

## REVIEW SUMMARY

## ECOLOGY

# Ecological and evolutionary consequences of changing seasonality

Daniel Hernández-Carrasco\*, Jason M. Tylianakis, David A. Lytle, Jonathan D. Tonkin\*

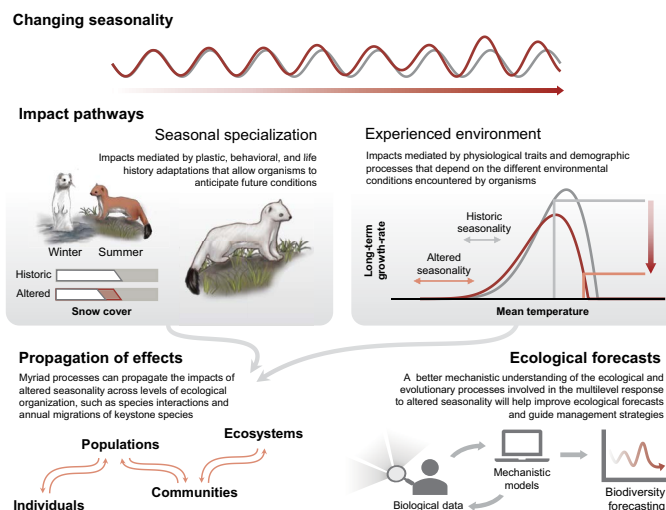


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**BACKGROUND:** Climate change is rapidly altering seasonal regimes in terrestrial, freshwater, and marine realms, disrupting the natural rhythm of ecological processes. Seasonality is so fundamental to ecosystems that these shifts threaten the maintenance of biodiversity and its contributions to society. Recent advances across several fields in ecology and evolution have identified links between environmental seasonality and processes affecting natural systems at different levels, from the genetic structure of populations to whole ecosystem functions. These connections reveal unexplored pathways through which changes in seasonality could affect biodiversity and propagate across multiple levels of ecological complexity. At the same time, ecological and evolutionary processes governed by seasonality can determine species' ability to adapt to changing seasonal patterns. Yet, despite the potential pervasive consequences for biological systems, changing environmental seasonality remains a largely overlooked dimension of climate change. We explore the diverse ways in which altered seasonal patterns can produce cross-level ecological responses. Given the prospect of further seasonal shifts over the next decades, it is imperative to identify and quantify the mechanisms that underpin biological responses to seasonal regimes and the potential for species to adapt.

**ADVANCES:** We synthesize theoretical and empirical evidence to identify two broad pathways through which altered seasonality affects living systems: the demographic response to the experienced environment, and adaptations that allow the synchronization with environmental fluctuations. The former is closely linked to the physiological constraints and adaptations determining populations' demographic rates in different environmental conditions, whereas the latter depends on plastic, life-history, and behavioral traits that allow organisms to track seasonal fluctuations. We show that both pathways can propagate the effects of changes in the amplitude, timing, and predictability of seasonality, though the mechanisms may depend on the average conditions of the environment. This interplay provides a means for climate change to affect ecological processes linked to seasonality, including population phenology and species interactions, even when other attributes of seasonality remain unchanged. Furthermore, previous adaptations to seasonality, such as the use of environmental cues, could limit species' tracking of environmental changes through evolutionary adaptation and latitudinal range shifts. Recent developments in modeling enable the inclusion of complex interactions among processes operating at different levels. Such models can predict emergent properties such as biodiversity change by allowing the propagation of known effects across levels—an area ripe for advancement in the context of changing seasonality.

**OUTLOOK:** The pervasive effects of seasonality and the interactions between processes operating at multiple levels increase uncertainty around the future of biodiversity in the face of global disruptions to



## Rapidly changing seasonal patterns can generate complex ecological impacts.

These impacts arise through (i) adaptations that allow a proactive response to periodic shifts in the environment (e.g., coat color changes with environmental cues) and (ii) individual performance under conditions experienced throughout the year (e.g., temperature-dependent growth). Such impacts propagate across levels of organization, often producing nonlinear responses, which require mechanistic approaches to anticipate.

seasonality. A deeper understanding of the effects of altered seasonality will help build tools to forecast ecological dynamics into a no-analog future. Empirical work is thus necessary to uncover and quantify these effects, but consensus between applied and theoretical studies is paramount. Such consensus can be achieved by using more ecologically informative measures of seasonality that incorporate the critical components to which biodiversity responds. The resulting theoretical knowledge can be used to inform mechanistic models that allow the propagation of effects across levels of ecological organization. Although part of the information required to build fully mechanistic models might currently be lacking, our synthesis suggests that including species' phenology and their demographic response to the environment can already improve current predictions. Understanding the mechanisms that allow the propagation of impacts opens new avenues for improving conservation planning, invasive species management, large-scale restoration, and biodiversity forecasting. □

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## ECOLOGY

# Ecological and evolutionary consequences of changing seasonality

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Climate change and other anthropogenic drivers alter seasonal regimes across freshwater, terrestrial, and marine biomes. Seasonal patterns affect ecological and evolutionary processes at different ecological levels through changes to gene frequencies, species traits, population dynamics, species interactions, and different facets of biodiversity. We synthesize the mechanisms that determine biological responses to seasonality, to demonstrate how their interconnections can propagate impacts of altered seasonal patterns and complicate predictions. Given the potential for nonlinearities and the propagation of impacts across levels of ecological complexity, we advocate the use of mechanistic approaches that acknowledge species-specific responses to the environment and potential seasonal adaptations.

Seasonality is a fundamental aspect of Earth's environment, driven by its tilt and annual movement around the Sun. From tropical forests to abyssal depths, seasons generate cyclic changes in environmental conditions, including temperature, daylight duration, precipitation, and resource availability (1, 2). These seasonal fluctuations shape natural systems at multiple ecological levels, ranging from the genetic structure of individual populations (3) to whole ecosystem functions (4). The timing of life-history events such as reproduction, growth, and migration is tightly tied to the specific annual pattern and across-year consistency (predictability) of seasonal fluctuations experienced by organisms (5). Furthermore, seasonality underpins the biodiversity observed in natural communities through the coexistence of organisms that exploit different conditions throughout the year (6, 7).

Climate change is disrupting many seasonal patterns, generating observable shifts in the timing, amplitude, and predictability of key environmental drivers (2, 8–11). These changes pose a threat to Earth's biodiversity and thus its key contributions to society, such as food security (12, 13), climate regulation (14), and the biotic control of diseases (15). However, the ecological consequences of changing seasonal patterns may be greater than previous syntheses (16–20) have identified, because biological responses to seasonality may propagate across levels of ecological complexity. Cross-level mechanisms could amplify the direct effects of seasonality and generate nonlinear responses that would be impossible to predict when looking at individual levels only, as has been shown for other aspects of climate (21, 22). For instance, species' adaptations to seasonality and their interactions with other species can mediate impacts on the carbon cycle (23), whereas changes in seasonal migration patterns can result in the restructuring of whole food webs (24, 25). Although

the effects of seasonal fluctuations at single levels are often well understood, at least in theory (17–19, 26), a framework is needed to account for the complex mechanistic connections between genetic and ecological processes across levels. Understanding these cross-level links between seasonality, species' ecology, and both rapid and longer-term evolutionary processes will enable more accurate predictions of emergent biological responses to environmental change.

