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IDEA AND PERSPECTIVE

Temporal ecology in the Anthropocene

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Abstract

Two fundamental axes – space and time – shape ecological systems. Over the last 30 years spatial ecology has developed as an integrative, multidisciplinary science that has improved our understanding of the ecological consequences of habitat fragmentation and loss. We argue that accelerating climate change – the effective manipulation of time by humans – has generated a current need to build an equivalent framework for temporal ecology. Climate change has at once pressed ecologists to understand and predict ecological dynamics in non-stationary environments, while also challenged fundamental assumptions of many concepts, models and approaches. However, similarities between space and time, especially related issues of scaling, provide an outline for improving ecological models and forecasting of temporal dynamics, while the unique attributes of time, particularly its emphasis on events and its singular direction, highlight where new approaches are needed. We emphasise how a renewed, interdisciplinary focus on time would coalesce related concepts, help develop new theories and methods and guide further data collection. The next challenge will be to unite predictive frameworks from spatial and temporal ecology to build robust forecasts of when and where environmental change will pose the largest threats to species and ecosystems, as well as identifying the best opportunities for conservation.

Keywords

Autocorrelation, climate change, ecological forecasting, events, non-stationarity, scaling, spatial ecology, temporal ecology.

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INTRODUCTION

Thirty years ago a transformation in ecological thinking was underway, precipitated in part by questions of how anthropogenic habitat loss and fragmentation affected populations, communities and ecosystems. Addressing these questions required ecologists to work at scales far larger than their traditional plot sizes, statistical methods and theories allowed, and required integrating perspectives and methods from other disciplines (e.g. geography and evolution) to build upon and develop a body of theories (e.g. island biogeography, metapopulation) and concepts (edge effects and corridors). The field of spatial ecology subsequently emerged from this as an integrative, multidisciplinary science adept at developing concepts and theory to address both basic and applied ecological challenges. Indeed, a major strength of spatial ecology has been its ability to generalise and tackle questions across a broad range of scales, from single-species metapopulations to multi-species metacommunities (Pillai *et al*., 2011) and from local to global scales (Bell, 2001). As the field has matured, a suite of dedicated journals (e.g. *Diversity and Distributions, Ecography, Journal of Biogeography, Landscape Ecology*) has provided forums for the exchange of ideas and cross-pollination between the formerly disparate disciplines that spatial ecology now encompasses.

Alongside the human modification of space and rise of spatial ecology, anthropogenic forces have also shifted the temporal dynamics of many systems. Large-scale human modification of the earth system, the hallmark of the epoch known as the Anthropocene, has impacted the temporal dynamics of many populations and ecosystems via alteration of disturbance cycles (e.g. fire), introduction of exotic species and even habitat modification itself – for example, by affecting dispersal or altering microclimates. Such impacts are especially apparent with climate change, which – from arctic to temperate biomes – has extended growing seasons, and altered the phenology and behaviour of many organisms. In these and myriad other ways climate change has fundamentally altered how organisms experience time. It has also spurred a new body of research and pressed ecology to revisit fundamental questions of how temporal dynamics structure ecological systems, and thus is our focus here.

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Much as questions related to habitat fragmentation pressed ecologists to work at larger spatial scales, climate change and related issues have challenged ecologists to better understand temporal processes over longer timescales. Facilitated in part by improved integration of climate science, evolution and paleobiology into ecology, addressing these questions has yielded data at larger scales than previously available. For example, researchers studying phenology have brought together hundreds of thousands of time series data sets to understand the impact of climate change on the timing of animal and plant life cycle events (Menzel *et al*., 2006).

With the increasing availability of long-term data, however, new challenges have arisen. These include creeping timescale issues: population dynamics that appear more complex when examined in longer time series (Ziebarth *et al*., 2010), selection that weakens when integrated over longer periods (Schoener, 2011; Uyeda *et al*., 2011), as well as shifts in trends, including responses that reverse over time (Yu *et al*., 2010). Yet a unified field of temporal ecology – with robust theory to explain these issues – has yet to emerge. Instead, within and across disciplines, vocabularies have diverged, often producing different terms for similar concepts [e.g. lag effects *sensu* Reichmann *et al*. (2013) or carry-over effects, *sensu* Betini *et al*. (2013)], highlighting the need for a common interdisciplinary forum.

We argue that there is a compelling current need to develop a unified framework for temporal ecology – one that builds on new data and methods and provides a new focus for predicting how shifting environments shape populations, species, communities and ecosystems. Such a framework could follow the successful, interdisciplinary model of spatial ecology, but would specifically address time. Here we offer a starting point by reviewing the important attributes shared between temporal and spatial ecology, alongside the unique aspects of time that will require new perspectives and methods for robust ecological forecasting.

TIME AS A FUNDAMENTAL AXIS

Time is about order and events. In its classical definition, it is a dimension that allows: (1) sequencing of events from past, present to future and (2) the measurement of durations between these events. Time routinely features in many ecological models and the study of temporal ecology centers on change over time and how such change drives system dynamics. Units can be absolute (minutes, hours, days, months, years) or relative (heart beats, generation times, species life spans), and change can take different forms (cycles, trends, noise) and be of different magnitudes, but it is implicit in any ecological process that involves a rate. Ecologists are thus familiar with time as the denominator of many ecological properties, from physiological to community ecology (e.g. metabolic rates, population growth, migration, diversification). Yet time can also shape process, such as species coexistence or predator–prey dynamics.

Together with space, time therefore represents one of the fundamental axes that shapes ecological systems. In turn, these two axes have shaped many of the fundamental questions in ecology including how spatial and temporal variation in the environment control species' distributions, and how such environmental variation affects population dynamics and structures diverse communities. Such questions highlight that temporal and spatial ecology are intricately intertwined (Delcourt *et al*., 1983), and the two axes share many important similarities.

Similar to space, time in ecology is populated by conspicuous patterns. A common feature of these patterns in both space and time is autocorrelation, the tendency for individual observations to be similar (non-independent) to other observations (Legendre, 1993). The major distinguishing feature of temporal autocorrelation from its spatial counterpart, however, is directionality. A point in space can influence, and be influenced by, points in all three dimensions, while points in time can only be influenced by preceding points. Temporal autocorrelation can manifest in a variety of ways (Fig. 1); for example as regular cycles (e.g. daily, seasonal, interannual), or trends (whether linear or nonlinear). Even 'noise' (the remaining variance after the 'signal' has been extracted) may show autocorrelation, such as 'red' (positive autocorrelation) or 'blue' (negative autocorrelation) noise.

Understanding to what degree fluctuations or cycles in ecological systems are shaped by external temporal patterns or are driven by ergodic properties of populations and species interactions makes up a large portion of study in behaviour (MacArthur, 1958), physiology (Lambers *et al*., 2008), population (May, 1976) and community (Chesson & Huntly 1997) ecology. Trends through time underlie the concept of succession (Clements, 1916), while temporal 'noise' has long interested both population (Kaitala *et al*., 1997; Bjornstad *et al*., 1999) and community ecologists (Chesson & Huntly 1997). For example, classical community ecology has used temporal variation, including cycles and noise, to explain coexistence via temporal niche partitioning or small-scale differences in species' responses to a temporally variable environment (MacArthur, 1958; Chesson & Huntly 1997). Space and time are additionally linked via the importance of scale. Just as spatial patterns may change when examined at local versus regional scales (e.g. Fridley *et al*., 2007), temporal trends may appear as cycles, and parts of cycles as singular events, or noise, depending on the timescale.

