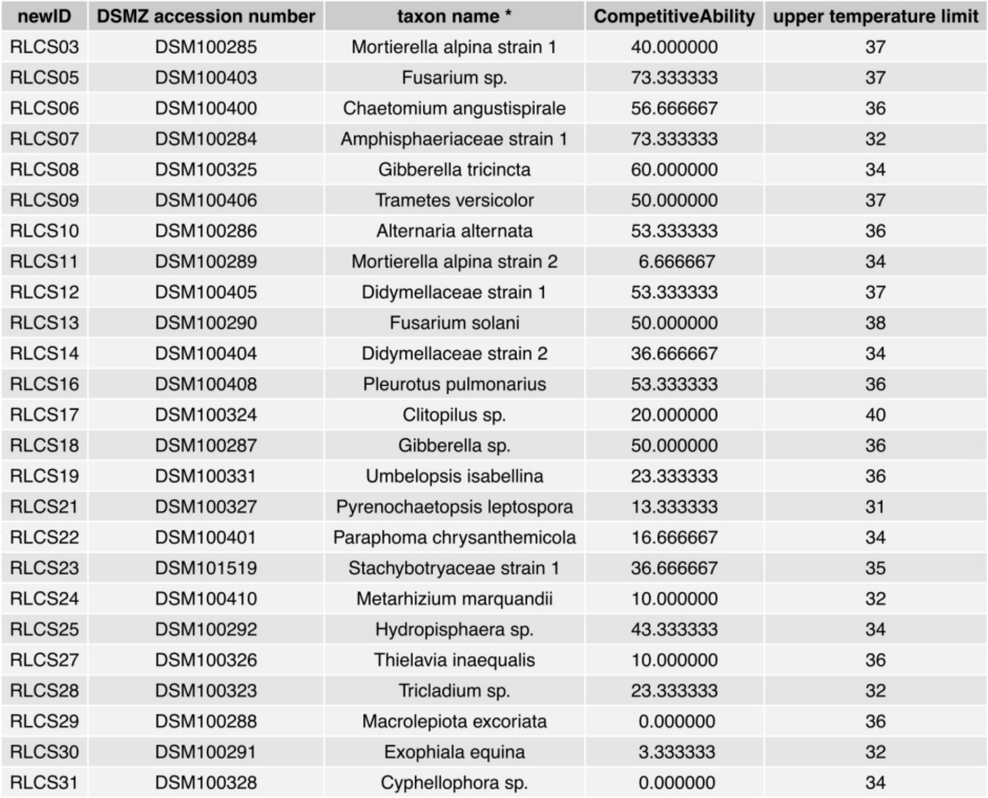
	Clear	Inter.	Tie
Cr	66.7	7.9	25.4
Ab	66.1	25.8	8.1
Gf	75.2	4.8	20
Gs	59.2	18.4	22.4

Figure 5 Experiment 3: competition outcome under temperature change for 3 different RoC.

(a) (of) The competition score is an overall estimation of the competitive abilities of the strains in this particular fungal subset consisting of seven strains, with 7 indicating the worst and 1 the best competitor. The y-axis shows the competition scores for each strain under each treatment. The x-axis shows the ranking position of each of the seven strains in the control treatment (based on their competition score in those conditions). Strains in the 7th and the 2nd and first positions are extreme competitors. In the complete set of the 29 fungi, extreme competitors are characterized by their strong loser or winner ranking in control conditions. The 2nd and first-ranked strains are winning against most other fungi in the 29 fungi set. The 7th ranked strain loses against most of the other fungal strains. competition scores by RoC treatment for the 7 strains; For the strongest (1st and 2nd-ranked) and the weakest competitor (ranked 7th), the temporal nature of treatments made little difference, but for the intermediate ranks, there were pronounced effects of temporal nature of treatments. **(b)** number of distance inhibition cases per treatment for the two fungi exhibiting this ability; distance inhibition only appeared in temperature stress treatments **(c)** percentages of competition outcomes in each treatment. Clear: clear competition outcome (“W” or “L” in SI 6.1), Inter. : intermediate competition outcome (“W1/2” or “L1/2 in SI 6.1).

4.6 SUPPLEMENTAL INFORMATION

SI METHODS



newID	DSMZ accession number	taxon name *	CompetitiveAbility	upper temperature limit
RLCS03	DSM100285	Mortierella alpina strain 1	40.000000	37
RLCS05	DSM100403	Fusarium sp.	73.333333	37
RLCS06	DSM100400	Chaetomium angustispirale	56.666667	36
RLCS07	DSM100284	Amphisphaeriaceae strain 1	73.333333	32
RLCS08	DSM100325	Gibberella tricincta	60.000000	34
RLCS09	DSM100406	Trametes versicolor	50.000000	37
RLCS10	DSM100286	Alternaria alternata	53.333333	36
RLCS11	DSM100289	Mortierella alpina strain 2	6.666667	34
RLCS12	DSM100405	Didymellaceae strain 1	53.333333	37
RLCS13	DSM100290	Fusarium solani	50.000000	38
RLCS14	DSM100404	Didymellaceae strain 2	36.666667	34
RLCS16	DSM100408	Pleurotus pulmonarius	53.333333	36
RLCS17	DSM100324	Clitopilus sp.	20.000000	40
RLCS18	DSM100287	Gibberella sp.	50.000000	36
RLCS19	DSM100331	Umbelopsis isabellina	23.333333	36
RLCS21	DSM100327	Pyrenochaetopsis leptospora	13.333333	31
RLCS22	DSM100401	Paraphoma chrysanthemicola	16.666667	34
RLCS23	DSM101519	Stachybotryaceae strain 1	36.666667	35
RLCS24	DSM100410	Metarhizium marquandii	10.000000	32
RLCS25	DSM100292	Hydropisphaera sp.	43.333333	34
RLCS27	DSM100326	Thielavia inaequalis	10.000000	36
RLCS28	DSM100323	Tricladium sp.	23.333333	32
RLCS29	DSM100288	Macrolepiota excoriata	0.000000	36
RLCS30	DSM100291	Exophiala equina	3.333333	32
RLCS31	DSM100328	Cyphellophora sp.	0.000000	34

Table SI -1.1 Overview of our fungal strains used in the three experiments. We present phylum, taxon name and “Deutsche Sammlung” von Mikroorganismen und Zellkulturen (German Collection of Microorganisms and Cell Cultures GmbH, DSMZ) accession numbers of the 29 fungal isolates. Competitive Ability as originally measured by Anika Lehman (personal communication) and thermal limits (°C) are given. For more details on the preliminary experiment generating the thermal limit data, please see section SI-1.2.

SI -1.2 Protocol of the preliminary experiment.

The upper limit was determined for the same strains with a gradient approach (not incubator replication) from 30°C to 38°C in 1° interval ; each +1°C interval was replicated 5 times (e.g. 5 plates at 35°C for every strain). When there was no growth seen over the course of 7 days then this was considered the thermal limit.

SI - 1.3 Selection of target temperatures

In order to study the effect of temperature RoC on our set of fungal strains, we first determined their thermal limits by growing each strain at temperatures ranging from 30°C to 40°C with 1°C increment and 5 replicates per strain. Thermal limits were unanimous among our 5 replicates (SI -1 for thermal limits). Based on these data, we chose 31°C (experiment 1 and 3; intermediate heat stress) and 36°C (experiment 2; strong heat stress) as target temperatures. At 31°, all strains grew but their growth was impaired. At 36°, 22 out of 29 strains did not grow anymore; they reached or exceeded their thermal limit. For the temperature controls we chose 25°C, the standard culture temperature for our fungal isolates (assumed to be near maximum performance temperature Dix and Webster, 1995).

SI - 1.4 Some depth in what the dose of temperature means, an example.

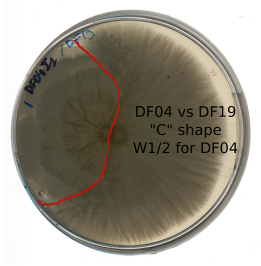
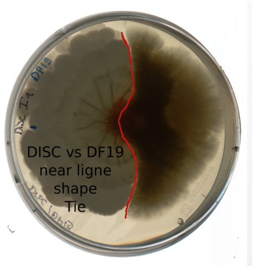
In the abrupt treatment of experiment 1, temperature rises almost immediately to the target temperature by 6°C (from 25°C to 31°C). Once reached, the target temperature remains constant for the following 6 days (which returns a total energy of 6°C x 6 days = 36 °C day). In the Gs treatment, the 6°C temperature increase occurred over 6 days followed by 3 days of stasis phase (+1°C x 6d + 6°C x 3d = 36 °C days) (Figure 1).