Here, we synthesize biological responses to changes in seasonal patterns across multiple levels of ecological organization and demonstrate that they depend on the components of seasonality that have been altered. We identify the primary pathways that mediate biodiversity responses to seasonality and how these can propagate across levels of ecological complexity. Our synthesis highlights that overlooking these multilevel processes can increase the uncertainty around biodiversity forecasts. In particular, we emphasize the need for a mechanistic understanding of the biological processes involved in the response to altered seasonality and pathways that generate and propagate impacts.

## Changing patterns of environmental seasonality

Different ecosystems exhibit different degrees of seasonality and predictability. Distinct rates of solar irradiation result in high latitudes having strong seasonal fluctuations, driven by changes in daylight and temperature, whereas seasonality in tropical regions is mostly related to rainfall, with alternating wet and dry seasons (27). The seasonality and predictability of environmental drivers are also modulated by local factors, including distance to the sea, land cover, altitude, continentality, and atmospheric circulation (28). Regions at similar latitudes can thus experience starkly contrasting seasonal patterns. For instance, although Spain and New Zealand are located at a similar distance from the equator (40°N and 41°S, respectively), the former presents strong rainfall seasonality typical of Mediterranean regions, whereas rainfall variability in the latter follows a much weaker annual pattern because of its maritime position (7).

Global patterns of seasonal environmental fluctuations are undergoing changes that are predicted to continue in the coming decades (8, 29, 30). These changes can primarily be attributed to climate change, including trends in the amplitude of thermal fluctuations (8, 10, 31), the variability and predictability of water availability (2, 9, 11), and the timing and duration of seasonal oceanic upwellings (32). European rivers have experienced shifts in the timing of seasonal floods of up to 14 days over the past 50 years, owing to altered timing of snowmelt, rainfall, and evapotranspiration (33). In the Southern Ocean, seasonal algal blooms have reduced their duration and predictability while increasing their amplitude (34). Local impacts can further modify seasonal fluctuations. For example, water resource management using dams modifies the natural frequencies of floods and droughts in rivers, with important implications for ecological processes (35, 36). Similarly, changes in land use, such as deforestation, urbanization, and different agricultural practices, can amplify, dampen, or shift seasonal patterns of temperature, nutrients, and water availability (37, 38).

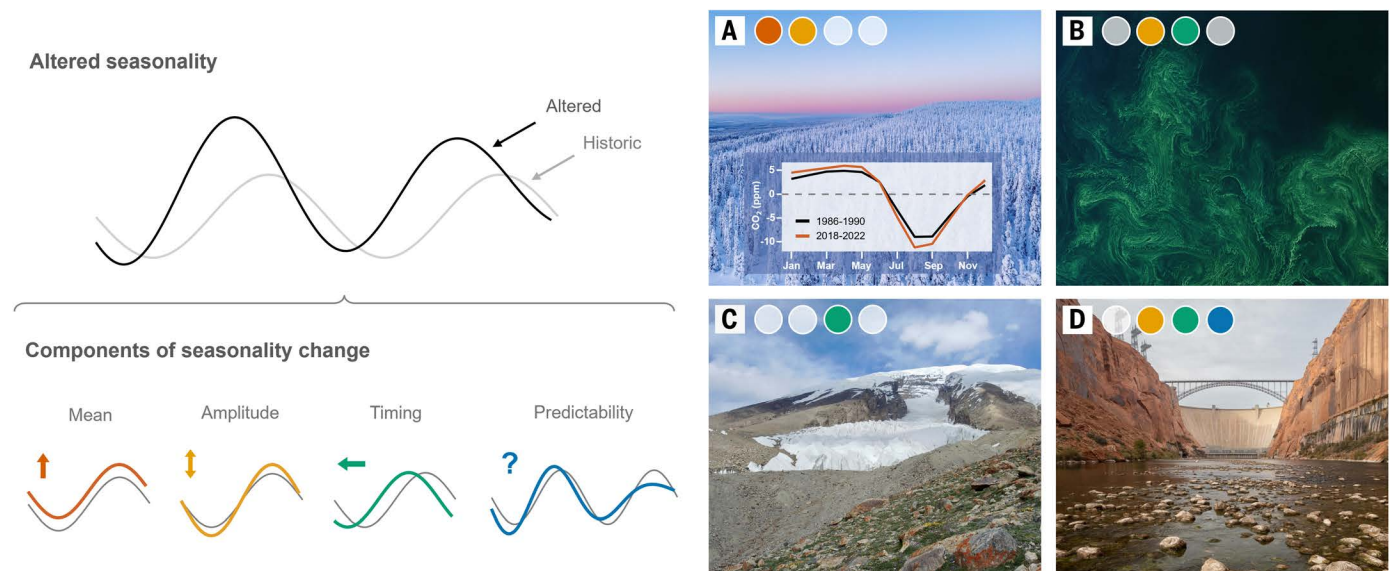
Changes in seasonality can be described as a combination of changes in the amplitude, timing, and predictability of fluctuations, in addition to the mean environment (Fig. 1). Here, we focus on these components because of their broad ecological relevance across systems, while acknowledging that other factors may be equally important in some cases. For instance, the rate at which environmental conditions transition between seasons can be altered by changes in the characteristic shape of the seasonal cycle (timing) or its amplitude, with potential ecological consequences including organisms' ability to respond in a timely manner (39), and species coexistence (40). Similarly, other forms of environmental variability contribute to the unpredictability of seasonal cycles among years, each with important attributes such as their degree of autocorrelation (41, 42).