Time is unique from space, however, in several important aspects. First, it is impossible to manipulate absolute time. While researchers have manipulated space at small (e.g. Huffaker, 1958) and large (e.g. Terborgh *et al*., 2001) scales, only relative time can be manipulated. Ecologists may adjust the timing of species' interactions (Yang & Rudolf 2010), the sequencing of events (Vannette & Fukami 2014) or underlying drivers of temporal processes to speed up or slow down rates, but they cannot fundamentally alter time itself. Next, temporal patterns are arrow-like – they have each a singular directionality. While space may have directional patterns (e.g. altitudinal and latitudinal trends) it is possible to view spatial patterns from almost endless directions and return to a place multiple times. In contrast, time flows. Once an event has unfolded all following patterns and processes may be impacted by it without any temporal recourse to return to it or examine it in another direction. While cycles might give the illusion of returning to a previous point, the temporal landscape has inexorably moved on. Finally, humans experience

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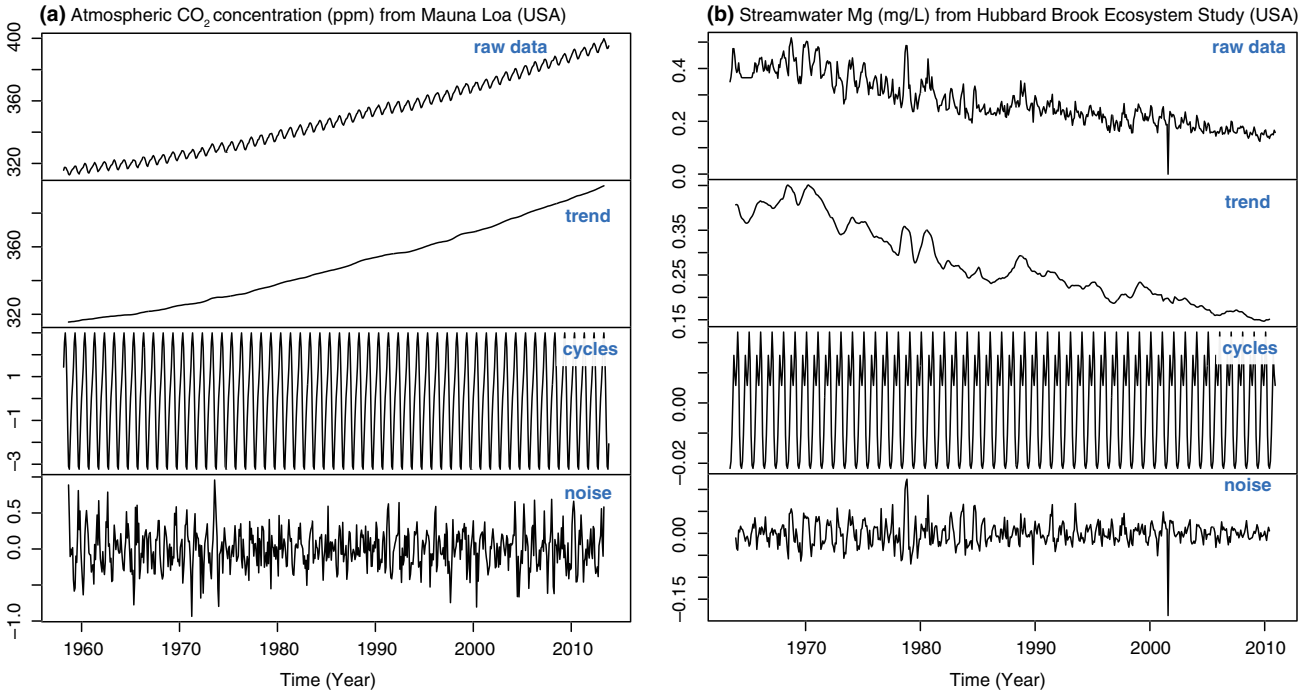

Figure 1 Time series are often a composite of different features of the underlying data and can be decomposed by various methods. For example, many ecological time series can be decomposed into regular cycles (e.g. daily, seasonal, multi-annual), longer term trends and remaining 'noise.' In (a), carbon dioxide data are from NOAA Earth System Research Laboratory, averaged with a 12-sample running mean; in (b), data are from watershed 1 (Hubbard Brook Ecosystem Study data: chemistry of streamwater at HBEF W-1, http://hubbardbrook.org/data/dataset.php?id=3, data accessed on 8 December 2013; data were provided by G.E. Likens with financial support from the NSF and The A. W. Mellon Foundation). Both data sets are decomposed using a simple additive seasonal decomposition by moving averages.

only a snapshot of time. While ecologists may cover the entire globe to map spatial patterns, temporal patterns over very short or very long timescales are inherently difficult to observe. In the words of Wiens *et al.* (1986), '[w]e get only a brief and often dim glimpse of the relevant processes.'

ANTHROPOGENIC FORCING & NEW CHALLENGES IN TEMPORAL ECOLOGY

While ecology has long embraced the importance of temporal dynamics, anthropogenic climate change has posed new challenges. Models of the most basic shifts – in species' ranges or phenologies, for example – are generally built on simple static correlations between ecological and environmental data. Such models tacitly assume stationarity – which refers to any stochastic process with a fixed, underlying probability distribution – and thus may not predict beyond the historical record. Further, they have little ability to extend across scales, for example between population, community or ecosystem levels. Part of this shortcoming may be due to chance: spatial ecology developed alongside a separate and increasing theoretical interest in space – providing ecologists interested in addressing questions related to habitat fragmentation with new theories and models of how space may structure populations and communities. Yet there has been no equivalent concurrence in temporal ecology and climate change. The main problem may be that climate change – a highly non-stationary phenomenon – challenges fundamental assumptions of many ecological concepts, models and approaches.

Climate change introduces into most systems a level of non-stationarity that is largely unprecedented over the last 200 years. In contrast, stationarity is a major assumption of most statistical methods and many major concepts and theories in ecology (Betancourt, 2012). All systems are inherently non-stationary at some scale, and assumptions of stationarity are often reasonable when the underlying rate of change is slow. For example, while certain environmental factors are still recovering from the last ice age (e.g. rebound of continents following retreat of the ice sheets) and thus non-stationary over long timescales, their trajectory is often so slow that they are effectively stationary when considered against ecological dynamics occurring at shorter timescales. Recent climate change, however, has altered both the magnitude and speed of environmental change in many systems – such that the rate of environmental change now clearly impacts biological systems (Fig. 2).

Improved integration of temporal non-stationarity in ecology requires a more widespread and persistent appreciation of the concept (Fig. 3). While climate change and other anthropogenic impacts have highlighted the importance of non-stationarity, such an appreciation should improve both basic and applied ecological study as non-stationarity is not confined to the Anthropocene and may occur on both very long or short timescales (Fig. 4). Recognizing when non-stationarity is relevant to ecological systems requires addressing issues of temporal scaling, including how processes with differing rates may interact, how species may respond to the same forcing over different time intervals (e.g. daily vs. annual vs. interannual

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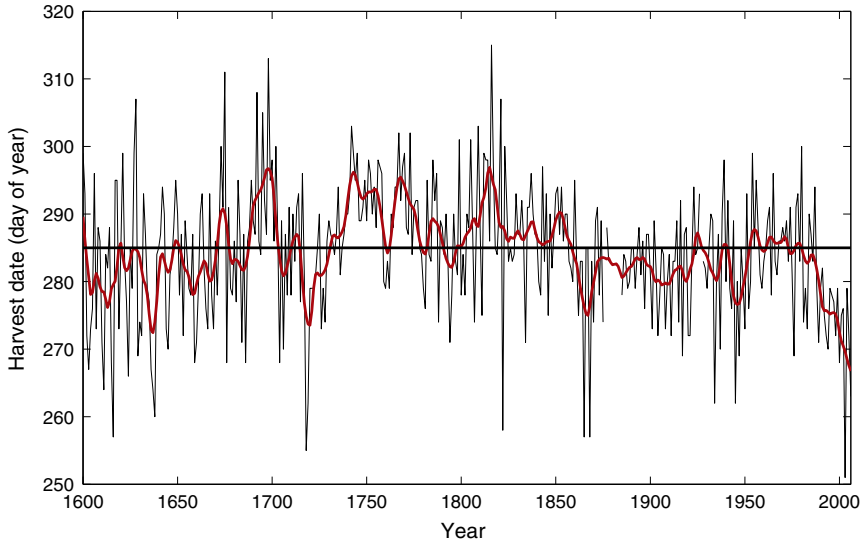