SI -1.5 Program description

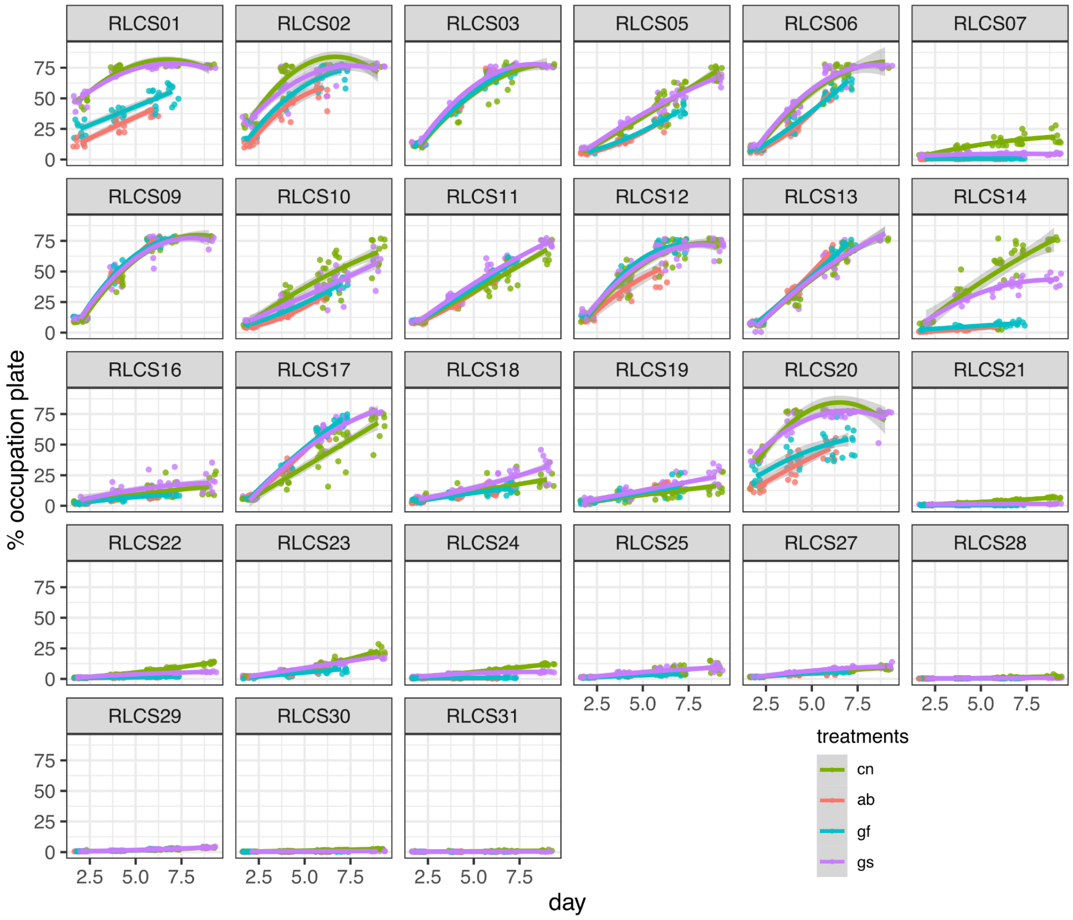
We cropped the scanned images in ImageJ (Schneider et al. 2012) so that every prepared picture had one Petri dish centered in the middle of the image. The process of identifying the fungal colony pixels in the prepared pictures worked as follows: For each picture, the program searched for the contour of the Petri dish by inserting a circle on the position of the Petri dish and searching for the dish's border inside this circle. The Petri dish's border is of the same color range as the fungus so they could be confused. For this reason, we implemented an additional step to remove the border when possible by using a smaller circle (80% of the petri dish area). For this step, we used only images of fungal colonies that did not overlap with the border of the Petri dish; thus we excluded images from our analysis, showing large colonies filling out the whole Petri dish. We also implemented a “cleaning” step to identify very small colonies of potential contaminations and air bubbles enclosed in the agar which would interfere with the image analysis. For this, we added another circle which cropped the image to exclude the affected pixels. Finally, the program distinguishes the pixels associated with the actual fungal colony by color. The remaining of the Petri dish pixels are colored in blue. The coverage of the fungus on the Petri dish is analyzed and reported as pixels. The program is available on GitHub (GitHub link).

Our image analysis program was successful in accurately extracting colony surface area values, differing from hand-measured values (the traditional method) by 0- 6%. The program values varied more greatly from hand-measured surface area values when the colony occupied more than 80% of the plate surface, thus these images were excluded from the analysis. In experiment 1, it was 130/4398 images, but most of those images belonged to the three Fungal strains we excluded anyway because we had noticed they had reached plate border before the end of the treatments in the control (72/130). Among the other pictures that were excluded (58/130) most of them correspond to day seven (17/58) and day nine (34/58) and are mostly from control (30/58) and gradual slow (20/58). DF24 (24/58) and C13 (14/58) represent the majority (38/58), most of the lost pictures are in the control with a maximum of lost pictures of five images on day nine for both fungus. This could have led to an underestimation of the size of control plate, an overestimation of the response ratio and thus would decrease the chance of seeing an effect of RoC of temperature for those two strains. For these reasons the loss of those images didn't impact the value of our results when it showed RoC effect but it might have masked it in some cases.

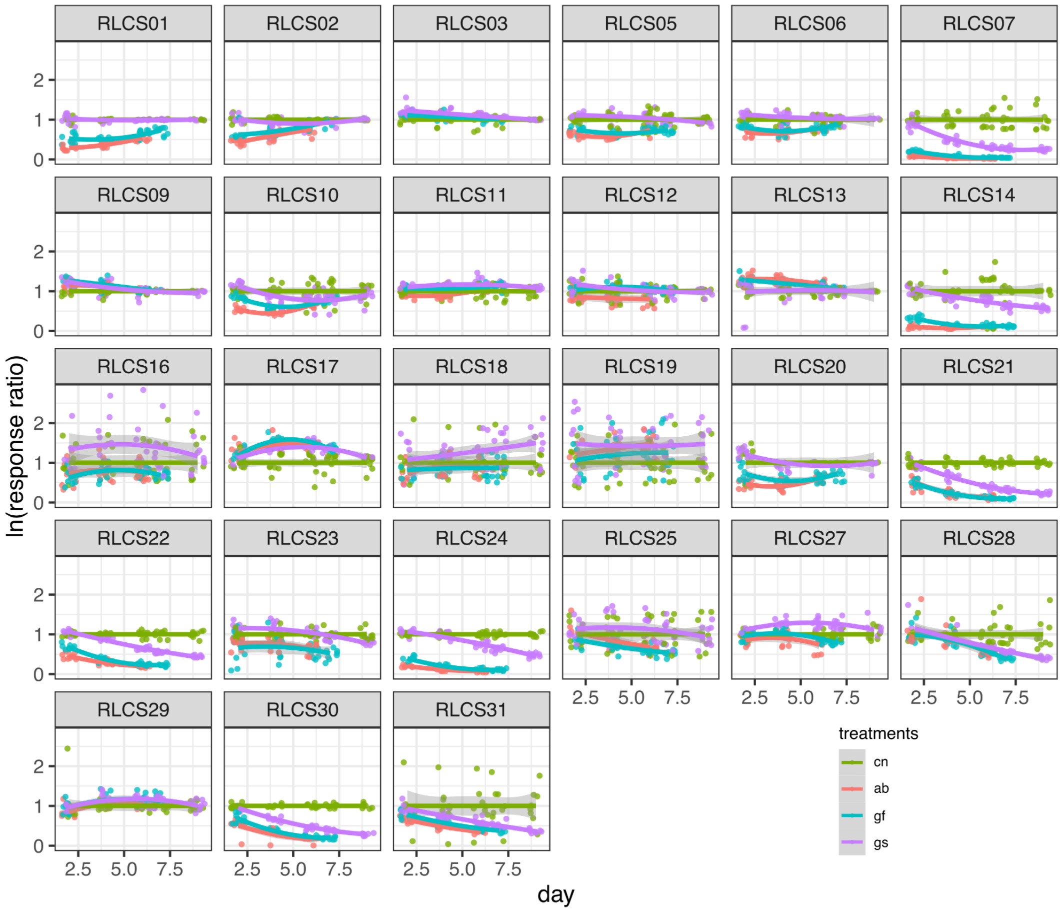
SI1.6 Criteria for categorizing fungal competitive outcomes

Competitive outcome	**Relative surface area criterion**	**Line of interaction criteria**	**Example**
Clear win/loss	the dominated colony is (eventually) completely covered by the winning colony	Interaction line forming a circular shape around the dominated colony	
Intermediate win/loss	One fungal colony partially overgrew the other	Interaction line forms a "C" starting to close on itself or a "V"	
Tie	(Near) equal surface occupation of both colonies	Straight or nearly straight line between colonies	

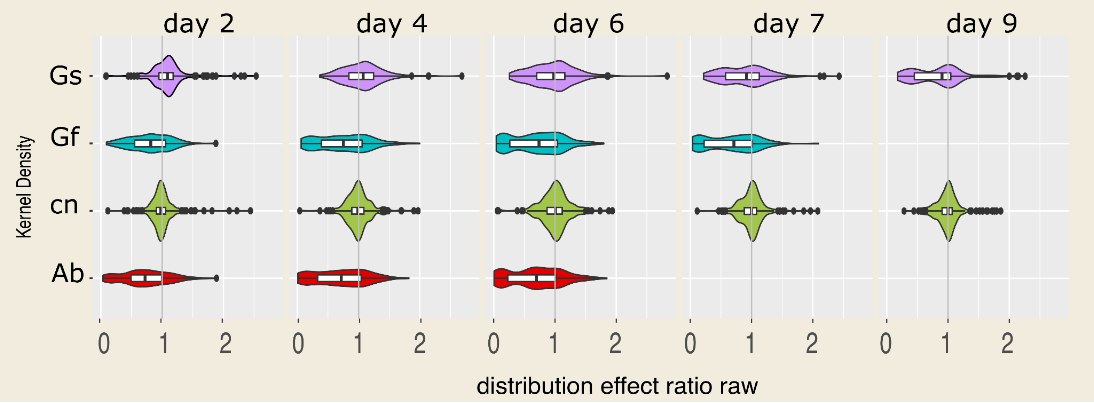
SI RESULT: EXPERIMENT 1



SI -2.1 Experiment 1 (from 25°C to 31°C): raw data . X axis is time in days and Y axis is in the upper panel, the surface occupancies of the fungus in % of the petridish (raw data). At 31°C all fungi were growing, except A in contradiction to our pre-experimental data (Table S1.1). At 31°C, we did not reach the stationary phase of the growth curves for most of the fungi but stayed in the active growth phase. For all strains being in the active growth phase and hence in a comparable stage, we could do meaningful comparisons between control and in our RoC treatments. This is essential for the usage of our response ratio approach. Those conditions were not met for DF25, DF56, DF58 and therefore, we excluded these strains from the analysis. It is noteworthy that data for the Gs treatment, in most cases, occupied an intermediate position between the temperature control on the one end and Ab and Gf temperature treatments on the other end, already indicating that RoC is relevant .