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**Fig. 1. Human impacts on seasonality are multifaceted.** (Left) Altered seasonal patterns can be described as a combination of changes in the mean (the average state of the environment during the year), amplitude (the magnitude of seasonal environmental variation), timing (the specific time during the year when certain environmental conditions occur), and predictability (the consistency of the seasonal cycle across years) of fluctuations. (Right) Examples of typically seasonal biotic and abiotic processes affected by climate change and localized human impacts. Circles indicate the main components of seasonality that have been affected. (A) Increasing amplitude of seasonal fluctuations in atmospheric CO<sub>2</sub> concentrations due to prolonged photosynthetic activity at higher latitudes (14), in addition to the global increase in mean concentrations. Panel shows detrended annual pattern in CO<sub>2</sub> concentration in Alert, Canada. Data from NOAA (<https://gml.noaa.gov>). [Panel image from ArtBBNV/Shutterstock.com.] (B) A combination of environmental and biotic factors have altered the amplitude and timing of seasonal algal blooms in the Baltic Sea (145). Satellite image from NASA Earth Observatory (<https://earthobservatory.nasa.gov>). (C) Increasing average temperatures have advanced the timing of spring snowmelt worldwide (146). [Image by J. D. Tonkin.] (D) Flow management using dams modifies the natural flow regimes of rivers around the world (35), including changes in the timing of peak flows, the amplitude of flow fluctuations, and the predictability of flow variation. Image shows the Glen Canyon Dam on the Colorado River. [Image by D. Herasimtschuk/Freshwaters Illustrated.]

### Cross-level biological responses to altered seasonality

Rapidly changing seasonality affects ecological and evolutionary processes across a range of levels of organization. Ecological dynamics in seasonal environments depend on a suite of adaptations that enable species to anticipate periodic changes in their environment (5, 43), and a combination of immediate and delayed responses to biotic and abiotic conditions experienced throughout the year (44, 45). Changing seasonality can therefore affect biodiversity through these two main pathways: species' seasonal specialization and the physiological and demographic response to the seasonally fluctuating environment (discussed in the following two subsections). These distinct but interconnected pathways are most tightly linked to different components of seasonality. Changes in timing and predictability interfere with species' seasonal specialization (e.g., seasonal reproduction or migration) by impairing their ability to anticipate future environmental conditions. Meanwhile, changes in amplitude and mean alter the range of conditions that organisms encounter throughout the year, influencing their performance through physiological traits and demographic processes that depend on the environment (e.g., temperature-dependent mortality). We review these different components and response pathways to identify how altered seasonality can have impacts that cascade across levels of biological organization.

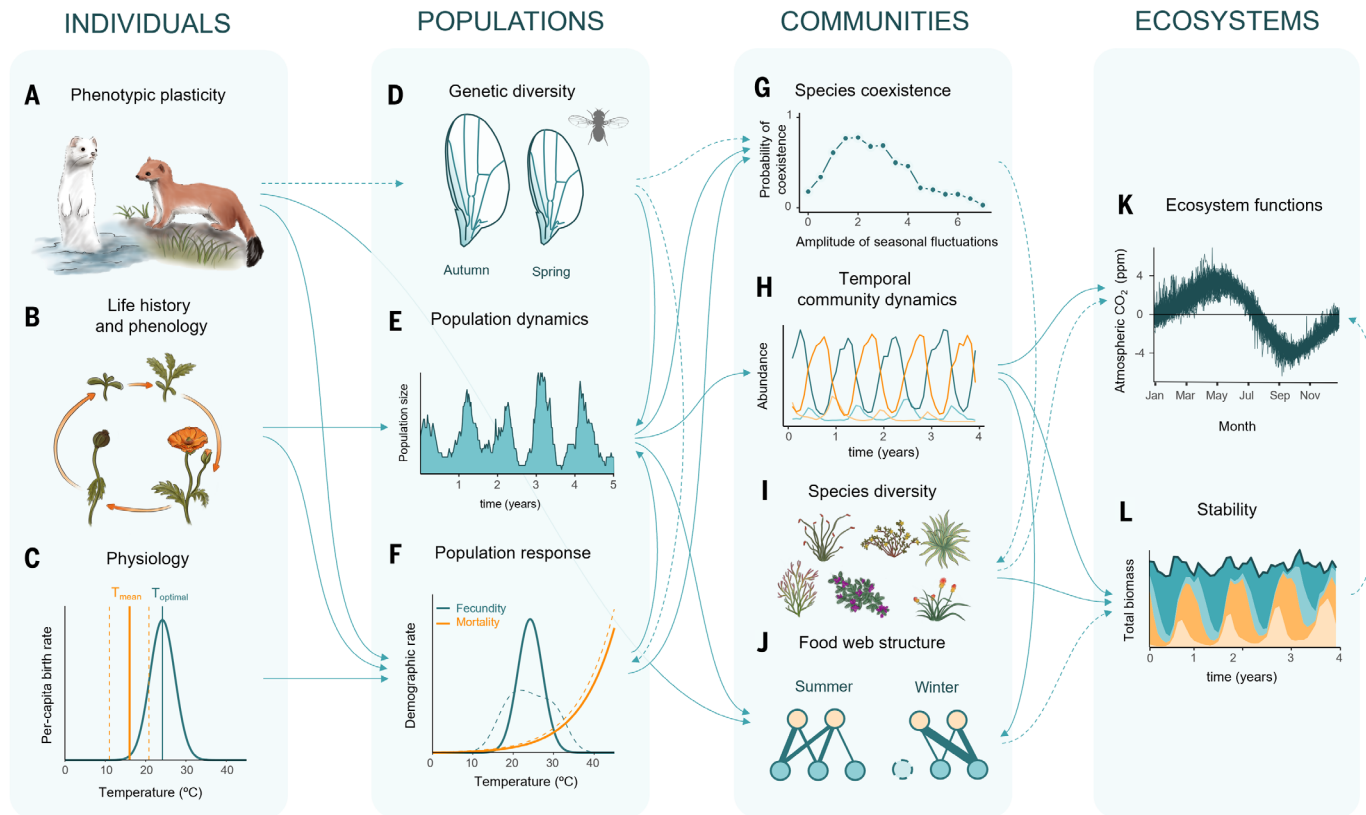
### Impacts mediated by species' seasonal specialization

Species' adaptations play a central role in shaping the impacts of changing seasonality on ecological systems, from species' fitness to whole ecosystem functions (13, 26, 46). Different species use different environmental cues to anticipate the timing of predictable seasonal changes, but day length and temperature predominantly determine phenological events including dormancy, flowering, and germination (47, 48). The mechanisms that allow proactive responses to future

environmental conditions can be an integral part of species' life cycles, allowing the synchronization of life histories to environmental fluctuations. For instance, individuals maximize gains in seasonal and predictable environments by scheduling growth, reproduction, energy storage, and development within the annual cycles of the environment (5). In addition, many species exploit environmental cues to time movement patterns with seasonally varying resources, while escaping unfavorable conditions (25). Seasonality can also promote intraspecific phenotypic variation in response to environmental cues through differences in the expression of single genotypes (adaptive phenotypic plasticity). This mechanism is found in birds and mammals that use day length as a cue to perform biannual coat color molting in response to seasonal snow cover (Fig. 2A) (49). Collectively, plastic, behavioral, and life-history adaptations allow a high degree of seasonal specialization, enabling individual-, population-, and community-level synchronization with seasonal fluctuations (Fig. 2, A, B, E, and H).