Figure 2 Temporal ecology is focused on understanding how, when and where time influences ecological systems; including examining when drivers and responses are stationary versus non-stationary. Non-stationarity occurs when the underlying probability distribution shifts across time (e.g. in its mean or variance). Until recently many systems appeared stationary over the timescale of ecological observations (i.e. the last 100–200 years), as seen here in grape harvest records from Switzerland (Meier et al., 2007). Yet systems have also appeared non-stationary outside of recent shifts in climate (e.g. shown here in the 1700s). Many systems now appear non-stationary due to climate change, which has resulted in a trend of increasing mean temperatures (Huntingford et al., 2013). Such shifts may impact biological processes, for example by advancing phenological events, as in the grape harvest over the last several decades. Data shown with a 10-year lowess pass smooth.

temperature fluctuations; changes in extreme events vs. the mean), and the appropriate temporal span and sampling frequency required to draw conclusions regarding trends, variability and periodicities (e.g. Delcourt *et al.*, 1983). This integration will, in turn, require revisiting basic ecological paradigms in a new light and adapting relevant theories and models.

Non-stationarity in current ecological models

Temporal non-stationarity is not a new concept in ecology. Many of ecology's major concepts are descriptions of temporal non-stationarity, including much work focused on disturbance (e.g. the shifting mosaic hypothesis), regime shifts and alternative stable states, as well as extinctions and extirpations. Ecology, however, has an uneven history of embracing temporal non-stationarity in both drivers of ecological systems and in ecological responses. This is perhaps best illustrated by changing views on the concept of succession (changes in the structure and function of ecosystems over time) and its relationship to the abiotic environment (Fig. 5), pitting Clementsian vs. Gleasonian versions of nature against one another (Clements, 1916; Gleason, 1926). In the Clementsian version, communities shift over time in a predictable sequence that is not highly impacted by the abiotic environment (Fig. 5a). This view is illustrated by temporally predictable sequence of primary succession, for example on newly deglaciated surfaces in Glacier Bay, Alaska (Cooper, 1923). Over this sequence, ecosystem properties changed over time (Chapin *et al.*, 1994), with the rate (but not the endpoint) of succession controlled by biotic interactions and a minimal or non-existent role for the abiotic environment (e.g. climate). Gleason (1926) offered an alternative view of succession, stressing the importance of the abiotic environment and, thus, expected far less predictable successional trajectories. This later view recognises that events such as climate extremes and other disturbances could reset successional clocks (Fig. 5b), and thus produce diverse ecological patterns across the landscape (Levin, 1992; Romme *et al.*, 2011). While succession is fundamentally about temporal non-stationarity in an ecological process, it is not, however, fully developed to handle temporal non-stationarity in underlying drivers. Rapid shifts in climate, for example could shift trajectories or make it impossible for systems to return to a given trajectory following a disturbance (Fig. 5c). In this way, temporal non-stationarity may be a key predictor of regime shifts in communities and ecosystems.

A framework for better incorporating non-stationarity into ecological models will require consideration of both non-stationarity in the forcings (e.g. climate, Fig. 5c) and also in the ecological responses (Fig. 6b.1, b.2). Non-stationarity in climate may push species outside of their normal response range. For example, many species will advance their phenology with warming in a linear fashion until a certain threshold, after which phenology may be dominantly controlled by photoperiod or snow cover (Iler *et al.*, 2013), resulting in non-stationarity in species' responses to climate change. Many current ecological models could be adapted to make predictions with climate change if stationarity assumptions were relaxed. This could include adjusting population ecology models to examine outcomes when life history parameters related to the environment (e.g. mortality due to drought etc.) are non-stationary or adjusting coexistence models built on temporal variability (e.g. Chesson & Huntly 1997) to examine the

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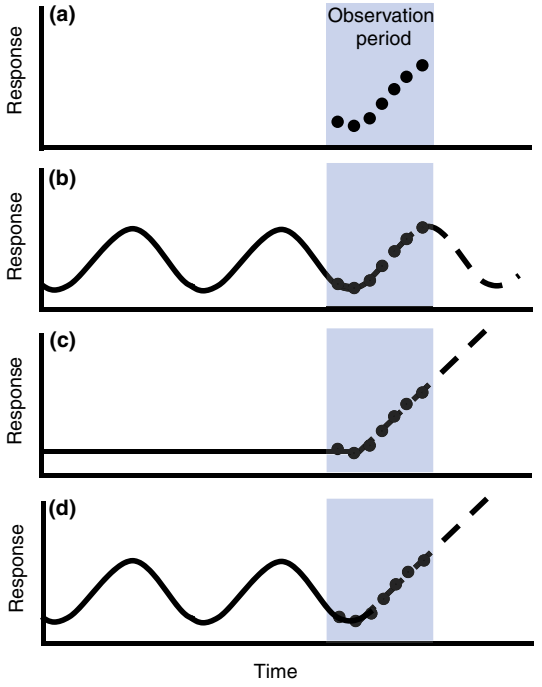

Figure 3 Long-term records in ecology such as repeated measures or observational data spanning at least 5–10 years are increasingly common. Such data provide an opportunity to improve our understanding and predictive capabilities, but also present a challenge regarding how best to interpret trends. Depending on the system and period of observation, what looks like a linear increase (a) could be part of a regular long-term cycle (b), indicative of a major shift in the system into a non-stationary period (c) or possibly part of both (d), especially if forcing on the system has changed – as seen in many systems with climate change. Temporal scaling and non-stationarity are, thus, inherently linked as any system or process can look stationary or non-stationary depending on the scale.

consequences of environmental non-stationarity on community structure.

Ecology must also become more aware of the temporal assumptions in many of its statistical methods, specifically that most assume: (1) a lack of temporal autocorrelation and (2) temporal stationarity. Autocorrelation – a common feature in time series data – violates the assumption of independence of observations in many statistical tests and can thus inflate Type I error (Brown *et al.*, 2011), while non-stationarity (itself a type of autocorrelation) may limit how well models can be applied beyond the range of recorded data. This latter issue may critically limit projections of ecological change in response to climate in the future given current ecological modelling methods. To combat these limitations, however, a variety of methodologies have been developed. General linear models can often be adapted to include temporal autoregression; this may accommodate some temporal non-stationarity, but could equally hide its impact. A better approach would be to explicitly model temporal non-stationarity, which will often require new model development and further integration of models from other disciplines that allow non-stationarity (e.g, Grenfell *et al.*, 2001; Lipp *et al.*, 2002). Such models are often also used in spatial ecology, with its increasing recognition of non-stationarity across space, and have led to new hypotheses and methods. For example, geographically weighted regression relaxes the assumption that process parameters (e.g. variance and mean) are independent of location and direction (Brunsdon *et al.*, 1998), allowing researchers to test questions of whether differing processes – which shift across space – could shape fundamental ecological patterns, such as species richness (Davies *et al.*, 2011).

Temporal scaling

Scaling issues in temporal ecology mirror many of the same challenges in spatial ecology, including the grain and extent of sampling. For example, while spatial ecology is concerned with how well observations at the plot level ($10^1 m^2$) scale to the landscape level (10^2–$10^3 m^2$), temporal ecology must harmonise across ecological processes that span disparate temporal extents and observation at various temporal grains (Fig. 7), from minutes (e.g. photosynthesis) to days and weeks (e.g. phenology, annual productivity) and upwards to centuries and millennia (e.g. successional dynamics, carbon cycle dynamics, evolution of species' niches). Scaling issues also highlight the intersection of temporal and evolutionary ecology. Evolutionary ecology – which explicitly incorporates the differential fitness of individuals into ecological processes – is a subset of temporal ecology occupying the macrobiotic scale (i.e. requires multiple generations, see Fig. 7). Temporal ecology is, however, distinct in its focus on responses to temporal dynamics – including cycles, events and non-stationarity – across scales such that many responses (e.g. phenology, behaviour, etc.) are not in themselves evolutionary, although they may be shaped by evolutionary processes.