SI -2.2 Experiment 1 (from 25°C to 31°C): response ratios. X axis is time in days and Y axis is the response ratio in fraction of the control surface occupancies at the same date (data used in the analysis).



SI -3.1 Experiment 1: over time response ratio distribution.

RESPONSES - RATIOS	Dose Based		Event Based			
			+ One day		+ Three days	
	mean	sd	mean	sd	mean	sd
control	1	0.226	1	0.257	1	0.222
Abrupt	0.681	0.434	0.721	0.380	0.681	0.434
Gradual fast	0.663	0.423	0.798	0.325	0.694	0.421
Gradual slow	0.824	0.409	0.891	0.385	0.824	0.409

SI 3.2 - Responses ratios means and standard deviations per treatments in experiment 1

	ab	cn	gf	gs
ab	[-0.8043]	**<.0001**	0.9835	**0.0077**
cn	-0.7844	[-0.0199]	**<.0001**	0.2021
gf	-0.0538	0.7307	[-0.7506]	**0.0218**
gs	-0.4898	0.2946	-0.4360	[-0.3145]

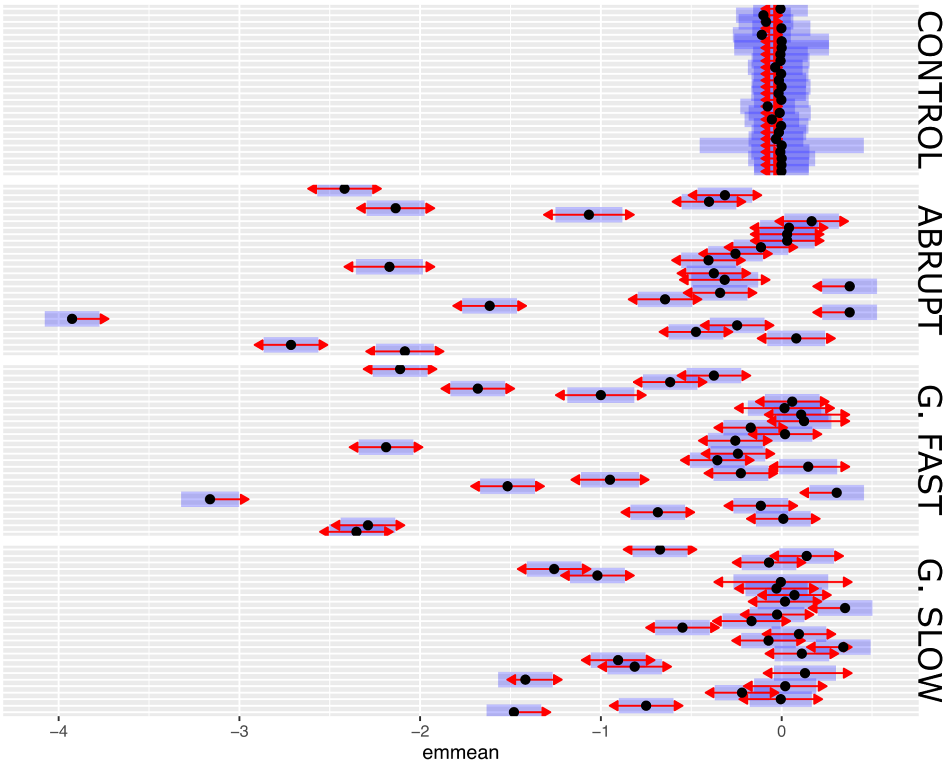
Row and column labels: treat
Upper triangle: P values adjust = “tukey”
Diagonal: [Estimates] (emmean)
Lower triangle: Comparisons (estimate) earlier vs. later

SI 3”- Dose based lmer model 1 (random effect)

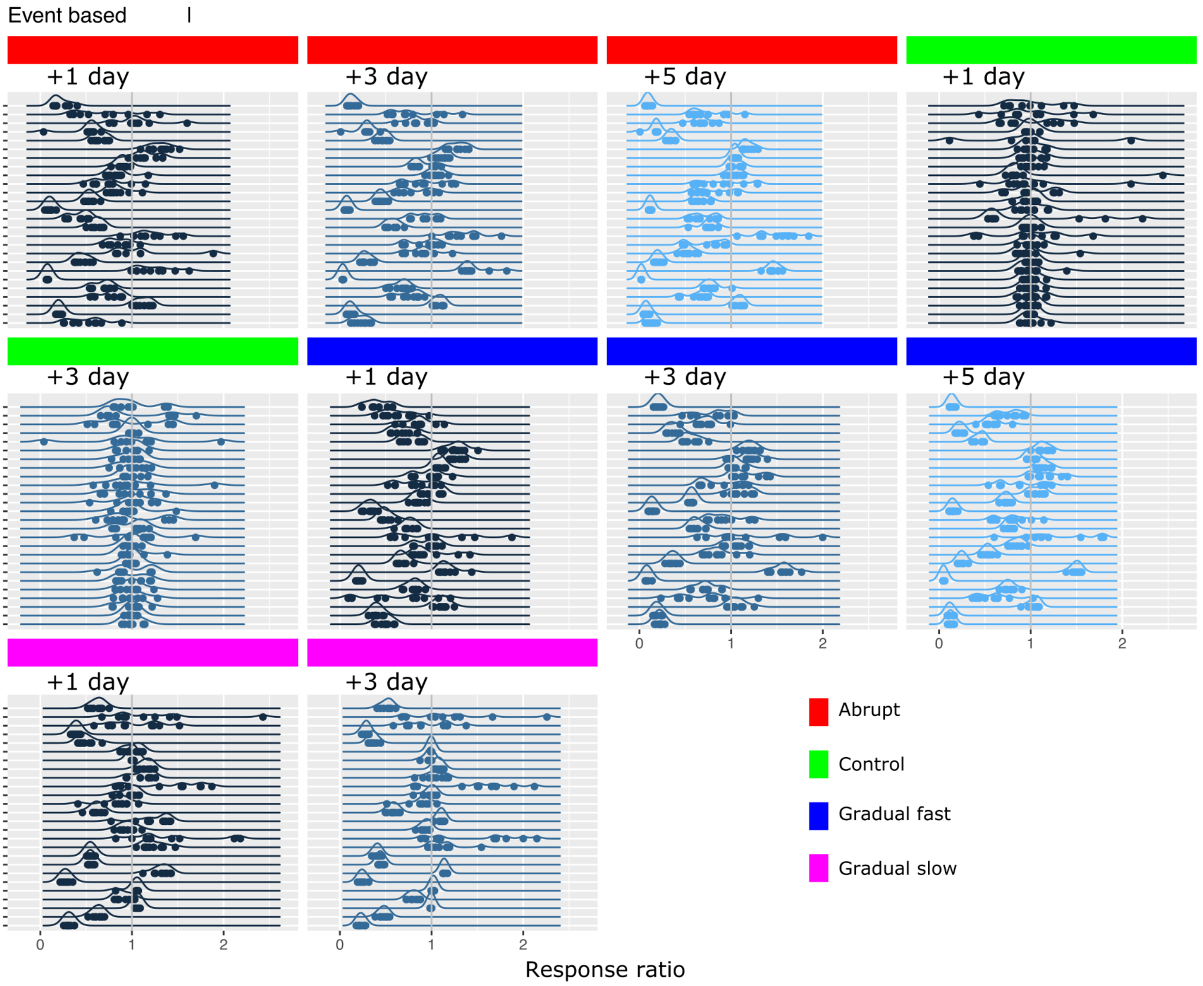
	ab	cn	gf	gs
ab	[-0.6488]	**<.0001**	0.4127	**0.0114**
cn	-0.623	[-0.0255]	**0.0011**	0.1144
gf	-0.176	0.447	[-0.4724]	0.3661
gs	-0.363	0.260	-0.187	[-0.2856]

Row and column labels: treat
Upper triangle: P values adjust = “tukey”
Diagonal: [Estimates] (emmean)
Lower triangle: Comparisons (estimate) earlier vs. later

SI 3.3 - Event based lmer model 2 (random effect)



SI- 3.4 Variability in fungal growth response (log response ratio) across different fungal strains for RoC treatments (Experiment 1, Model 2’).
Each horizontal facet presents data on a specific treatment group (cn = control, ab= abrupt, gf gradual_fast, gs = gradual_slow). Each point is a mean effect (log response ratio) of one fungal strain. The blue rectangles are confidence intervals and the red arrows are comparisons (Tukeys test); if red arrows overlap it means there is no significant difference (emmeans package).