By contrast, organisms living in less predictably seasonal environments adopt strategies that minimize risks, even if the strategy is suboptimal under average conditions. These bet-hedging mechanisms can be broadly described as "playing it safe" (conservative bet-hedging) or "not putting all eggs in one basket" (diversifying bet-hedging) (50). Species have evolved myriad bet-hedging strategies to minimize the risk associated with unpredictable conditions, such as continuous reproduction throughout the year, partial or facultative migration [but see (51)], and the generation of eggs or seeds with prolonged dormant stages (50, 52, 53). At the genetic level, environmental unpredictability may select against adaptive phenotypic plasticity and instead favor phenotypic variance (i.e., the production of a fixed proportion of each phenotype within the offspring) as a diversifying bet-hedging strategy (54, 55). Both conservative and diversifying bet-hedging strategies translate into a reduction in population-level variance of important





**Fig. 2. The ecological effects of seasonality propagate across levels of ecological organization, from individuals to ecosystems.** (A to L) Panels represent direct effects of seasonality, whereas arrows indicate potential cross-level consequences (many referred to in the main text). (A) Northern populations of stoats (*Mustela erminea*) shift their coat color to match seasonal changes in snow cover by tracking photoperiod changes (49). (B) The common poppy (*Papaver rhoeas*) is an annual plant that grows and reproduces during spring and summer but remains as seeds during winter. (C) Physiological response of an insect (*Murgantia histrionica*) to temperature. The difference between the temperature that maximizes per-capita birth-rate ( $T_{optimal}$ ) and the average temperature in the source location ( $T_{mean}$ ) is a potential adaptation to seasonality. (D) Seasonal fluctuations in the frequencies of alleles determining wing size generate differences between individuals of *Drosophila melanogaster* (147). (E) Demographic fluctuations of a hypothetical population with seasonally varying growth rates. (F) Effect of seasonal environmental fluctuations on average demographic rates. Solid and dashed lines indicate demographic rates under constant and seasonally fluctuating temperatures, respectively. (G) Effect of seasonal fluctuations on the probability of species coexistence. Small fluctuations allow coexistence mechanisms to operate, but large fluctuations increase the probability of stochastic extinction (96). (H) Seasonal fluctuations in species' abundances in a simulated community. (I) Diversity of annual plants from the Sonoran Desert. (J) Seasonal fluctuations can alter food-web structure through variation in species composition and strength of interactions (73). (K) Detrended seasonal fluctuations in global atmospheric CO<sub>2</sub> concentration. Each line corresponds to a different year. Data from NOAA (<https://gml.noaa.gov/obop/mlo/>). (L) Temporal biomass stability as a result of temporal community dynamics and species diversity. Illustrations (A), (B), and (I) by S. Brown. Demographic data (C) and (F) from (148). Community model (G), (H), and (L) from (96).

vital rates (56), allowing populations to perform moderately well in a wider range of environmental conditions.

These distinct adaptations to different levels of seasonality and predictability determine species' responses to changing seasonal patterns. Altered timing of seasonal fluctuations interferes with organisms' ability to exploit environmental cues (57), as demonstrated by mass losses of migrating bird populations (58, 59). Indeed, populations that have adapted their life cycles to predictable seasonal fluctuations are particularly vulnerable to changes in the timing and predictability of seasonal events. For instance, the life cycles of plants in fire-prone environments are tuned to minimize mortality, maximize recovery, and even capitalize on seasonal wildfires, which makes them vulnerable to increasing unpredictability of fire seasonality owing to climate change and human ignitions that occur randomly during the year (26). Similarly, riparian plants adapted to predictable seasonal flow variation are susceptible to changes in the timing of floods upon which they rely for successful recruitment (60).

The ability of a population to track shifting seasonal cues can mediate community-level consequences of altered seasonal patterns (Fig.

2, G to J). The phenological mismatch of interacting species owing to the advance of seasonal events is perhaps the most well-known case, including mutualistic, consumer-resource, and competitive interactions (43, 61, 62). For instance, a temporal mismatch between a flowering plant and its pollinator can lead to complete recruitment failure in any given year (63). However, examples of timing and predictability of seasonal patterns altering species interactions are plentiful, such as higher predation rates due to maladaptive plastic camouflage (64), changes in food-web structure due to modified prey preferences (65), and increased rates of attack due to host-parasitoid phenological synchronization (66). In addition, the presence of non-native species can exacerbate the effect of altered seasonal fluctuations at the community level, as they may outcompete native species under new patterns of environmental variation (67, 68). Non-native species with temporally flexible life histories may have an advantage over native species that follow more constrained environmental cues. This advantage has been illustrated in coastal scrub communities, where artificially advancing the growing season confers a competitive advantage to non-native species that can better respond to changes in the annual pattern (69).

Similarly, higher invasion rates by non-native freshwater fish and riparian plants across the USA have been linked to changes in the timing of river discharge (68, 70).

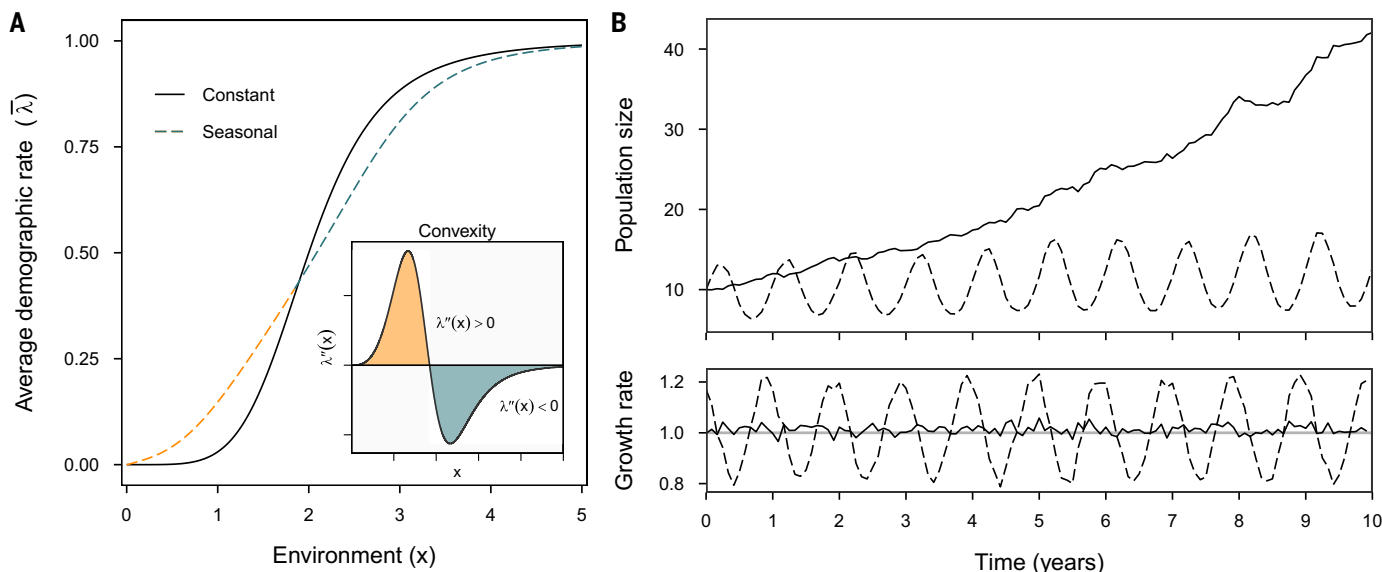
More generally, changes in the timing and predictability of seasonal fluctuations can threaten biodiversity by hindering individual- and population-level mechanisms that underpin species coexistence. Species in seasonal and predictable environments exploit the negative covariance between competition and relatively favorable conditions by specializing in specific time windows within the year (7), which is the basis for the so-called storage effect (whereby populations “store” gains from good periods to avoid extinction during bad periods) (71). This specialization generates characteristic seasonal shifts between entirely different community structures and food webs (Fig. 2, H and J) (72, 73). Thus, while a high amplitude of seasonal fluctuations could act as an environmental filter for some organisms (74), the specialization of different species in different seasons can increase the overall local diversity and the temporal variability of community composition (Fig. 2I) (7). Changes in the timing or predictability of seasonal fluctuations can consequently compromise species coexistence by decoupling populations’ seasonal cycles, increasing competition among species. Greater seasonal unpredictability could further affect biodiversity by benefiting generalist species with bet-hedging strategies that produce lower temporal variability in competition. These links between species’ seasonal specialization, species interactions, and biodiversity could consequently leave populations and whole communities vulnerable to sudden changes in the timing and predictability of seasonality.