Temporal dynamics observed at short timescales that do not appear to impact long-term dynamics have fuelled many of ecology's most vociferous debates (Wiens *et al.*, 1986). Mismatches in temporal grain are highlighted by the difficulties inherent in incorporating fast and slow processes in models of ecosystem dynamics (Carpenter & Turner 2000) or modelling temporal community coexistence via both seasonal (e.g. phenology) and interannual environmental dynamics (Chesson & Huntly 1997). Climate change has refocused ecological thinking on temporal scaling, providing a major new impetus to revisit fundamental questions and identify where scaling issues limit predictions. Particularly critical for understanding ecological responses to climate change is bridging from the shorter, more rapid temporal scales that characterise ecological responses to the longer timescales that encompass both evolution and other macro-temporal processes such as rock weathering, ecological succession and some climate system dynamics (Fig. 4).

Studying too short a timescale (narrow extent) can mean that important long-term cycles or slow processes are missed, which can hamper prediction. This problem is illustrated clearly in climatology by the failure to understand long-term variability in water budgets for the western US leading to over-allocation and persistent problems with sustainable water supply under the Colorado River Compact (Christensen *et al.*, 2004). In ecology, many annual population, community and ecosystem dynamics are at least partly driven by multi-annual climate cycles and variability. For example, the highest

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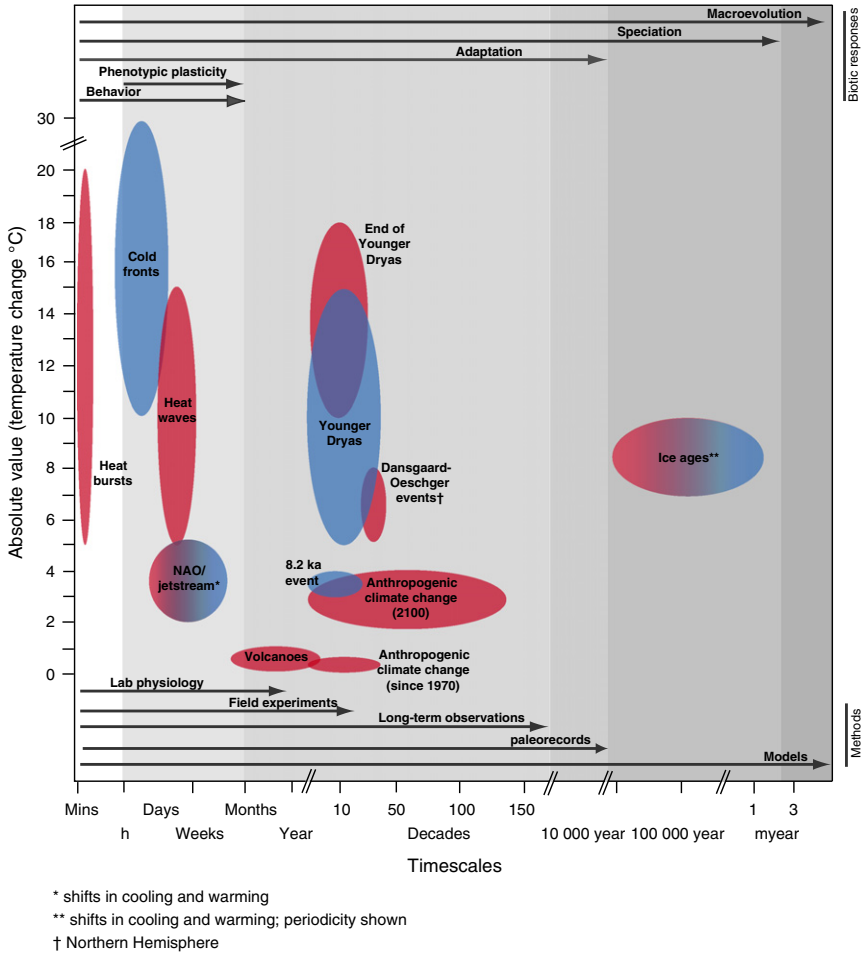

Figure 4 Robust forecasting in temporal ecology requires recognising the multiplicative dimensions of time inherent in most ecological processes (top arrows). For example, predictions of species' responses to climate change must consider: (1) that many species experience large shifts in temperature (blue indicates cooling, red indicates warming) on the timescale of hours to days (left) and (2) that over their evolutionary history many species have experienced climate swings similar in magnitude and rate to current and projected anthropogenic climate change (middle), in addition to the pressures of glaciation cycles (right). Differing methods in ecology (bottom) are optimised to differing timescales but ecologists are generally most adept at working in timescales of days to years. See Table S1 of the Online Supporting Information for details on data and references.

anomaly of global net primary productivity (observed in 2011) was attributable to high precipitation due to the strongest La Niña year recorded (Bastos *et al.*, 2013). Thus, consideration of the El Niño Southern Oscillation (ENSO) – a climate feature with approximately a 5-year periodicity – is essential in many ecological systems.

Conversely, observations collected at too large a temporal scale (coarse grain) rarely scale down to shorter timescales. For example, the temperature sensitivity of ecosystem respiration derived from annual data sets does not reflect the short-term temperature sensitivity calculated by extrapolating from night to daytime data (Reichstein *et al.*, 2005). For climate change responses, basal physiological timescales – such as daily metabolic or photosynthetic rates – are often more important for understanding ecological responses to the environment. Photosynthesis, for example responds to daily variations in temperature and light availability, which then integrates to gross and net primary productivity that will be additionally limited by weekly to monthly climate and weather variability (e.g. heat waves, frost events). Yet, despite the recognised importance of these basal scales, many ecological models have historically used climate data available at the monthly scale (Sitch *et al.*, 2003), leading to a disconnect between the timescale of ecological theory and the temporal resolution of the data.

This issue of temporal grain is perhaps most clearly illustrated by climate envelope models that are often used to predict species distributions. Such models frequently use seasonal and annual average temperatures as the primary constraints on species ranges, but much evidence indicates that ecological processes – including species' ranges – are limited not by mean climate, but rather the recurrence intervals of extreme events (e.g. fire, droughts) or higher order climatic moments (e.g. coldest winter day). For example, the distribution and population sizes of many insect pathogens are limited not by average summer or annual temperature controls on fecundity, but by mortality induced by minimum winter temperatures (Weed *et al.*, 2013). Further, increasing evidence from the paleorecord indicates that extant species have occupied quite different climate conditions in the past (e.g. Veloz *et al.*, 2012).

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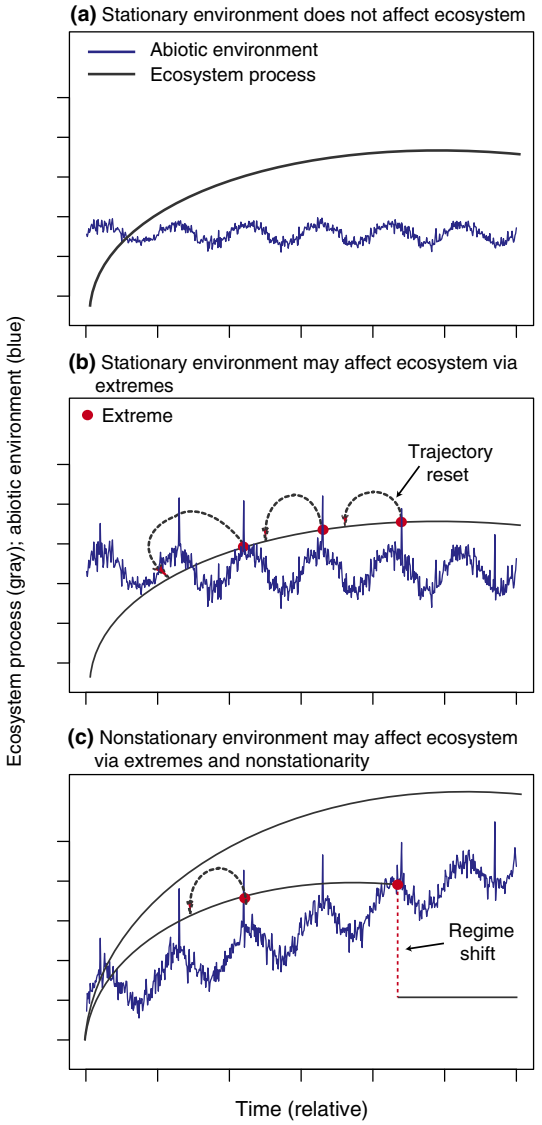