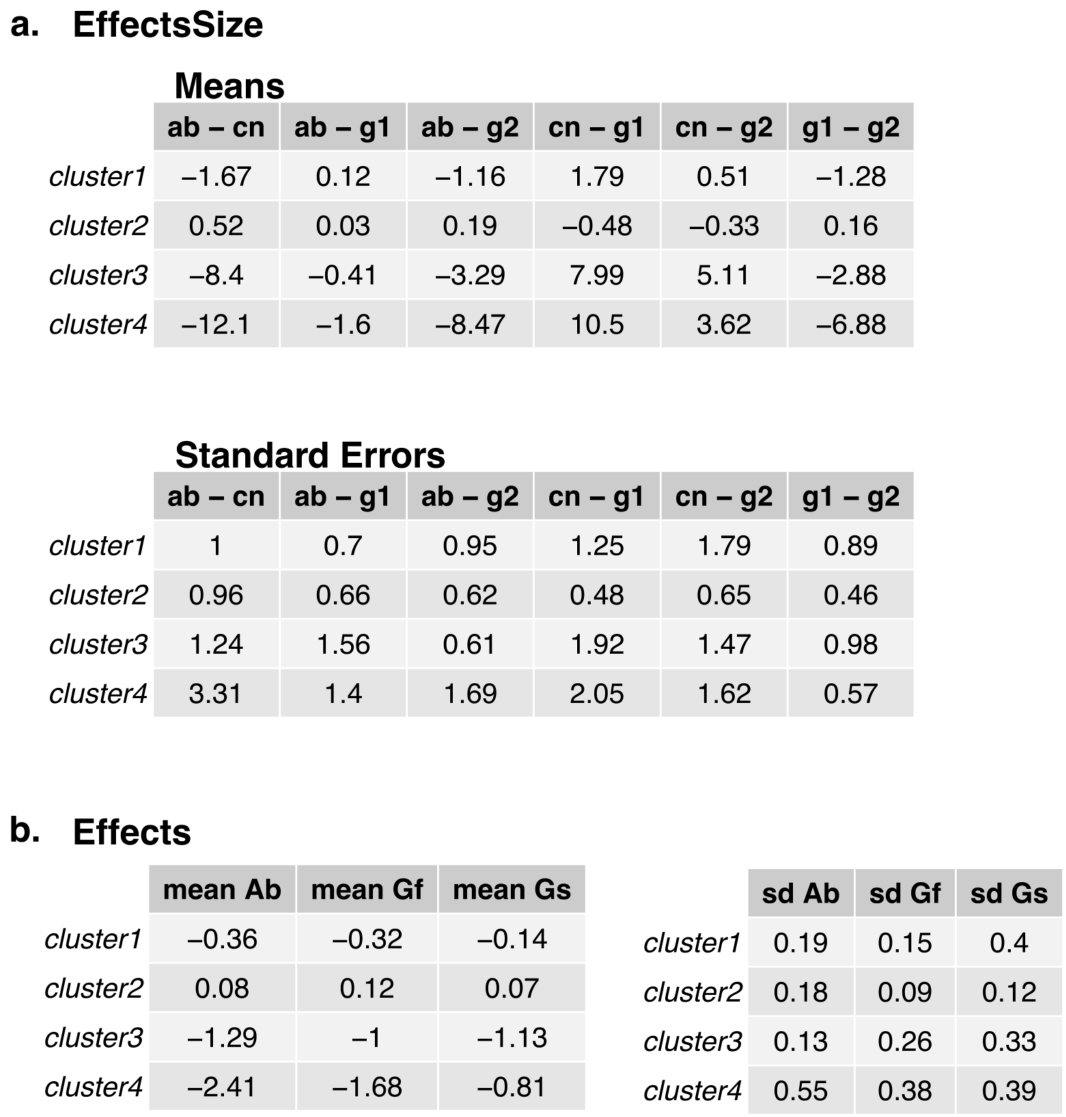


SI - 4.1 Variability in fungal growth response (response ratio) across different fungal strains for RoC treatments (event based approach, experiment 1, model 2).

In each panel, fungal strain specific data on response ratio is presented with (raw data and kernel density).Data are presented for the different RoC treatments and the day after reaching the target temperature. +5 days is not included in the final models (model 2 and model2 ’) because the data is only available for Ab and Gf.

cluster	statistique	Cn - Ab	Cn - Gf	Cn - Gs	Ab - Gf	Ab - Gs	Gf - Gs
1	**median**	**1.43**	**1.18**	**-0.07**	**0.17**	**-1.15**	**-1.46**
	minimum	0.34	0.50	-1.67	-0.64	-0.64	-2.37
	maximum	4.14	3.87	3.93	1.32	1.32	0.08
2	**median**	**-0.26**	**-0.37**	**-0.04**	**0.21**	**0.23**	**0.19**
	minimum	-1.96	-1.38	-1.81	-1.18	-0.99	-0.84
	maximum	1.09	-0.04	0.12	0.99	1.07	0.76
3	**median**	**9.01**	**7.26**	**5.44**	**-0.43**	**-3.47**	**-3.04**
	minimum	6.97	6.55	3.50	-1.97	-3.79	-3.77
	maximum	9.23	10.17	6.40	1.16	-2.61	1.83
4	**median**	**11.08**	**9.68**	**9.60**	**-1.59**	**-8.02**	**-6.87**
	minimum	9.38	9.10	2.37	-3.30	-10.84	-7.54
	maximum	16.84	3.54	6.00	0.08	-7.01	-6.22

SI 4.2- Table Size effect median and range for cluster



a. EffectsSize

Means

	ab – cn	ab – g1	ab – g2	cn – g1	cn – g2	g1 – g2
cluster1	–1.67	0.12	–1.16	1.79	0.51	–1.28
cluster2	0.52	0.03	0.19	–0.48	–0.33	0.16
cluster3	–8.4	–0.41	–3.29	7.99	5.11	–2.88
cluster4	–12.1	–1.6	–8.47	10.5	3.62	–6.88

Standard Errors

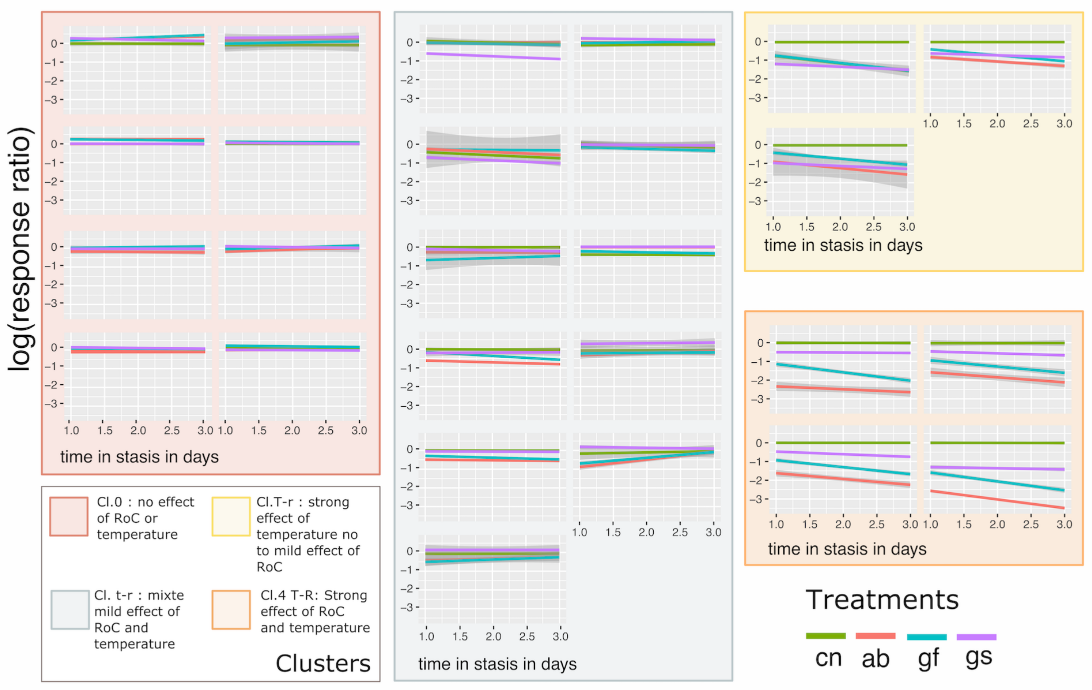
	ab – cn	ab – g1	ab – g2	cn – g1	cn – g2	g1 – g2
cluster1	1	0.7	0.95	1.25	1.79	0.89
cluster2	0.96	0.66	0.62	0.48	0.65	0.46
cluster3	1.24	1.56	0.61	1.92	1.47	0.98
cluster4	3.31	1.4	1.69	2.05	1.62	0.57

b. Effects

	mean Ab	mean Gf	mean Gs
cluster1	–0.36	–0.32	–0.14
cluster2	0.08	0.12	0.07
cluster3	–1.29	–1	–1.13
cluster4	–2.41	–1.68	–0.81