### Impacts mediated by demographic responses to the experienced environment

In addition to species’ seasonal specialization, the effects of seasonality on populations’ demographic rates can mediate the propagation of impacts across biological levels. Such effects depend on the characteristic

shape of the relationship between demographic rates and the environment (response curve), which integrates population-level consequences of life-history strategies, genetic diversity, behavioral and plastic responses, and physiological constraints (75, 76) and determines important community dynamics such as species coexistence (77). For populations, the effect of seasonality on demographic rates can be positive, negative, or neutral (Fig. 3). Seasonality has no direct effect on average demographic rates when the response curve is strictly linear, but it generates lower or higher than average values when response curves are nonlinear, with an effect size proportional to the amplitude of fluctuations. This interaction between the amplitude of seasonal fluctuations and the linearity of species’ responses can drive the evolution of species’ responses to their environment. For instance, wide seasonal fluctuations promote thermal optima that are higher than the mean temperature experienced by organisms, because temperatures higher than species optima have a disproportionately negative effect on species’ performance compared with lower temperatures (Fig. 2C) (78).

Although seasonal fluctuations can positively affect demographic rates under certain conditions, the long-term growth of populations is negatively affected by its temporal variability (Fig. 3). Thus, adaptation to seasonal fluctuations can flatten response curves to minimize temporal variation in vital rates, with consequent impacts on population growth (75). This strategy, the demographic buffering of vital rates, is in fact the manifestation of bet-hedging mechanisms whereby the arithmetic mean growth rate is sacrificed for a reduction of its temporal variability. The opposite strategy, demographic lability, can nonetheless be favorable in cases where the positive effect of nonlinear response curves offsets the negative effect of temporal growth-rate variation by substantially increasing average growth (44). For instance, populations of soft-shell clams depend on disproportionately high recruitment under certain environmental conditions



**Fig. 3. Nonlinear demographic responses to the environment and temporally varying growth rates mediate population-level effects of seasonality.** (A) Direct effect of seasonality on a demographic rate  $\lambda$  (e.g., births, deaths, or overall growth). The effect of environmental fluctuations on the average demographic rate ( $\bar{\lambda}$ ) can be positive, negative, or neutral depending on the shape of the demographic response to the environment [ $\lambda(x)$  in the range of fluctuation of  $x$ ]. Environmental fluctuations have no direct effect on average demographic rates when  $\lambda(x)$  is strictly linear, but it generates lower values of  $\bar{\lambda}$  when the function is concave [ $\lambda''(x) > 0$ ; blue line] and higher when the function is convex [ $\lambda''(x) < 0$ ; orange line]. Panel shows the value of the second derivative of  $\lambda(x)$  (convexity) along the hypothetical environmental gradient  $x$ . (B) Effect of fluctuating growth rates on long-run population growth. (Bottom) Growth rates of two hypothetical populations. The dashed line depicts a population that experiences wide seasonal fluctuations in growth rates, whereas the solid line depicts a population with milder growth-rate variation. The average growth rate is the same for both populations (1.0122). (Top) Population growth as a consequence of fluctuating growth rates. A life cycle with continuous reproduction throughout the year is assumed. Because population growth is a multiplicative process, wider variability in growth rates implies lower overall growth, even for equal average growth rates.