Figure 5 The evolution of how ecologists view time and the role of the environment in shaping temporal dynamics can be seen partly in the maturation of theory on succession – a fundamentally non-stationary ecological process. Early work (a) tended to focus on one trajectory and outcome, driven by a consistent, predictable turnover of species; mean climatic factors shaped the species pool, but climate was otherwise generally unimportant. As work progressed (b), ecologists recognised that multiple trajectories were possible – often triggered by climate extremes and other related disturbances (e.g. drought, fire) that reset the relative temporal position of an ecosystem along its development curve. More recently, ecologists have layered onto this an appreciation of factors that may yield diverse trajectories, endpoints and have highlighted that some events may transition ecosystems to fundamentally different states; non-stationarity in climate (c), or other ecosystem drivers, may contribute to such tipping points.

These observations suggest that at the very least, a more explicit consideration of time might lead to caution in the use of species distribution models under conditions very different than modern.

Related upscaling issues can be seen in attempts in evolutionary ecology to link short timescales on which ecological dynamics often occur to the longer timescales that shape species and lineages. For example, Lavergne *et al.* (2013) related rates of evolution derived from phylogenetic trees to species' current sensitivities to recent environmental change; this tacitly assumes information from two very different temporal scales – millions of years vs. decades to centuries – can be simply and directly linked. Timescale issues have also hampered efforts to estimate evolutionary rates (Schoener, 2011; Uyeda *et al.*, 2011). Over short timescales observations suggest rapid, but bounded evolution, consistent with population divergence over a fluctuating adaptive landscape within an adaptive zone (Uyeda *et al.*, 2011). While, over the longer timescales, sufficient for speciation, variance increases slowly, but more or less linearly – consistent with rare niche shifts that reconfigure the adaptive landscape. Reconciling this apparent disjunct seems a critical step before phylogenetic information can be robustly incorporated into ecological models of species responses to climate change.

Several basic approaches in ecology can help to identify and reconcile temporal scaling issues; in particular complementary timescales provided by differing approaches can be leveraged to address the same question. Ecological approaches have often been abstracted into experiments, observations, long-term observations and modelling (Carpenter, 1992). Experiments are often conducted on the shortest timescales – from days to weeks in the laboratory, to weeks and years in the field – and may only capture transient dynamics. Experiments generally allow, however, the most powerful tests of mechanisms (Chapin *et al.*, 1995; Wolkovich *et al.*, 2012; Laube *et al.*, 2014). Such tests are buoyed by comparisons with observational data, both short term (e.g. a single growing season or several years) and long term. Modelling can help to understand dynamics and generate predictions beyond the scale of observations, and incorporate longer-term dynamics such as climate cycles. Today, ecology has a significant advantage in integrating across timescales through increased interdisciplinary work with other fields, especially climate science, paleobiology and evolution.

For studies focused at a single temporal scale, the key is to match the timescale of observation with the timescale of the process (Fig. 7). Just as landscape ecology requires identification of the relevant spatial scale for sampling, temporal ecology requires identification of the relevant temporal grain and extent for addressing the ecological question of interest. As a first step this means recognising the relevant timescales – including the generation times of the study organisms, frequency of disturbance, as well as the period of climate oscillations – and then placing the study in the relevant part of these cycles. Improved integration of temporal scaling in ecological studies, however, will require continually cross-checking approaches of varying timescales, modelling studies to extend beyond currently available data and more integration of disciplines that have sometimes worked separately because of their underlying disparate timescales (Fig. 4).

Events: at the intersection of scaling & non-stationarity

Rapid bouts of evolution that reshape niches, extreme frosts that limit species' ranges and disturbances that alter community trajectories all highlight a major feature of temporal ecol-

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ogy: events. Events – the presence in time series data of non-cyclical and/or abrupt, and often non-stationary temporal patterns – are one area where temporal ecology diverges from spatial ecology. While the term 'event' has taken multiple meanings in the literature (see Box 1: Defining events), within ecology it typically refers to single, discrete occurrences, such as seed dispersal (Higgins *et al*., 2003), establishment of a new species (Blackburn *et al*., 2011), an extreme forcing such as a frost or drought (Jentsch *et al*., 2009) or a much larger climate shift, like the Younger Dryas (Jackson *et al*., 2009). Here, we view events more holistically (Fig. 8), and recognise that forcing events may be discrete (e.g. a frost or drought) or persistent (e.g. long-term warming trends), and the ultimate ecological responses may be transient (temporary) or persistent (continuous). Importantly, any ecological response to a forcing will depend on the system dynamics, including feedbacks (positive or negative), and resistance or resilience inherent to the system of interest. Events highlight temporal scaling issues as detection depends on three sampling features: the temporal frequency of sampling (grain), the duration of the sample period (extent) and the magnitude of the event or departure from previous samples. Events may not be detected or perceived as events if any of these three features is insufficient (Fig. 9).

Box 1 Defining events

Time is fundamentally about events, with research often aimed at quantifying their occurrence, duration and sequencing, however, a precise definition of the term is difficult to find in the ecological literature. For example, a variety of biotic and abiotic phenomena, including fire, establishment of invasive species, drought, insect irruptions, frosts, etc. are often referred to as events. Improved understanding of temporal events in ecological systems would benefit from clearer and more precise language. Thus, we suggest a more holistic view of ecological events (Fig. 8) as forcings or responses that may be short-lived (transient) or persistent (continuous). Considering forcings, a transient ecological forcing encompasses most short-lived disturbance (such as a fire or insect outbreak) that may lead to a variety of ecological responses (e.g. a persistent shift in community composition, a temporary reset of the successional sequence, etc.). These can be differentiated from more persistent, continuous changes, such as the introduction of an invasive species or climate change that may also induce short lived, or more permanent, ecological responses. One area of temporal dynamics that is of particular interest is how quickly and persistently ecosystems respond to these two types (transient vs. persistent) of forcings (see Fig. 6) and how such forcings may drive transient or persistent ecological responses.

Critically, the permanence and velocity of ecological responses depend not only on the nature of the forcing (e.g. its severity and duration), but also on the inherent capacity for resistance, resilience and feedbacks within the ecosystem or community of interest. Thus, events may be better specified in terms of whether they are related to the forcing or response, and whether they are transient or continuous. For example, vegetation may quickly return to its previous state following transient disturbances, such as a fast growing grassland recovering after a fire or drought (e.g. Weaver & Albertson 1936; Albertson & Weaver 1944), or a plant down-regulating initial photosynthetic enhancement in response to elevated CO_2 concentrations (Leakey *et al*., 2012). Both responses can be considered transient, regardless of the nature of the forcing, and may indicate either some inherent resilience in ecosystem structure and function (in the grassland example), or fundamental shifts in the importance of the resource limitation and environmental stressor space (as in the CO_2 example). Ecosystems may also respond in persistent ways to either transient or persistent forcings. A relatively recent example is the switch from a ponderosa pine forest to a piñon-juniper woodland in southwest North America following a major drought in the 1950s (Allen & Breshears 1998). This new woodland persists to this day, despite a subsequent return to more normal moisture conditions. In another example, during the Mid-Holocene the Sahara permanently shifted from a woodland savanna to a hyper-arid desert in response to changes in Northern Hemisphere summer insolation, with the ecosystem collapse happening much more quickly than the forcing change (Foley *et al*., 2003). Clearly, the nature of forcing events (fast or slow, discrete or persistent) does not necessarily map clearly onto ecological responses, presenting a challenge for better prediction of the speed and persistence of ecosystem responses.