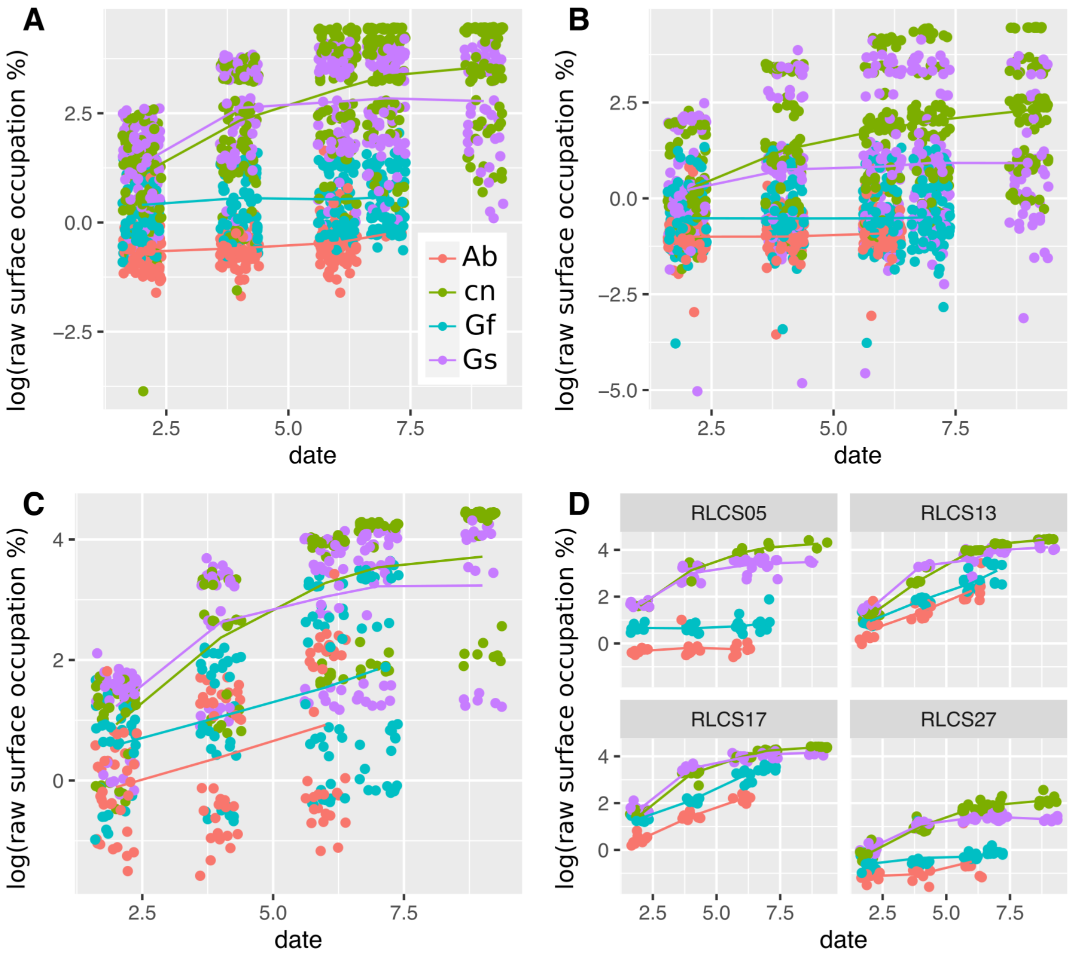
	sd Ab	sd Gf	sd Gs
cluster1	0.19	0.15	0.4
cluster2	0.18	0.09	0.12
cluster3	0.13	0.26	0.33
cluster4	0.55	0.38	0.39

SI 4.3- Table effects size & effect in cluster means and standard errors



SI - 4.4 Experiment 1 (25°C to 31°C). (a) Comparison plot of the event-based linear model (model 6) used to categorize the strains into 4 clusters. We see how much of the overall variability in “behavior” (estimate effect per treatment and effect size pairwise comparison) is explained by 4 clusters and more or less. (b) is our interpretation of the 4 “behavior” associated with our 4 clusters. (c) shows how much our 4 clusters explain the variability in the parameters extracted from the event-based linear.

SI - RESULT: EXPERIMENT2



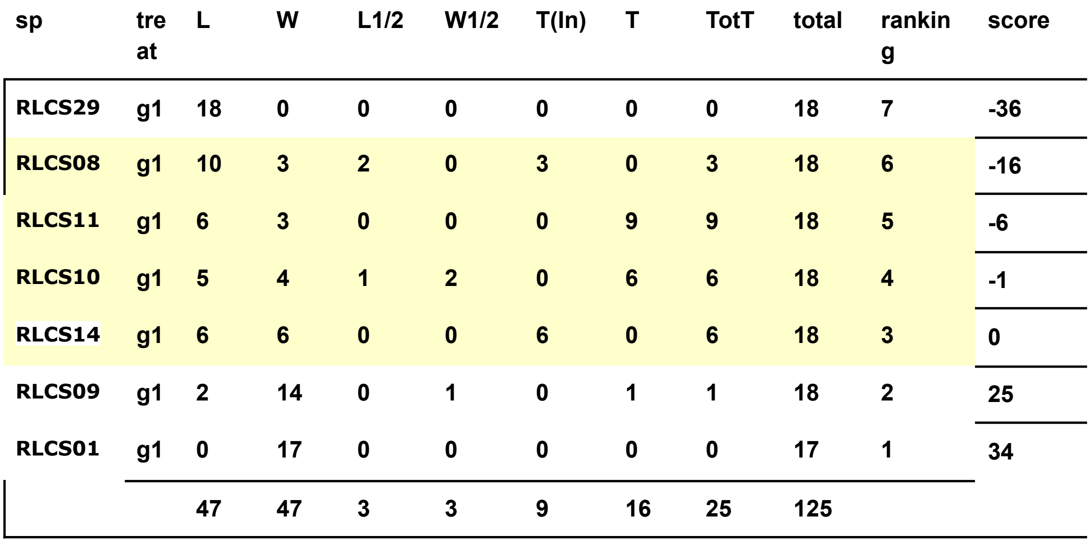
SI 5- Experiment 2 (from 25°C to 36°C): a. Fungal response (log of the percentage of the area occupied by the fungal strain) to RoC treatments over time (5 sampling dates: day 2, 4, 6, and 9). The plot shows the data for all fungi that have a thermal limit of 35°C or 36°C. Panel b presents data for fungal strains with a thermal limit below 35°C. Panel c shows data for fungi that have a thermal limit above 36°C. For these, panel d gives detailed growth curves.

SI RESULT: EXPERIMENT 3

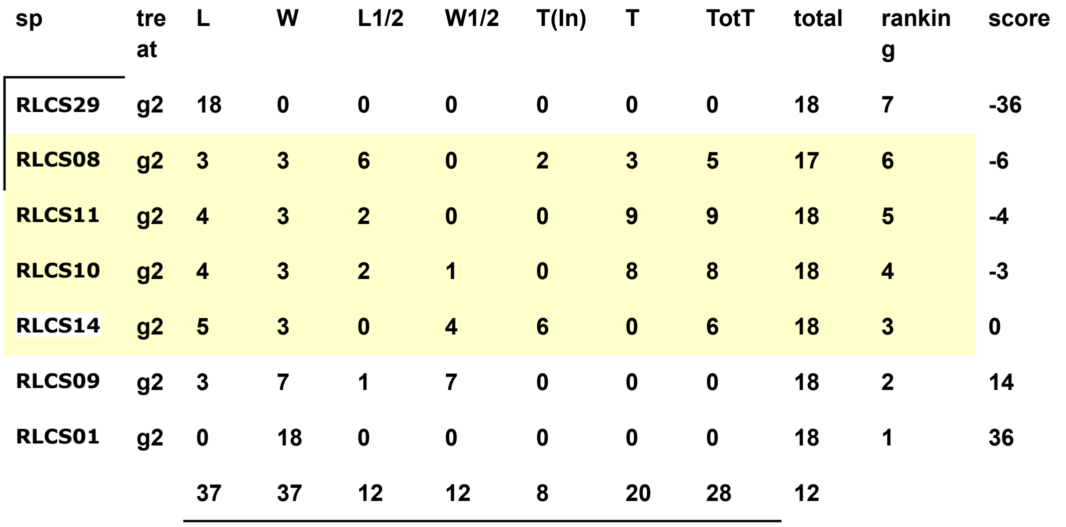
SI 6.1- Experiment 3 data on competition qualitative analysis, the classification of every interaction. In yellow are intermediate competitors.

sp	treat	L	W	L1/2	W1/2	T(In)	T	TotT	total	ranking	score
RLCS29	cn	18	0	0	0	0	0	0	18	7	-36
RLCS08	cn	8	3	3	1	0	3	3	18	6	-12
RLCS11	cn	4	3	7	0	0	3	3	17	5	-9
RLCS10	cn	5	4	3	3	0	2	2	17	4	-2
RLCS14	cn	3	6	3	4	0	2	2	18	3	7
RLCS09	cn	3	7	0	8	0	0	0	18	2	16
RLCS01	cn	0	18	0	0	0	0	0	18	1	36
		41	41	16	16	0	10	10	124		