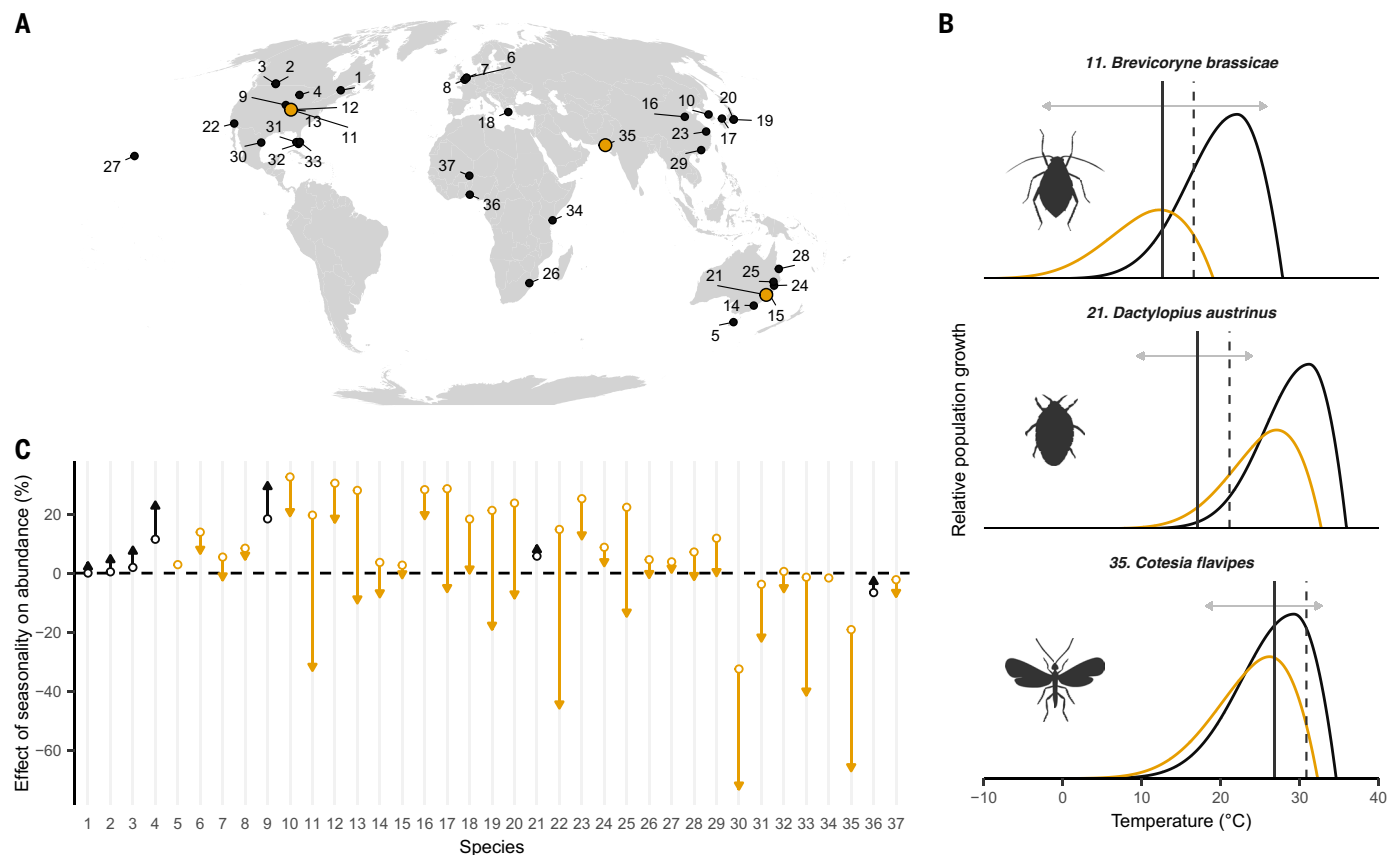
(i.e., recruitment follows a nonlinear response curve), which generates an overall positive effect of environmental variability on growth rates (44, 79).

These mechanisms—the nonlinearity of response curves and the negative effect of growth-rate variability—guarantee that the projected changes in the mean and amplitude of seasonal environmental fluctuations in the coming decades will directly influence population dynamics (80). Particularly for species with continuous reproduction throughout the year and environment-dependent vital rates, lower amplitudes could negatively affect population performance when the relationship between environmental conditions and demographic rates follows a convex function, whereas greater amplitudes negatively affect populations with concave responses, or with increased growth rate variability (44). Of course, reversing these scenarios would lead to a positive effect of changes in the amplitude of seasonal fluctuations on demographic rates (Fig. 3).

Directional changes in the mean environment can further modify the magnitude and direction of the effect of seasonality on demographic rates and long-term growth rates by moving the range of seasonal fluctuations to a different region of the response curve (Fig. 4). This could be the case for populations experiencing trends in their environments because of climate change, such as rising temperatures or decreasing water availability, because survival tends to decrease exponentially under such extreme conditions (87). Consequently, even if

the effect of seasonality on populations is currently positive or neutral, it could become negative through a combination of higher growth-rate variability and a disproportionately negative effect of extreme environments (Fig. 4).

The nonlinearity of response curves and the negative effect of growth-rate variability have been sufficient for representing population dynamics of short-lived organisms (80, 82), but species with longer life cycles will likely display more intricate responses to changing seasonality. For instance, the environment experienced during a given season can affect organisms' performance and population dynamics in later seasons (seasonal carry-over effect), as observed in vegetation growth patterns in the Northern Hemisphere (45). These lagged effects can interact with populations' density-dependent growth (83) and affect multiple generations through parental effects (84). Seasonal life cycles and plastic responses will also determine species' vulnerability to changes in the mean and amplitude of seasonal patterns. For instance, the specialized physiology of overwintering stages in some insects implies greater mortality with increasing winter temperatures, even if adults can cope with those conditions (85, 86). The response of populations to changes in the mean and amplitude can be even more complex when processes such as sexual selection and sex determination are influenced by the environment (87, 88), leading to further indirect effects. Thus, accounting for the environmental responses of different sexes, ages, and life stages—and the mechanisms



**Fig. 4. Temperature seasonality can have opposing effects on population performance.** (A) Insects were collected from 37 locations around the world. The source location of species in (B) has been highlighted. (B) Temperature-dependent population growth rate of three species: *Brevicoryne brassicae*, *Dactylopius austrinus*, and *Cotesia flavipes*. Black curves represent population growth at constant temperatures, whereas orange curves indicate population growth under seasonal fluctuations that match those in the source location. Arrows indicate the range of seasonal fluctuations. Solid and dashed vertical lines indicate current average temperatures and an increase of 4°C at the source location of each species. Monthly average temperature data come from WorldClim (149). (C) Effect of seasonality on species' abundances under current and increasing temperatures (4°C). For most species, the effect of seasonality on long-term average abundance depends on average temperature, and it becomes more negative with increasing temperature. Model and data from (80). Data were originally published in (150).

driving lagged and indirect effects—is crucial to fully understanding how structured populations will respond to altered seasonality.

Seasonality effects on demographic rates scale to the community level, where population-specific responses to the environment facilitate the coexistence of species that outperform one another in different seasons (71). For instance, rivers with highly seasonal flow variation generate distinct conditions throughout the year that allow the time-sharing of habitats by species with different adaptations (storage effect) (89). The storage effect has also been linked to the stabilization of genetic diversity within populations in seasonal environments, allowing for the long-term maintenance of multiple alleles that are favored in different seasons (3, 90) (Fig. 2D). Depending on how species respond to a given resource or condition, environmental fluctuations can also promote coexistence through the relative non-linearity of their response to competition (91). If the best competitor under average conditions presents a more concave response, environmental fluctuations promote coexistence because variability is more detrimental for such species (92). Moreover, within-population trait variation through genetic diversity or phenotypic variance can interact with the relative nonlinearity of species' response curves to promote or hinder coexistence (77). This mechanism allows genetic-level effects of seasonality, such as the maintenance of polymorphisms and the evolution of plastic traits (93, 94), to propagate across multiple levels of ecological complexity.

