

## Opinion

# Food Web Structure in Temporally-Forced Ecosystems

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**Temporal variation characterizes many of Earth's ecosystems. Despite this, little is known about how food webs respond to regular variation in time, such as occurs broadly with season. We argue that season, and likely any periodicity, structures food webs along a temporal axis in an analogous way to that previously recognized in space; predators shift their diet as different resource compartments and trophic levels become available through time. These characteristics are likely (i) central to ecosystem function and stability based on theory, and (ii) widespread across ecosystem types based on empirical observations. The temporal food web perspective outlined here could provide new insight into the ecosystem-level consequences of altered abiotic and biotic processes that might accompany globally changing environments.**

### A Call for Temporal Food Web Studies

Species behaviors are shaped by temporal environmental fluctuations that are ubiquitous in nature [1]. Such periodicity occurs at a variety of scales (e.g., seasonal, inter-annual, decadal), and encompasses fluctuations in both abiotic (temperature, precipitation, light, nutrients) and biotic processes (migration, growth, reproduction, trophic interactions). Anthropogenic stressors such as climate change and river impoundment are directly altering the timing and magnitude of these existing temporal signals [2–4] and providing new opportunities for invasive species [5,6]. These global environmental changes are removing key ecosystem services on which human societies depend, and threatening the underlying species interaction networks (i.e., food webs) that sustain essential ecosystem functions (Box 1). Managing ecosystems for sustained function in the face of changing conditions is a daunting task, but one that demands consideration of how food webs are structured around existing temporal changes (e.g., seasonality). Given that human impacts often modify the nature of these existing environmental drivers, it is imperative that ecologists prioritize studies to better understand how food webs respond to and maintain function in the face of changing conditions [7].

Based on existing theory, for example, the capacity of consumers to forage across spatially variable habitat boundaries is important for food web structure [8,9] and **stability** (see **Glossary**) [10]. However, few food webs have been studied on a year-round or even on a two-season basis and how consumers switch their diet through time remains rarely tested. Discounting how temporal variation structures food webs could be detrimental for anticipating and mediating the consequences of novel periodicities on ecosystem functions.

Here, we combine existing food web theory with empirical examples from seasonal food web studies to generate a conceptual framework for how temporal variation might structure food

### Trends

Temporal environmental variation is ubiquitous in nature and appears to consistently structure food webs in many ecosystems.

Such abiotic variation drives different resources to become available during different times. Consumers buffer this variation via dormancy, migration, or by temporally shifting their diet towards abundant resources.

These temporal food web characteristics likely sustain ecosystem functions in the face of naturally-variable conditions.

Global environmental changes are threatening these existing abiotic signals and the biotic processes that are structured around them.

Failure to study food webs on a temporal axis represents a missed opportunity to better understand ecosystem structure and function in a changing world and could be detrimental for efforts aimed at anticipating and mediating the consequences of novel periodicities on key ecosystem functions.

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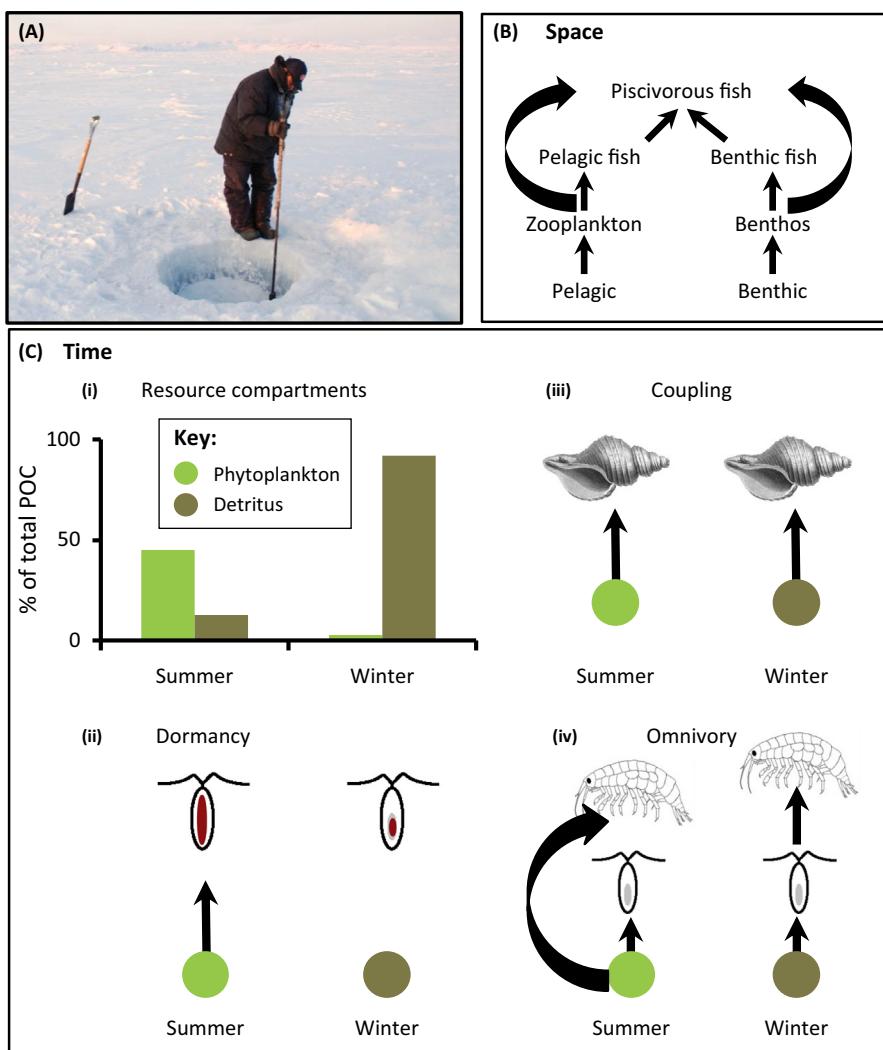
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**Box 1. A Food Web Perspective on Variation in Space and Time**