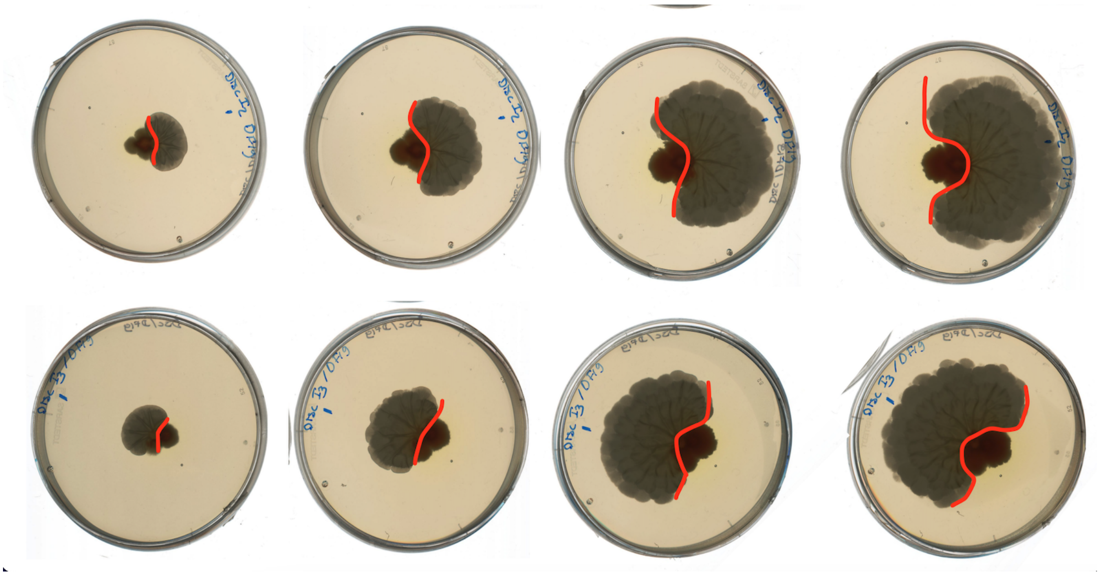
sp	treat	L	W	L1/2	W1/2	T(In)	T	TotT	total	ranking	score
RLCS29	ab	18	0	0	0	0	0	0	18	6	-36
RLCS08	ab	6	3	1	0	6	2	8	18	5	-7
RLCS11	ab	6	3	1	1	5	2	7	18	4	-6
RLCS10	ab	6	3	0	0	0	9	9	18	4	-6
RLCS14	ab	3	3	3	1	0	8	8	18	3	-2
RLCS09	ab	3	12	0	3	0	0	0	18	2	21
RLCS01	ab	0	18	0	0	0	0	0	18	1	36
		42	42	5	5	11	21	32	126		



sp	treat	L	W	L1/2	W1/2	T(In)	T	TotT	total	ranking	score
RLCS29	g1	18	0	0	0	0	0	0	18	7	-36
RLCS08	g1	10	3	2	0	3	0	3	18	6	-16
RLCS11	g1	6	3	0	0	0	9	9	18	5	-6
RLCS10	g1	5	4	1	2	0	6	6	18	4	-1
RLCS14	g1	6	6	0	0	6	0	6	18	3	0
RLCS09	g1	2	14	0	1	0	1	1	18	2	25
RLCS01	g1	0	17	0	0	0	0	0	17	1	34
		47	47	3	3	9	16	25	125		



sp	treat	L	W	L1/2	W1/2	T(In)	T	TotT	total	ranking	score
RLCS29	g2	18	0	0	0	0	0	0	18	7	-36
RLCS08	g2	3	3	6	0	2	3	5	17	6	-6
RLCS11	g2	4	3	2	0	0	9	9	18	5	-4
RLCS10	g2	4	3	2	1	0	8	8	18	4	-3
RLCS14	g2	5	3	0	4	6	0	6	18	3	0
RLCS09	g2	3	7	1	7	0	0	0	18	2	14
RLCS01	g2	0	18	0	0	0	0	0	18	1	36
		37	37	12	12	8	20	28	12		



SI - 6.2 Example of distant inhibition (in gf DF19 inhibited by DISC)

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5

GENERAL DISCUSSION

In the early twentieth century, the field of biology was grappling with the concept of phenotypic plasticity. Diversity of study types was employed to investigate how different magnitudes and timescales of environmental factors influence organismal responses to their environment. From this diversity of experimental designs, the field eventually focused on the magnitude of environmental factors, as illustrated by performance curves. This streamlining of plasticity studies within a common framework led to an explosion of biological knowledge. However, some of these early studies reported that temporal factors influenced biological responses, which has been overlooked (cf. chapter 2). Environmental change, particularly climate change, is occurring far more quickly today as opposed to a 100 years ago. Accordingly, it is critical to build models with strong predictive power to inform conservation and policy decisions to prevent biodiversity loss and maintain ecosystems in our rapidly changing world. Nevertheless, do we have sufficient predictive power with such insufficient information about the temporal influence of global change factors on organismal and ecological responses?

Experimental ecology has recently begun to contend with incorporating temporal aspects of global change into experimental designs. However, there is no widely accepted framework, often precluding the translation of results between systems and across levels of ecological hierarchy. Theoretical work has suggested that depending on the rate of change (RoC) of an environmental driver, the nature of biological responses can be profoundly different. Although seemingly intuitive, data on driver RoC effects are scarce and difficult to synthesize (cf. chapter 2). To address this gap, we (1) performed a systematic literature review to identify publishing trends in studies reporting on the RoC of global change drivers from the level of individual organisms to ecosystems and (2) experimentally investigated the influence of temperature RoC on soil fungal individuals and interactions. Our experimental work implemented a multidimensional temperature treatment design that included a gradient of different RoCs (imitating instantaneous, daily, and seasonal temperature changes) and two different heat stress levels compatible with possible climate change scenarios. Furthermore, we applied two different analytical approaches (dose-based and event-based) for distinguishing the effects of magnitude and RoC on individual and interactive responses.

Our systematic literature review revealed a dearth of studies at higher levels of ecological organization (i.e., the community and ecosystem levels) and limited experimental data above the level of individual organisms. Few studies applied a gradient RoC approach, with most using only "abrupt" and "gradual" treatments, impeding insights into nonlinear trends and system thresholds. In our experimental work, we found that slower temperature RoC buffered the adverse effects of heat stress on fungal growth but did not alter thermal limits. Those results indicate that different performance curves would be expected under different temperature RoCs. Fungal responses to temperature RoC correlated with traits relating to mycelial architecture and thermal limits. More instances of competitive exclusion were observed under faster RoCs, while more ties were observed under slower RoCs, particularly for intermediate competitors. Building on our first chapter and based on our review (cf. chapter 2) and experimental work (cf. chapter 3), we built up a framework for experimental RoC studies, which highlighted the need for: reporting of parameters, and creation of experimental designs that can be applied to any organism (group) and/or level of ecological organization. We will summarize this framework here again and extend it (1). To finish this thesis we will discuss how RoC studies could generate new hypotheses and experiments for temporal ecology using our cross-scale approach (2).

5.1 HOW TO APPROACH THE ROC QUESTION EXPERIMENTALLY

5.1.1 *Why do we need to switch to a RoC approach: from the Abrupt vs. Gradual to a gradient approach.*

"There's something that doesn't make sense. Let's go and poke it with a stick." - 11th Doctor in Doctor Who

Incorporating time into the existing experimental framework represents a technical challenge. Some recent studies have revived this idea through applying 'abrupt' and 'gradual' treatments (reviewed in chapter 2); however, used RoC as 'abrupt' or 'gradual' treatment are often seemingly randomly selected and not based on 'real-world' relevant timescales (cf., chapter 2). We employed a study design with multiple rates of temperature change (i.e., how quickly the temperature increased from ambient to target/heat stress). Using a gradient of RoC allows to capture nonlinear trends and information about thresholds – information that cannot be obtained with the 'abrupt' and 'gradual' framework (only two measurements implies a linear relationship). If one takes two points of comparison, the relation will be linear regardless of the actual relationship because there is simply no other model possible. We recommend, at the very least, to include 3 RoC treatments and, if possible, more.

5.1.2 *What's the treatment in a RoC study and how to describe it*

"she said the mystery of life isn't a problem to solve, but a reality to experience." -Reverend Mother in Dune

As we already highlighted, a general framework is needed to allow the synthesis of the knowledge and generate hypothesis driven experiments. We have argued that the first step is to incorporate a gradient-based approach of RoC drivers (cf. Figure 1). More practically, this means that the treatment's RoC should be described as a combination of a technical RoC and a step increase, so one can fully understand and replicate the temporal structure of the treatment (cf. chapter 1). In some cases, there is no need for step-increase, for instance, when it is possible to create a constant RoC or if it can be proven that the stepping is negligible. In this latter case, the Roc is described fully as a technical RoC (the rate of change in the driver as it can be measured per sec. or min. as the technical flux of mechanical devices generates it). Consequently, the technical RoC, the magnitude of the step increase, and its interval can describe precisely the treatment's RoC and should be explicitly mentioned.