Additional difficulties may be presented by a special class of events known as 'Black Swans'. A Black Swan event is defined by two components: (1) that it has dramatic effects on the system, but is extremely rare, such that (2) it is effectively impossible to predict using current methods. These two components lead to the third aspect of Black Swan theory: owing to their large impact on the system there is a strong tendency to believe such events can be predicted – when, instead, by their extreme rarity this is often impossible. There is already evidence for ecologically important 'Black Swan' events. One example is an 18th century drought in eastern North America that has shaped successional trajectories to this day (Pederson *et al*. in press). While another, more well-known example, is the Salton Sea, an inland body of water in southern California that formed during a large flood event in the early 20th century, and subsequently became a critical habitat for wildlife and migratory birds (Cohn, 2000). Identifying these events and their importance for ecological processes in historical and paleoecological data, however, remains challenging.

Events may also be characterised by significant non-stationarities in ecological systems. Examples include regime shifts in aquatic communities caused by changes in food web

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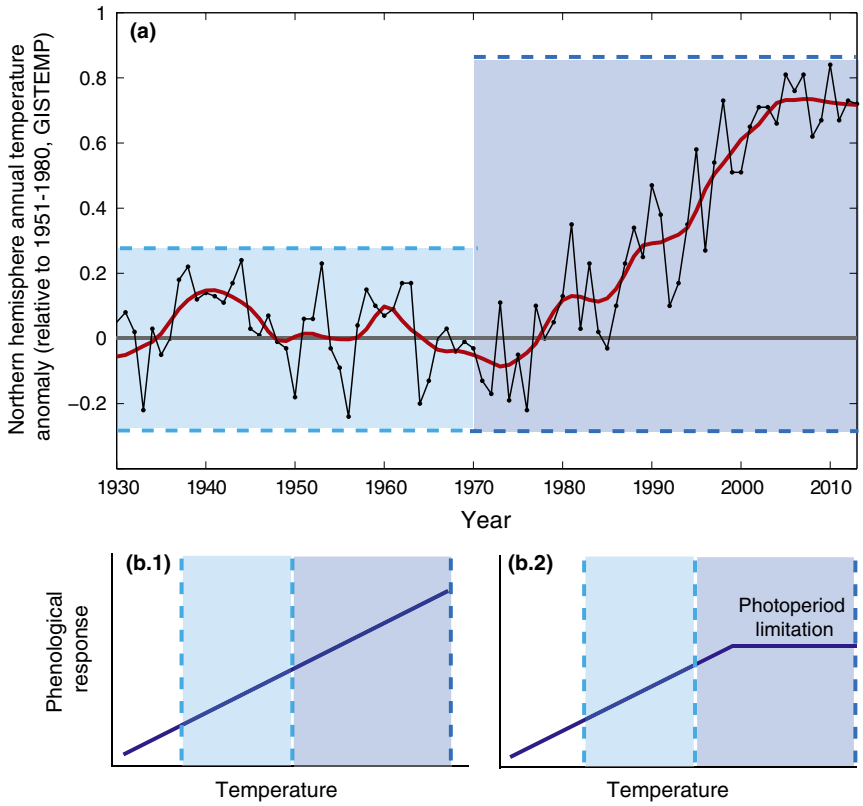

Figure 6 Forecasting ecological responses to climate change requires layering projections of complex physiological responses onto non-stationary drivers, such as increasing temperatures (a), shown with a 10-year loess spline in red. Much research has focused on projecting phenological responses to this increasing temperature (b), which requires understanding whether responses are approximately linear (b.1), where higher spring temperatures yield progressively earlier leafing or flowering, or nonlinear (b.2) where responses to temperature are limited at higher values by additional factors, for example photoperiod, though drought, nutrients or other factors could also be critical. Such responses may look identical under a stationary climate regime (lighter blue shading), but would diverge once the threshold is crossed under non-stationary climate (darker blue shading).

structure (Carpenter *et al.* 2011), irreversible ecosystem changes caused by disturbance events (Allen & Breshears 1998) or changes in ecosystem structure and function with the removal of key species (Mumby *et al.*, 2007). Because many extreme transient forcing events (e.g. droughts, heat waves) and their consequences (e.g. community shifts, extinctions) are often rare, predicting their occurrence and ecological impacts has been difficult. Recent efforts, however, to test models of regime shifts (Carpenter *et al.* 2011; Boettiger *et al.*, 2013) and to predict the outcomes of contingency events in shaping communities (Vannette & Fukami 2014) have shown promise.

Forecasting ecological systems in non-stationary environments

The ultimate goal of any mature science is prediction. Thus, while many of the questions that structure temporal ecology address fundamental issues in ecology, they are also critical for ecological forecasting. These questions follow naturally from the topics already discussed: which attributes of events and temporal non-stationarity create persistent shifts in ecological systems? How can we relate processes that occur at differing timescales (e.g. differing resolutions or durations)? How do events and different types of autocorrelation, including non-stationarity, affect our ability to extend inferences from one time period or timescale to another? Additionally important are questions related to the interaction of abiotic and biotic timescales (Fig. 7) including: How do abiotic and biotic processes interact across temporal scales? How important are the different scales of interaction for long-term ecological dynamics? What are the timescales and temporal dynamics (e.g. events, non-stationarity etc.) when abiotic vs. biotic drivers dominate ecological dynamics?

Addressing these questions would make fundamental contributions to expanding and improving predictions in ecology. They would critically help answer whether inferences drawn from contemporary and historical data are appropriate for forecasting under quantitatively different boundary conditions. For forecasting, researchers must also address scaling issues with the often coarser (i.e. larger grain) temporal data available for model calibration and prediction. For example, understanding how a species responds to climate change must consider how a species' response to a persistent increase in mean temperatures over many years may differ from the much larger – but shorter term – fluctuations that many populations and species experience on a daily or weekly basis (Fig. 4), and whether responses across such timescales are linked. Relatedly, given that most species ages are 1–10 million years (Lawton & May 1995) the best projections would

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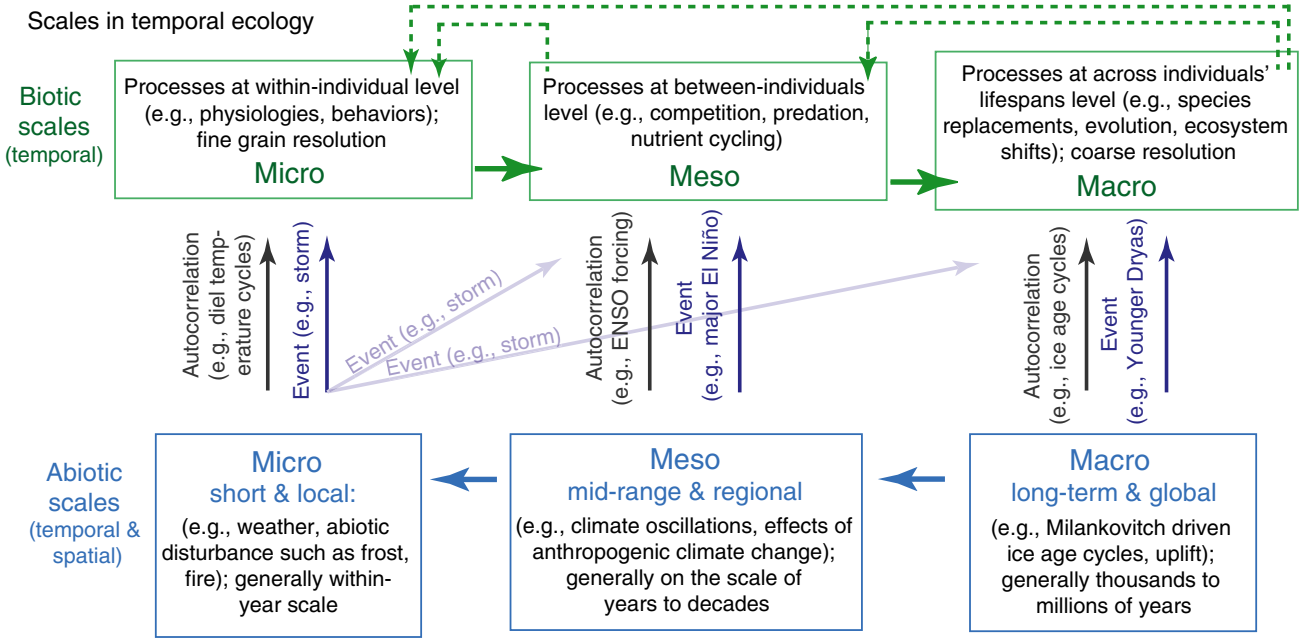