Changes in the mean and amplitude of environmental fluctuations can modify these community dynamics through mechanisms operating at different levels. For instance, increasing the amplitude of seasonal variability might increase the contribution of coexistence mechanisms to the maintenance of species diversity. Yet, wider seasonal fluctuations could negatively affect species diversity if they generate strong demographic fluctuations, because populations are more likely to face stochastic extinction during periods of low abundance (95). Whether changes in the amplitude of seasonal fluctuations have a positive or negative effect on coexistence and species diversity therefore depends on the interplay between deterministic processes at the community level and stochastic processes at the population level (Fig. 2G) (96). The mechanisms that promote or hinder coexistence under seasonal fluctuations depend on species' relative response to the environment and could have opposing effects under new ranges of fluctuation if population responses are different in the new range. Changes in the mean environment can consequently alter seasonal community dynamics.

### Consequences of cross-level processes for ecosystems

The impacts of changing seasonality on individuals, populations, and communities propagate to the ecosystem level, including the destabilization of ecosystem functions. The stabilizing role of taxonomic and genetic diversity on ecosystem functions through the diversity of responses to environmental conditions (Fig. 2J) can be lost when more extreme seasonal fluctuations homogenize species' responses and reduce genetic and taxonomic diversity (97–99). This potential destabilization is exacerbated by the dependence of taxonomic and genetic diversity on natural seasonal fluctuations (6, 7). In ecosystems dominated by a few species, the dynamics of abundant populations become more relevant for ecosystem functions (100). The stability of these ecosystems will therefore depend on whether mechanisms that allow the demographic buffering of key species to environmental fluctuations, such as bet-hedging strategies, adaptive phenotypic plasticity, and genetic diversity, operate under new seasonal patterns at the necessary timescales.

Despite the existence of ecological mechanisms that stabilize ecosystems, many functions undergo strong seasonal fluctuations. Annual patterns of plant growth and organic matter decomposition in the Northern Hemisphere produce seasonal oscillations in atmospheric CO<sub>2</sub> concentrations noticeable at the global scale (Fig. 2K) (101). Similarly,

ecosystem services provided by freshwater ecosystems, such as the retention of nutrients and toxic substances, vary seasonally with light, temperature, and water flow (102). These large-scale phenomena are emergent properties of processes and interactions across multiple ecological levels, including species' seasonal specialization, physiological constraints, and community dynamics. For example, fluctuations in the gross primary productivity of peatland ecosystems result from a combination of seasonal species turnover, their phenology, and their physiological response to the environment (46).

The propagation of effects of altered seasonal fluctuations can consequently produce complex, unexpected changes in ecosystem functions that can only be anticipated through a mechanistic understanding of the processes involved. In marine environments, changing seasonality is expected to affect marine productivity and carbon absorption through changes in the timing and duration of algal blooms worldwide (23). The mechanism underpinning these impacts is the temporal decoupling of phytoplankton growth and zooplankton predation, partly because phytoplankton's growth matches the current environmental conditions, whereas zooplankton's life cycles are more constrained by evolutionary adaptations to seasonality (23, 103). Cascading and interconnected impacts on the productivity of fisheries emerge as a result, because many species rely on environmental cues to time reproduction with periods of high phytoplankton and zooplankton abundance (13).

Local changes to ecosystem functions can also arise from shifts in seasonal migration patterns. The annual migration of thousands of species connects Earth's ecosystems and underpins ecological processes at all levels of organization (25). For instance, the seasonal migrations of trillions of insects globally provide critical functions to the ecosystems they visit, such as plant pollination and pest control (104). Animal migrations can also be fundamental for coupling ecosystem functions at smaller spatial scales, as observed in the nutrient transport between lakes and river systems, provided by migratory fish species, which sustains whole food webs (105). However, changes in the timing and predictability of seasonality are reducing the fitness benefits of performing annual migrations for many species owing to the lower reliability of environmental cues (24). Derived shifts in movement patterns can have consequences for recipient ecosystems, including the decoupling of spatially distant locations and the loss of important ecosystem functions.

### Constraints on evolutionary responses to changing seasonality

Species' adaptations to seasonality will influence their ability to track rapid shifts in seasonal patterns. In the short term, microevolutionary processes and phenotypic plasticity will play a key role. Populations whose individuals possess evolutionary adaptations such as phenotypic variance within the offspring or adaptive plasticity could persist under new seasonal fluctuations, allowing beneficial mutations to occur over longer timescales. For instance, plastic physiological traits of the brown algae *Fucus vesiculosus* enabled its initial survival outside the native range of water salinity, thereby providing the necessary time for colonizing populations to develop specific adaptations to such conditions over the following 8000 years (106). Still, the low genetic variation for seasonal plasticity observed in some natural populations and the fact that multiple plastic phenotypes may belong to a single genotype limits populations' ability to genetically track environmental changes that fall out of the historic range of variation (107, 108). Some populations have been able to track seasonal shifts over a few generations through adaptive plasticity and microevolution (109), but these mechanisms may not operate under further seasonal changes as they are constrained by the preexisting variability within the population. Moreover, the short-term response to directional selection induced by changing seasonal patterns can reduce within-population trait variability (110), with potential effects on species' performance (76), community dynamics (77), and ecosystem functions (98). Thus, although



short-term responses to new patterns of environmental seasonality are likely governed by ecological processes, adaptive plasticity, phenotypic variance, and microevolutionary dynamics contribute to determining a population's persistence over the following generations.

Species' success in responding to rapidly changing seasonality will also depend on the pace at which beneficial mutations arise and are selected within the population in relation to the rate of seasonal change, which is crucial for long-term adaptation. Crops such as rice, wheat, maize, and soybean have only been successfully cultivated under seasonal patterns that differ from those of their home range after artificially selecting for mutations that suppress the expression of genes related to the seasonality of their life cycle (*111, 112*). Such examples suggest that the pace of adaptation of natural populations could lag rapid seasonal shifts—such as those related to sudden local impacts and climate change—when the genetic response to seasonal cues is complex (*113*). Ecological and environmental mechanisms that determine the pace of evolutionary adaptation in relation to the rate of seasonal change could in turn depend on genetic changes related to seasonality. Examples include population dynamics (*114*), the complexity of the biotic selective landscape (*115, 116*), generation time (*117*), the genetic architecture and pleiotropy (*118*), and trade-offs involved with plasticity (*27, 107*). However, no general consensus exists about how adaptive plasticity affects evolution (*108, 119, 120*), and plasticity can itself evolve rapidly in some cases (*121*), suggesting that its role in determining the pace of adaptation under rapidly changing seasonality could be context specific.

The potential for timely adaptation to altered seasonal patterns may depend on the components of seasonal fluctuations that have been altered. Populations might be able to track changes in the timing of seasonal fluctuations by adjusting the response to seasonal cues. By contrast, changes in amplitude or mean could entail adapting the physiological response to environmental conditions (*78*), and adaptation to increasing unpredictability might require developing complex bet-hedging strategies. Still, adaptation to changes in timing can be slow in some cases (*48, 112*), whereas adaptations to increased unpredictability such as phenotypic variance have been observed to evolve rapidly in experimental settings (*122, 123*), suggesting that bet-hedging mechanisms could be a faster evolutionary response to rapid changes in seasonal fluctuations.