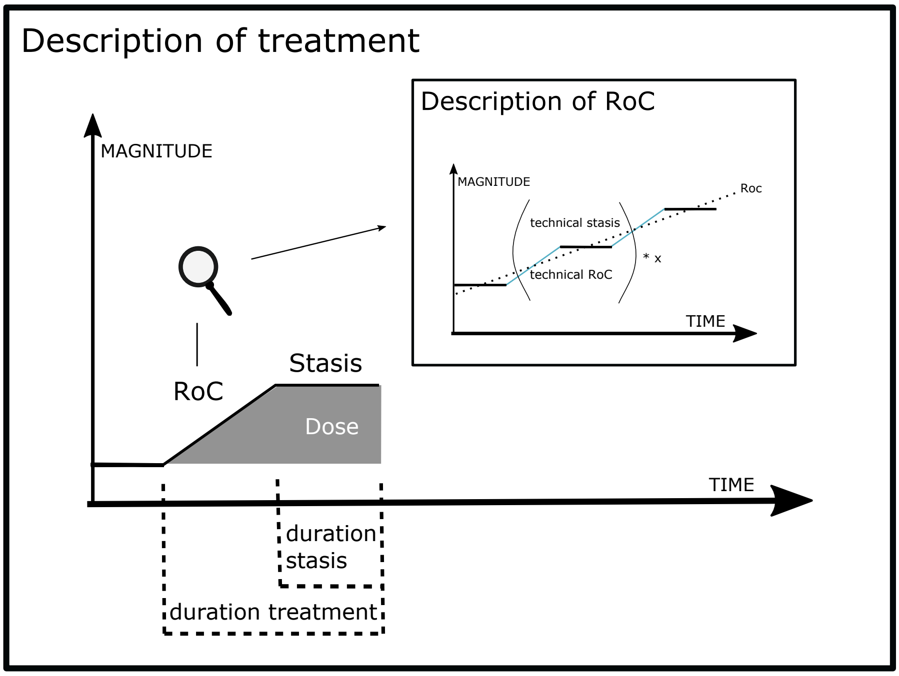
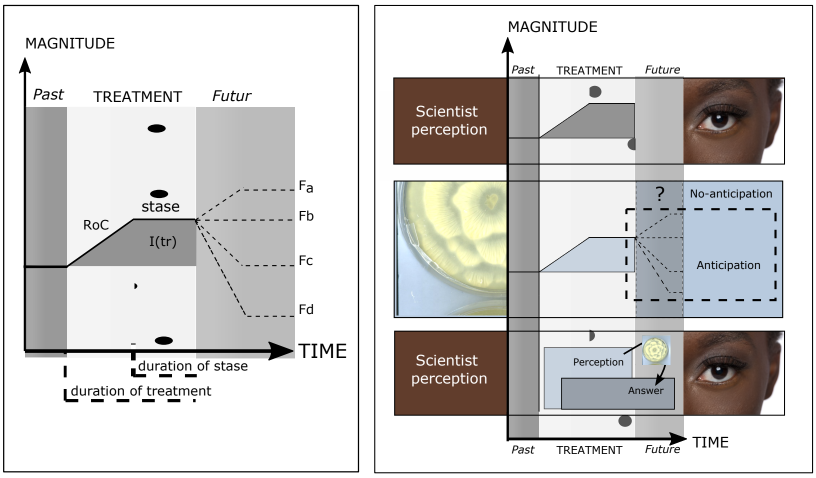


Figure 1: Adequately describing an environmental rate of change in experimental treatments.

Now to take a larger point of view, the complete treatment in a study of RoC-effects is composed of the RoC (technical rate and step increase parameter), the dose (explicitly represented as I(tr) in Figure 2a), and the duration of the stasis when one is included (Figure 2a). It is essential to understand that the duration of the stasis is part of the treatment and a parameter limiting the observed and measured response (Figure 2b). Additionally, when confronted with a dose and a particular temporal distribution of a treatment (RoC, duration of the ramp, and duration of the stasis), the kind of responses an organism can produce is likely to be influenced by the evolutionary context. This influence is evident when an organism has anticipatory mechanisms (e.g., phenology, Figure 2b). For example, fast RoCs may be associated with more disturbance-like change (driver returns to baseline; see curve Fc in Figure 2a), while slower RoCs may be associated with more continuous change as depicted with curve Fb or further change like Fa (Figure 2a). Their associated responses would be selected to fit those different timelines of change. As a result, when one chooses the range of the RoC and the duration of the stasis of their treatments, one also assumes the observed response type (Fa, Fb, Fc, and Fd in Figure 2), which should always be explicitly considered.



a. Time line of the driver

b.Time line of different perceptions

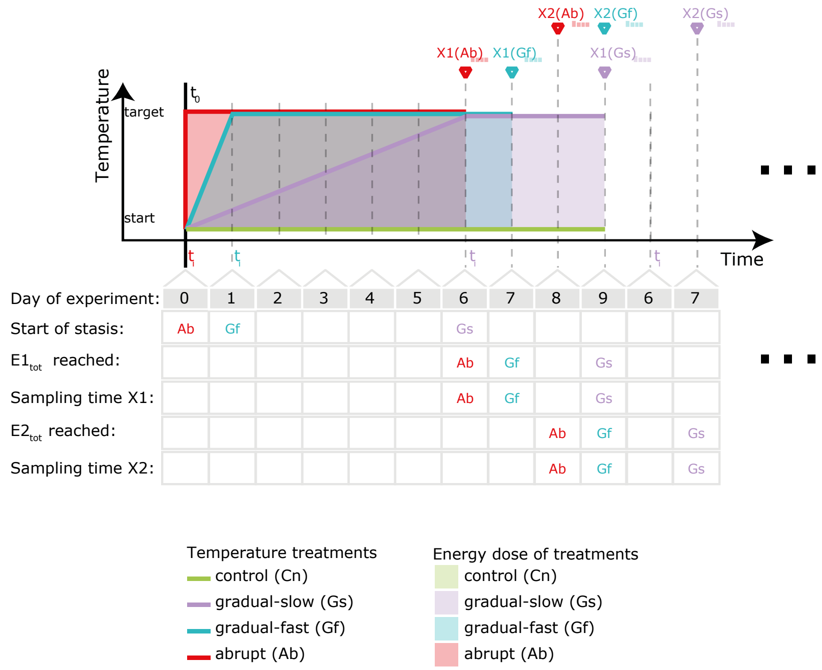
Figure 2: Description of the different time components of the treatment and how they are placed in the general temporal context of the experiment (Scientist perception) and of the organism studied (life history, timeline of the answer, and anticipation mechanisms). Panel a decomposes all the different components of the treatment: ramping phase (RoC), static phase (stasis,) the dose (I(tr)). F(a,b,c,d) represent the type of development that could follow in nature but are not part of the treatment. Those potential futures trajectories of the environmental driver determine the response at least partially, as some organisms have anticipations mechanisms (i.g. phenology). The past is anything that could have happened to the organism (i.g. Starting temperature). A scientist who studies RoC should explicitly consider all these parameters in the design. In panel b: the different timelines that enters into account in the experimental vs. natural context in temporal ecology. The experimental context means one chooses to reduce the windows of development of the answer, that does not mean that the answer is reduced. This should be particularly carefully taken into account in the case of known anticipatory mechanisms.

5.1.3 *Sampling strategies for the studies of RoC effect*

"If wishes were fishes, we'd all cast nets." - Gurney Halleck in Dune

An additional challenge is the selection of sampling times and the subsequent data analysis when studying RoC effects: is it better to compare samples taken at the same time point or samples that have received the same dose? We attempted to resolve the analytical complications by applying both 'dose-based' and 'event-based' sample comparisons, and they showed similar results. We do not recommend choosing only one approach based on these results for other types of organisms or biological systems because we only tested these approaches on fungal strains. In further work with other biological objects, both approaches still need to be tested, especially at a higher level of organization. Of course, the best data would describe the entire response timeline, complete with continuous data, however acquiring this kind of data is costly in terms of time, energy, and is sometimes impossible due to destruction of samples.

We could not consider a third option in our experimental work (cf. chapter 3), a through-time dose-based comparison that combines both approaches. Due to the size of the petri dish used, the maximal duration of the experiment was limited. As a result of the duration limitation, we could not include a sampling design that looks at more than one time-point in the dose-based comparison paradigm (cf. chapter 3). We would recommend this approach for further experimental work as it combines both aspect dose and event approach (Figure 3).