Figure 7 Timescales in temporal ecology vary greatly across species and systems, but are united by the same fundamental biotic timescales relevant to organisms in the system. These include generation times that define the microscale and – considering biotic interactions and related processes (e.g. nutrient cycling) – the mesoscale, as well as longer timescales required for major ecosystem and evolutionary shifts. Biotic timescales inherently build up (e.g. micro affects meso etc.), though feedbacks (dashed arrows) are also important. In contrast, abiotic timescales generally build down (e.g. ice age cycles can affect ENSO dynamics, which can affect local weather). Biotic and abiotic timescales are intrinsically linked, often through autocorrelation (shown in gray arrows, though additional effects are possible), and events (dark blue arrows), which may often transcend scales (see 'storm' example). Additionally, not shown but important are potential feedbacks between from biotic to abiotic processes (e.g. vegetation altering the global carbon cycle and climate).

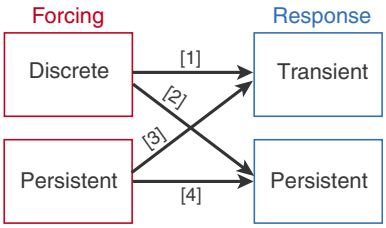

Figure 8 Understanding the role of events in shaping ecological systems could benefit from an improved classification of events. In particular, ecosystem responses to discrete events (e.g. fires, droughts, insect defoliation, etc.) may be either short lived and transient [1], or persistent and continuous, reflecting changes in the background state (e.g. climate change, introduction of invasive species, habitat fragmentation, etc.) [2]. Similarly, however, persistent forces may give rise to transient ecological responses [3] or persistent responses [4].

also consider how a species has responded to previous major climatic shifts, which are often equal in magnitude and rate to current climate change (Fig. 4).

Autocorrelation presents its own set of challenges for prediction, and may either help or hinder depending on – ultimately – what the autocorrelation represents and how it is resolved. For example, if autocorrelation in a population time series manifests as some intrinsic year-to-year persistence or robust cyclicity, incorporating this information into a predictive model may improve model skill. Alternatively, if autocorrelation is not accounted for correctly, it may undermine model development and lead to less useful projections. The significance of a statistical relationship between two time series may be overestimated, for example if the autocorrelation is not accounted for correctly, and thus lead to an inaccurate predictive model.

Projecting shifts in communities with non-stationarity would benefit from increasing recognition of how temporal non-stationarity structures ecological communities. For example, research on historical contingencies and temporal legacies may help forecast communities in non-stationary systems. Studies of community and ecosystem stability (Boettiger *et al.*, 2013), paleoecological systems and modern disturbance ecology have provided foundational work on the role of contingency in driving ecological systems and highlighted that historical contingency is often more common than predictable, deterministic sequences over time. Moving forward, the challenge is to build theory that incorporates contingency and develops more robust tests of how contingencies operate (Vannette & Fukami 2014). More research is also needed on the role of multiple or compound disturbances in altering trajectories and on how environmental non-stationarity may make regime shifts more common by effectively moving the underlying environmental track (Fig. 5c). Given the importance of non-stationarity, and the increasing evidence that ecological trajectories are often not deterministic, ecological forecasting may additionally benefit from probabilistic, rather than deterministic, modelling approaches, such as those used in the field of climate science (Tebaldi & Knutti 2007). Probabilistic sampling and modelling allow for better understanding of the internal, unpredictable variability in the system. Such

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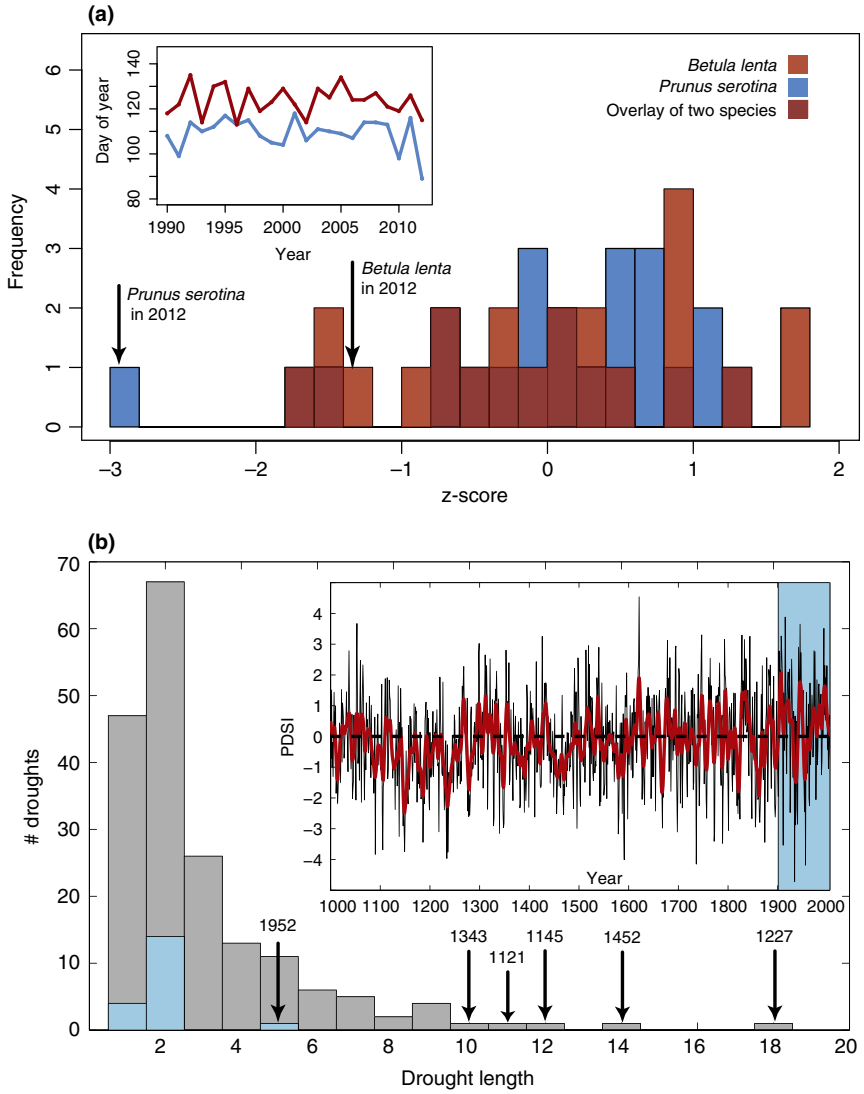

Figure 9 Paralleling grain and extent in spatial ecology, in temporal ecology both the frequency (a) and duration (b) of sampling are important. In phenology research (a), increasing the frequency of sampling to study more species can affect the interpretation of a climate event. For example, 2012 was an extremely warm spring in northeastern North America and typically early-season species flowered very early (see *z*-scored data – where negative indicates earlier and positive later, inset shows raw time series data), while other species that flower later did not show as extreme a response. Duration of sampling also can affect how extreme an event appears (b). Considering only the 20th century (b, light blue bars in histogram, light blue shading of Palmer Drought Severity Index – positive indicates wetter and negative indicates drier than normal), a 5-year drought in central North America appears uniquely long. Far longer droughts occurred, however, over the last 1000 years. See Online Supporting Information for details on data and references.

an approach may also allow for detection and attribution of controversial topics in ecology for which data are limited, such as CO_2 fertilisation and invasive species, as well as understanding the importance of very rare events, such as Black Swans (Box 1).

