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Review

Basic Principles of Temporal Dynamics

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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.

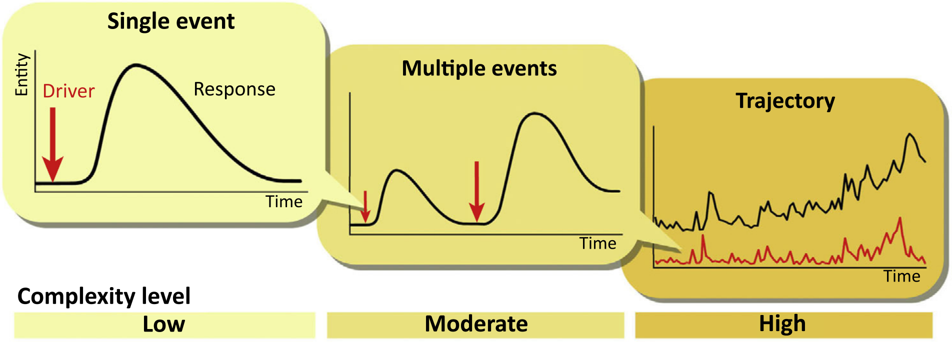

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Figure 1. Hierarchical Complexity. The idea deals with driver–response relationships in time-series across three levels of complexity. The levels are hierarchically nested, as single-event (i.e., one driver and one response) is a subset of multiple 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

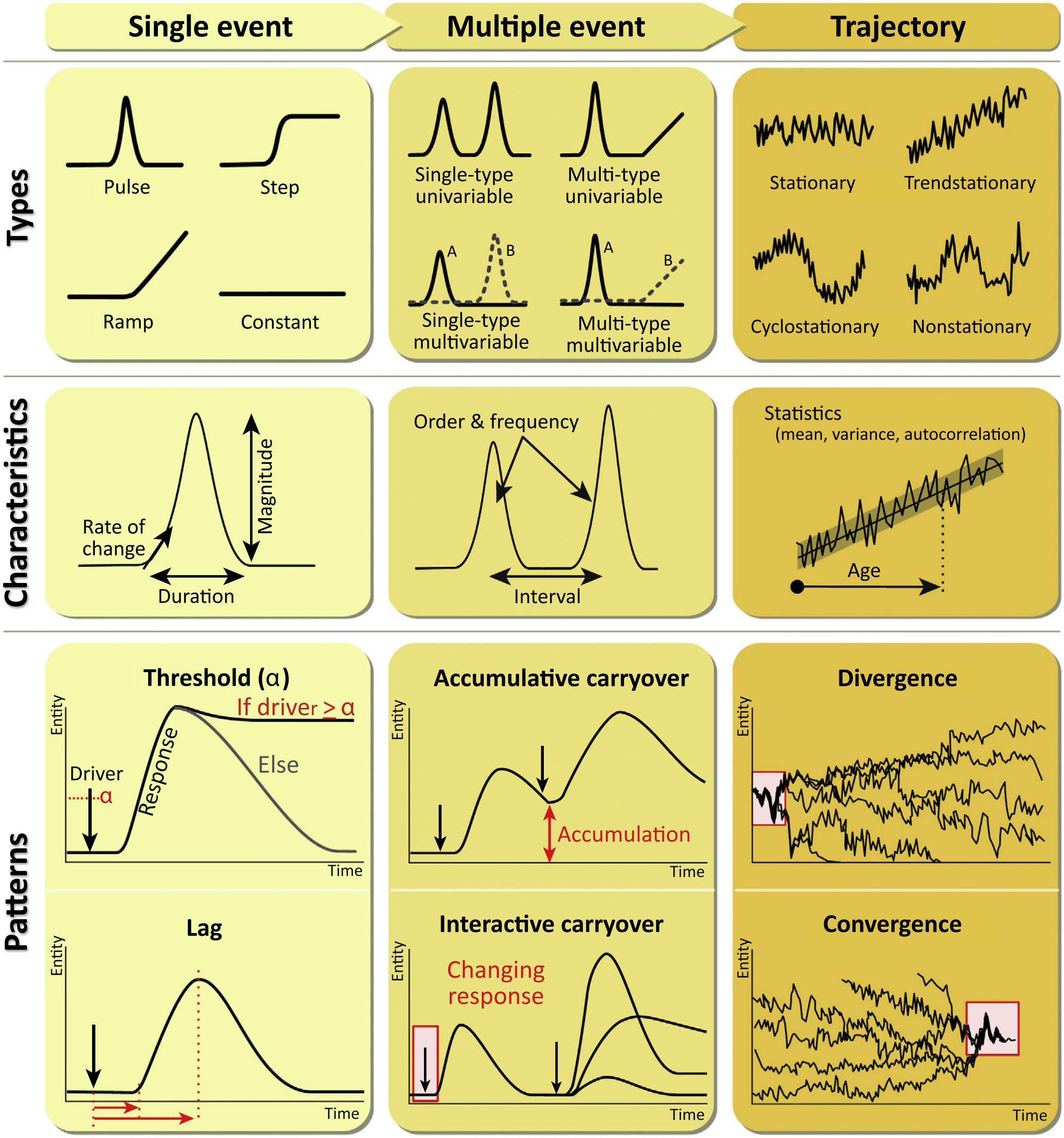

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Figure 2. Basic Principles of Temporal Dynamics. At each level of complexity, some unique properties are summarized. At single-event level, for instance, there are four different types of patterns, three quantifiable characteristics, and two important 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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