Species' ability to adapt to new seasonal patterns could also determine their ecological potential to escape from unfavorable conditions by undergoing latitudinal range shifts in response to global warming (*124*). The correlation between cues and the environment varies with latitude, which limits range shifts in populations that are not able to adjust their response (*125, 126*). Moreover, patterns of temperature and rainfall seasonality at different latitudes have different means and amplitudes, so populations undergoing range shifts need to adapt their physiology and life cycles accordingly. The evolution of traits such as thermal breadth could even limit some populations more than adaptation to altered seasonal cues (*125, 127*). Thus, population persistence under changing environmental conditions through latitudinal range shifts requires a suite of combined physiological and life-history changes related to environmental seasonality.

### New directions for understanding and predicting ecological impacts

We have shown the complexity of ecological responses to changing seasonal regimes, including the potential propagation of effects. However, understanding the links between seasonality and biodiversity remains a frontier research topic. Mathematical models have helped unravel ecological consequences of seasonality, but some fields are ahead of others in testing hypotheses empirically (*19*). Predictive models of species distributions and biodiversity routinely incorporate indices of temperature and rainfall seasonality from global climatic databases as predictors (*128–130*). These indices, which often explain a

great proportion of variability, are usually measures of within-year variability regardless of its periodicity or predictability and could confound models by amalgamating components of seasonality with potentially opposing effects. Moreover, the estimated effect of seasonality could change under new conditions (Fig. 4), leading to biased projections. The increasing use of these indices highlights the urgency for a common framework for the study of seasonality in ecology that allows the transferability of hypotheses across theoretical and applied studies. We have highlighted that the mechanisms whereby seasonality affects the different facets of biodiversity are tightly related to four components: the mean, amplitude, predictability, and timing of seasonal fluctuations (Fig. 1). Testing the effect of these components could help close the gap between empirical and theoretical studies by providing a more mechanistic interpretation of the observed effects of seasonality on population and community dynamics.

As seasonal patterns continue to change globally, accurately predicting complex biological responses is a critical challenge for the protection of biodiversity. Further theoretical and technical advancements are necessary for understanding and predicting ecological impacts, which could unlock widespread benefits for ecosystems and human society. From invasive species management (*69*) to the design of environmental flow regimes (*36*) to scientifically informed ecosystem restoration (*131*) and optimized management of key resources for human populations (e.g., fisheries, crops, and wood) (*111, 132*), managers will be better placed to provide targeted action toward biodiversity, climate, and food security goals. Moreover, better understanding the biological responses to altered seasonality could improve our ability to predict the dynamics of global climate through the role of such biotic processes in the carbon cycle (*133*).

However, the utility of statistical models that extrapolate correlations between variables at a single level is limited for these tasks because the existence of cross-level mechanisms tends to generate nonlinear responses that cannot be accurately predicted using correlative models (*134, 135*). Processes influencing the biological response of interest may operate at different levels and thus require models that enable the propagation of mechanisms across them. Failing to account for cross-level mechanisms might lead to an over- or underestimation of the effects of altered seasonal patterns, confound the results of empirical studies, and limit our ability to generate sound predictions under new conditions.

Models that integrate mechanisms at multiple ecological levels, such as reproduction, phenology, physiology, dispersal, biotic interactions, and evolution, offer a promising alternative for forecasting beyond the observed range of environmental conditions (*134, 135*). However, the application of these methods for predicting the impacts of changes in seasonality is currently limited by our theoretical understanding of the relevant processes at each ecological level. Progress can be achieved by systematically laying out and testing potential mechanisms through experiments and observation. Studies in which different components of seasonality are artificially manipulated (e.g., changing snow cover or rainfall patterns), or where individuals are moved to locations with different seasonality, are needed to identify relevant processes and quantify impacts (*63, 69, 136*). Assessing the potential for genetic adaptations may require more tailored strategies, as some effects are only observable at larger temporal scales. Resurrection studies can provide valuable insight into species' ability to genetically track changes in seasonality (*127, 137*), but this will only be feasible for taxa with dormant stages. Comparative studies of populations under different seasonal regimes (*126*), analyses of the current genetic diversity, and a more detailed understanding of the molecular basis underpinning adaptations to seasonality (*48, 111, 112*) could help anticipate under which conditions evolution will be relevant at ecological timescales. Finally, advancing understanding of the impacts of seasonality change necessitates the continuation of long-term ecological research programs and the collection of fundamental natural history information



with which to parameterize models, such as the study of species' life cycles, environmental responses, and the demographics of structured populations (134, 135).

Theoretical understanding of mechanisms underpinning responses to altered seasonality at individual levels (e.g., physiology) can be coupled with mechanistic ecological models that can integrate multiple mechanisms and reproduce emergent properties of the system (e.g., species diversity). Such mechanistic approaches enable pinpointing parameters with a strong effect on the response to altered seasonality and that should therefore be investigated with further empirical work (135). Based on our synthesis, we highlight two types of information that should be prioritized in mechanistic models: (i) the timing of phenological events and underlying mechanisms and (ii) species-specific responses to their environments through immediate and delayed changes in vital rates. Even simple mechanistic models incorporating these pieces of information can allow the emergence of complex responses to changes in seasonality within and across levels. For instance, accounting for species' thermal response has improved predictions of population extinction risk under projected changes in temperature fluctuations (80). Similarly, linking recruitment success to the timing of peak flow has helped forecast riparian plant population and community dynamics under altered flow regimes (138). We also stress the need to consider the multitude of ways in which the impacts of changing seasonality can propagate through levels of ecological organization (Fig. 2). Species migration and interactions provide pathways for such propagation, potentially over great distances, though the variables governing this propagation require further research (139).

Because mechanistic understanding of the response to altered seasonality remains incomplete, statistical approaches are necessary for testing and quantifying unknown processes. However, inferring causal relationships necessitates accounting for cross-level knowledge when designing experiments and statistical models (140). Advances in statistical modeling provide new opportunities for assessing ecological dynamics under changing seasonality, including specialized tools that facilitate the task of fitting and interrogating complex models (141). Researchers can incorporate existing biological knowledge at different ecological levels, merge disparate data sources, include prior knowledge about parameter values, and update models iteratively as new information arises (142, 143). In addition, mechanistic knowledge can be exploited to improve predictions when biological information is only partially available using hybrid approaches that combine statistical and mechanistic components (144). We highlight the importance of an explicit consideration of temporal dynamics in statistical and hybrid models, including population growth, phenology, and delayed demographic effects to altered seasonal cycles. Together, these advances will help researchers to understand and predict the complex, multilevel ecological responses to Earth's rapidly changing rhythms.

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