COMBINING THE AXES OF SPACE & TIME

A more robust framework for temporal ecology will help unite the predictive – and intertwined – frameworks of spatial and temporal ecology, allowing researchers to better address one of the most fundamental questions in ecology: how do we link spatial and temporal patterns and concepts to improve ecological theory and forecasting? We argue that advances in temporal ecology could be motivated by the example of spatial ecology in recognizing and understanding hidden dimensions in ecological models and theory. While in turn, decades of progress in understanding the consequences of spatial processes have resulted in a return to the importance of temporal dimensions in ecology. For example, island biogeography theory predicts species richness based on several basic spatial metrics – but temporal dimensions of the controlling processes – immigration, extinction and speciation – are also fundamental to predictions (Wiens, 2011). Similarly, disease models have advanced through incorporating both spatial and temporal models of travelling waves as disease prevalence varies both with population density and temporal fluctuations in that density (Grenfell *et al.*, 2001) and climate (Lipp *et al.*,

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2002). In paleoecology, research has advanced to visualise past vegetation assemblages in both space and time by combining data from across diverse sites and spanning 10 000 years (Brewer *et al.*, 2012). Perhaps the current best example of spacetime integration comes from outside of ecology from climatology, where methods such as empirical orthogonal function analysis allow the simultaneous exploration of temporal and spatial patterns in climate data, and could be employed in examining some of the longer term, spatially explicit data sets in ecology.

These recent advances represent, however, only a small foray into the potential benefits possible from fully embracing the interconnectedness of spatial and temporal dynamics in ecology. Consider coexistence theory – long stymied by models that required *n* different axes to produce *n* coexisting species alongside empirical examples of many co-occurring species that appeared quite similar when examined from one snapshot – it advanced when the role of variability in species' responses to the temporal dimension was re-examined (Chesson & Huntly 1997). Under the storage effect model, highly similar species coexist via small differences in how they respond to temporal variability in the environment. Since its introduction the storage effect model has been ported to spatial dimensions – where species coexist via reduced competition from spatial variability. Tests for such models have found support separately for temporal (Angert *et al.*, 2009) and spatial (Sears & Chesson 2007) storage effects, but we expect most communities function based on a constantly shifting mix of the two mechanisms. For example, studies of community change in the Great Plains during the years of the Dust Bowl show dramatic shifts in abundance of dominant vs. rare species, suggesting a role for the temporal storage effect (Weaver & Albertson 1936), while recent work in the same habitat suggests spatial variability via microclimates is also important (Craine *et al.*, 2012). In such cases, temporal storage effects may be built on buffered population growth maintained by spatial dynamics. Further, by modelling the environment explicitly, such models could make predictions of how fundamental coexistence mechanisms may shift with climate change and help answer critical questions of how communities built on coexistence mechanisms via a temporally and/or spatially variable environment will respond when that environment switches from stationary to non-stationary.

Finally, robust projections of climate change impacts on populations and species will require an adjustment to the most classic spatial metaphor for a temporal process: adaptive landscapes. Non-stationarity in climate has resulted in rapid and effectively continuous shifts to most populations' adaptive peaks and valleys. Climate change has thus highlighted how rapid evolution may be and has brought it firmly into an ecological timescale, but theory as to how such non-stationarity may affect evolutionary outcomes remains a challenge (Schoener, 2011; Bailey, 2014).

Spacetime in conservation ecology

While habitat loss has been the main driver of extinctions historically, climate change poses perhaps the biggest threat to biodiversity in the future, and has been our focus here. Nonetheless, multiple anthropogenic forcings, including habitat fragmentation and modification, the alteration of disturbance cycles, and the widespread dispersal of invasive and exotic species, can all result in non-stationarity over ecologically relevant timescales. Yet we lack general theories and paradigms to shape and guide research efforts on shifting temporal dynamics. We believe a unified field of temporal ecology that integrates across methods, concepts and theories while focusing on issues of scaling, non-stationarity and the detection and role of events would help address this gap. Recent advances within subfields incorporating environmental variability into coexistence models (Chesson & Huntly 1997), bridging ecological and evolutionary timescales (Schoener, 2011), revisiting the role of climatic events in setting range limits (Khai Tran *et al.*, 2007) and in modernising paleoecology (Brewer *et al.*, 2012) indicate that the discipline of ecology is up to the challenge.

A renewed temporal ecology framework has particular relevance for conservation science in the Anthropocene, where ecological dynamics operate in increasingly non-stationary environments dominated by rising rates of anthropogenic change. Traditionally, conservation biology has focused on space – identifying the best locations to conserve species or habitats (e.g. Cincotta *et al.*, 2000), motivating the establishment of reserves, refugia and corridors (e.g. Doak, 1989). However, non-stationarity in climate highlights the necessity of also considering changes over time (Hannah *et al.*, 2002). For example, species range shifts associated with climate change suggest that policies for setting conservation areas must not only consider current suitable areas, but also how these areas might change in the future. Within a climate change scenario, the very concept of conserving biodiversity within fixed protected areas may be misguided (Rutherford *et al.*, 1999). A joint consideration of space and time may help resolve some of the current debates on trade-offs between prioritising species conservation for habitat loss (space) and climate change (time), and a dual consideration of both space and time will allow the identification of where and when the best opportunities exist for mitigation and conservation.

A broader temporal ecology perspective may also help inform the probability and potential impact of extreme events, such as Black Swans (see Box: Defining events), and the resistance and resilience of ecosystems to these events. For example, a species or ecosystem may adapt to long-term changes in the average climate (e.g. long-term warming), but recent shifts in many landscapes (e.g. Anderegg *et al.*, 2013) highlight that the frequency and impact of extreme events (such as drought and insect irruptions) may fundamentally alter ecological responses. Conservation strategies must additionally consider how such events may impact the resistance and recovery of ecosystems to further events in the future. Insights into these issues can be gained from historical and paleoecological data but projecting into the future will require recognising the non-stationary nature of these processes.

CONCLUSIONS

The two greatest threats to ecological systems in the Anthropocene – habitat degradation and climate change – represent

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human modifications of space and time, shifting the fundamental axes of ecological systems. As ecology is challenged to better understand and predict these changes gaps in our body of concepts, theories and methods have appeared. Such gaps, however, also highlight opportunities for advances in both basic and applied ecology. In the twentieth century, classical Newtownian physics gave way to Einstein's theory of relativity with the recognition that time is not simply a fourth dimension orthogonal to space, but a relative metric, inherently intertwined with space. Ecology now has an opportunity to build a similarly integrative spatiotemporal framework. Clearly, ecology has progressed significantly in recent decades as data spanning years, decades and centuries have become increasingly available in paleo-, conservation, community and ecosystem ecology. The challenge remains, however, to develop a holistic structure that will allow for cross-disciplinary sharing of methods and ideas to leverage the strengths of these disparate fields. Encouragingly, such work is being developed in areas including phenology (Pau *et al*., 2011), paleoecology (Brewer *et al*., 2012), and conservation (Mooers *et al*., 2008), suggesting there is great potential for rapid advances.

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AUTHORSHIP

EMW conceived of and wrote the manuscript; BIC, KKM and TJD wrote sections of the manuscript, edited it and assisted with figures; in particular, BIC wrote Box 1 and contributed to Figs. 2 and 4-9. KKM conceived of Fig. 3.

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