Day of experiment:	0	1	2	3	4	5	6	7	8	9	6	7
Start of stasis:	Ab	Gf					Gs					
$E1_{tot}$ reached:							Ab	Gf		Gs		
Sampling time X1:							Ab	Gf		Gs		
$E2_{tot}$ reached:									Ab	Gf		Gs
Sampling time X2:									Ab	Gf		Gs

Figure 3: Dose-based AND Event-based

5.2 CUTTING THE TEMPORAL SALAMI AND SOME FOOD FOR THOUGHTS

5.2.1 *Environmental drivers set the time - driver RoC and responses are coupled*

"It's wrong to think that the past is something that's just gone. It's still there. It's just that you've gone past. If you drive through a town, it's still there in the rear-view mirror. Time is a road, but it doesn't roll up behind you. Things aren't over just because they're past. Do you see that?" - Johnny and the Dead Terry Pratchett

The capacity of a community to adjust to environmental change is dictated by the plastic and evolutionary responses occurring within the community (individual and population responses, see chapter 2), as well as by biotic and abiotic interactions (Fortelius et al., 2015; **Fortelius2015ab**; Klironomos et al., 2005; Blasio et al., 2015). The RoC of environmental drivers strongly matters for the appearance of temporal equilibrium at the community or ecosystem level because couplings are results of coevolution under a particular time dynamic in the drivers (chapter 2). The coupling of environmental conditions and biological agents occurs through the ability of organisms to perceive change and, at some time, accommodate (e.g., plasticity) or even pre-accommodate to it (e.g., phenology). This also occurs through direct effects on organisms and populations, for instance, regarding food intake or damages (Reed et al., 2010 and chapter 2). In the specific case of synchrony and asynchrony in ecosystems, it was even shown that environmental drivers have more impact than biotic interactions (Tredennick et al., 2017).

We hypothesize that organismal responses synchronize with recurring, predictable driver RoC over time and subsequently that driver RoCs are an important element of stability of the system. Thus, for an ecosystem, there should be a specific rate of RoC for an environmental driver with which the system could deal without major dissonances. Accordingly, this should be related to the historical range of variation of the RoC of the driver. Support for our hypothesis lies in evidence that species that evolve in a more variable environment (e.g., more prone to "out of normal range" RoC) rather than in a stable environment are more capable of responding to higher variability in high driver RoC (Reed et al., 2010 , Seneviratne et al., 2009).

5.2.2 *Predictability of RoC - perception of the response*

"The Great Conjunction is the end of the world! Or the beginning. Hm! End, begin, all the same. Big change. Sometimes good, sometimes bad !"- Aughra in Dark cristal

Environmental changes and organismal changes are thus synchronized, but the change in the driver and the process unfolding the response are not necessarily ordered with the change in the driver occurring first (Reed et al., 2010).

On the other hand, unpredictable changes are changes for which the organismal responses co-occur with the change in the driver because the response is then a direct reaction to the change (e.g., stress responses). In this situation, there is a more direct relationship between the RoC of the driver and the RoC of the responses. Some evidence suggests that those types of temporal plasticity have been selected under more variable environments (chapter 2,Reed et al., 2010, Seneviratne et al., 2009).

In a review of evidence across multiple ecological levels (cf. chapter 2), we highlighted that biotic responses could be classified across scales of organization by the predictability of the various RoC of environmental drivers (Table 1). When a driver final change is predictable based on his RoC, organisms or populations can pre-accommodate to becoming environmental conditions with plastic mechanism, like in phenology (Table 1). Those anticipation mechanisms are the result of selection on temporal plasticity by recurrent environmental events of approximately constant RoC (Reed et al., 2010, cf. chapter 2). In the case of phenology, organisms sense cues announcing seasonal changes and initiate plastic change (responses) for building a new phenotype before the environmental conditions manifest for which the phenotype is actually adapted. The response is an anticipation of the change (Reed et al., 2010).

Time scale also structures response interactions between hierarchical levels. The response to the rate of environmental change is transmitted between levels of the ecological hierarchy. For example, Seebacher and Grigaltchik, 2015 showed in a frog model system that developmental thermal plasticity modifies predator-prey interactions (i.e., the organism-level response affects the community). Conversely, at the population level, environmental change initiates selection processes. This leads to genetic adaptation, and yet again, the speed of evolution and its outcome (characteristics of the resulting population) are dependent on the RoC (Gienapp et al., 2008; Jezkova and Wiens, 2016). Such adaptations could be based on sensitivity or directly "targeting" plasticity (). At this level, plasticity and evolution interact (Reed, Schindler, and Waples, 2011). Another example of such processes is how diurnal cues can influence the phenology of trees (Flynn and Wolkovich, 2018).

In general, detection of environmental change depends on the time scale of the change (e.g., diurnal cycle versus seasonal cycle for organism level, see Table 1). It must be noted that by applying a fast RoC treatment to predict the consequences of changes that naturally occur over more extended periods, there is a high likelihood of missing the effective mechanism that would develop in response to gradual change (cf. chapter 2). Therefore, it is crucial to clearly take into account the RoC when conducting experiments at any level of ecological organization.

Cues sensed by organisms to initiate pre-adapted plastic responses in predictable cyclic environments (phenology) are not directly bound to the environmental factor to which they are adapted (Kronfeld-Schor et al., 2017, Putten, Macel, and Visser, 2010). If environmental changes become irregular or unpredictable, this pre-adaptation sys-

	Organism		Population		Community & Ecosystem	
RESPONSES TO PREDICTABLE CHANGE:	Responses	TS	Responses	TS	Responses	TS
anticipation mechanisms,	Diurnal or circadian clock1,2	++	Migration7	+	Ecosystem coupling 6,15	na
cycles,	Seasonal clock1,6	-	Phenology6,10,11,12	-		
systems			Life cycle*	- -		
RESPONSES TO UNPREDICTABLE CHANGE:	Response to stress3,4,5	++	Plasticity8,9	++	Resistance	na
reaction mechanisms,	Hardening-like3,4,5	+	Maternal effects	+	Resilience	na
linear-like processes	Acclimatization-like3,4,5	-	Dispersal /ranging7	-		
			Evolution and Niche change13,14	- -		

Table 1: Characterization of ecological responses to environmental events and stressors and different types of functions.
TS: Temporal scale ("++": faster, "- -" : slower, "na": not absolute), where the relative speed depends on the organism(s) under study
Cited literature: 1 Dunlap, 1999, 2 Kidd, Young, and Siggia, 2015, 3 Bowler and Benton, 2005, 4 Loeschcke and Sørensen, 2005, 6 Kronfeld-Schor et al., 2017, 7, 8 Reed et al., 2010, 9, 10 Visser et al., 2010, 11 Forrest and Miller-Rushing, 2010, 12 Reed et al., 2012, 13 Cang, Wilson, and Wiens, 2016, 14 Jezkova and Wiens, 2016, 15 Putten, Macel, and Visser, 2010

tem may become a handicap (Reed et al., 2010), and this is likely to be predictable by the range of the RoC of the environmental driver.

Such mechanisms allow organisms to "pre-adapt" to environmental change (phenology) (Reed et al., 2010). In order to be effective, it would be assumed that a fixed RoC of the driver is related to reliable cues about this change. When coupled organisms (i.e., couple indicates dependencies in an exclusive or reciprocal way of the organisms considered) react to cues related to different drivers (e.g., temperature vs. light), and in the case of environmental change that desynchronized the RoC of these drivers, the organisms may develop maladaptive plastic responses to their abiotic and biotic context. For instance, when light and temperature are desynchronized, those organisms that base their anticipation of phenotypic needs on light change (e.g., reproduction initiation for Hamster or various plants phenology) will experience a mismatch with their phenotypic needs regarding imminent temperature change (Kronfeld-Schor et al., 2017, Putten, Macel, and Visser, 2010). This leads the organism using light cues to be desynchronized with abiotic conditions (Kronfeld-Schor et al., 2017, Putten, Macel, and Visser, 2010). Furthermore, in general, light cue-supported mechanisms are likely to be less plastic to environmental change (Lyon, Chaine, and Winkler, 2008). A lack of plasticity in terms of the ability to discriminate between RoC with a single threshold-based mechanism could also lead to mis-match.

In the case of responses associated with non-predictable driver changes, we hypothesize lesser impact on ecosystems of the change in the RoC of the drivers because of their very nature, i.e., magnitude is more important. Such types of mechanisms are directly linked to the RoC of their driver. Although even for them, the behavior may not be linear (chapter 1 and 2), leading to potential mismatches in the interaction network.

In addition, if climate change does not result in homogenous temporal change through space, a more mis-match could occur. At the regional scale, climate change effects occur in a non-homogeneous manner (Xia et al., 2014). Therefore, biotic and abiotic modifications linked to those changes are also likely to occur in a non-homogeneous manner (Xia et al., 2014, Maclean et al., 2017). Thus, the mis-match between different compartments of the meta-ecosystem, particularly stocks and fluxes, could significantly impact nutrient cycling and biodiversity (Xia et al., 2014, Maclean et al., 2017).

"Cats make ideal time travellers because they can't handle guns. This makes the major drawback of time travel– that you might accidentally shoot you own grandfather – very unlikely." -in Time Terry Pratchett

Finally, we want to point out that understanding the relationship between the rate of an environmental change and the response of an organism, a population, or a community is important for an audience broader than ecologists. Stevenson et al., 2015 reviewed how biological temporal changes (particularly seasonal changes) and human activities are connected. The effects of the rate of environmental changes are also crucial for economic theories that consider ecology (Walker et al., 2006; Murray, Skene, and Haynes, 2015 and see also Lambin and Meyfroidt, 2010 "flow" and "RoC" in land-use transition). The temporal relationship between environmental changes and biotic responses needs to be explored and integrated across scales in ecology with the view of being used as a trans-disciplinary tool to serve the epistemological turn our democratic societies need to survive global changes.

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Part I

APPENDIX

A

FUNGUS–BACTERIUM ASSOCIATIONS ARE WIDESPREAD IN FUNGAL CULTURES ISOLATED FROM A SEMI-ARID NATURAL GRASSLAND IN GERMANY

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