Climate change will directly remove important ecosystem services for human societies (Figure 1A). Beyond these direct effects, a food web perspective seeks to understand the inherent structures present within complex species interaction networks that allow for nutrients to cycle and energy to flow through ecosystems in the face of changing conditions. Based on existing theory [10], one such characteristic structure that promotes stability and function in space (Figure 1B) is that of a generalist predator (e.g., piscivore) feeding omnivorously on lower trophic position prey (thick curved arrows) and coupling across different habitat compartments. Although rarely considered, seasonal fluctuations in the availability of different resources could set up analogous food web structures in time (Figure 1C). In Arctic seas, for example, brief but intense summer phytoplankton production occurs during open-water periods, whereas detritus (of predominantly phytoplankton origin) dominates total particulate organic carbon (POC) flux during ice-covered winter (Figure 1C, i; data adapted from [14]), forming the basis for asynchronous temporal resource compartments. In response to this variation, some species (e.g., herbivorous copepods [56]) are known to enter a non-feeding, dormant state in winter by relying on stored lipid reserves (red ovals, Figure 1C, ii). Other generalist consumers, such as grazing gastropods [17], remain active and could temporally couple phytoplankton and detrital energy pathways (Figure 1C, iii), or feed omnivorously on abundant, lower trophic level resources in summer and on higher trophic level prey in winter (Figure 1C, iv), as occurs in some Arctic amphipods [20].



**Figure 1.** Spatial and Temporal Shifts in Food Web Structure Could be Central to Sustained Function. (A) Climate-driven losses in sea ice threaten important ecosystem services (transportation, fishing, and hunting) and the food web interactions that maintain important functions (photo credit: Bailey McMeans). (B) Food web model based on distinct spatial resource compartments being coupled by a generalist predator (e.g., piscivore). (C) Proposed analogous food web structures in time.

**Glossary**

**Asynchrony:** refers to the dynamics of different resources being out of phase with one another. When one resource is at high density, a different resource is at low density and vice versa.

**Carnivore:** a species that feeds on animals.

**Coupling:** feeding on resources from multiple resource compartments. Can exist in space if foraging occurs across habitat boundaries [8] and in time if different resources are consumed during different times of the year [29].

**Decoupling:** when a consumer stops feeding on a resource.

**Omnivore:** a species that feeds on multiple trophic levels.

**Omnivory:** feeding on multiple trophic levels. Can occur spatially if different trophic level prey are exploited in different habitats [53] and seasonally if different trophic levels are exploited during different times of the year [54].

**Primary consumer:** a species that eats primary producers or detritus.

**Resource compartment:** stronger interactions in a subgroup of the entire food web, for example, among a resource and its direct consumers. Can arise between distinct resources in space [55] or time [23].

**Stability:** defined generally here as how variable the dynamics of a system are. For example, systems having higher coefficients of variation (CV, a common stability metric) are less likely to persist and therefore considered less stable than systems with lower CV.

webs in ways that are central to their sustained function. We focus on season as an illustrative example of how environmental periodicity structures food webs because it is ubiquitous, widely recognized to shape species behaviors, and under direct threat due to environmental change [1,2]. After first discussing emerging notions about the relationship between food web structure and function in space, we explore a strongly seasonal ecosystem, Arctic seas, as a case study of how analogous food web structures manifest along a temporal axis. We conclude by arguing that these temporal food web characteristics are important for stability and widespread across ecosystem types. Our goal is to provide a general framework that motivates and guides future temporal food web research, which could ultimately help better protect the characteristics of food webs that matter most for sustained function in the face of changing environmental conditions.

### Existing Notions: Food Webs in Space

For decades, ecologists have sought to understand how structure helps maintain function in food webs [11]. Owing in large part to the emergence of ecological tracers, such as stable isotopes, that drastically reduced the work involved in configuring food webs [8], emerging efforts have uncovered a relatively simple and common patterning within the complex web of trophic interactions. Against a backdrop of spatial environmental heterogeneity, which drives **asynchrony** of different resources across a landscape, consumers tend to be flexible in their feeding and move across habitat boundaries to forage on the most abundant resources [10]. This food web patterning of generalist consumers **coupling** across different **resource compartments** and exhibiting **omnivory** by feeding on different trophic levels has the potential to buffer and stabilize the whole food web by preventing runaway resource growth and dynamics [10,12]. It is also empirically common and widespread across system types [13].

### Seasonal Food Webs: A Case Study of Arctic Marine Ecosystems

#### Evidence for Temporal Compartments

The strongly periodic nature of light and sea ice in Arctic seas is recognized to drive primary producers (e.g., ice algae, phytoplankton, or macroalgae) to peak in their availability during ice break up and open water, and detritus (originating from these living sources) to become relatively more abundant during ice-covered periods. For example, phytoplankton availability peaks during summer and phytodetritus dominates total particulate organic carbon (POC) flux during winter in these polar systems [14,15]. The differential availability of these resources through time sets up asynchronous temporal resource compartments, analogous to previously identified compartments in space (Box 1).

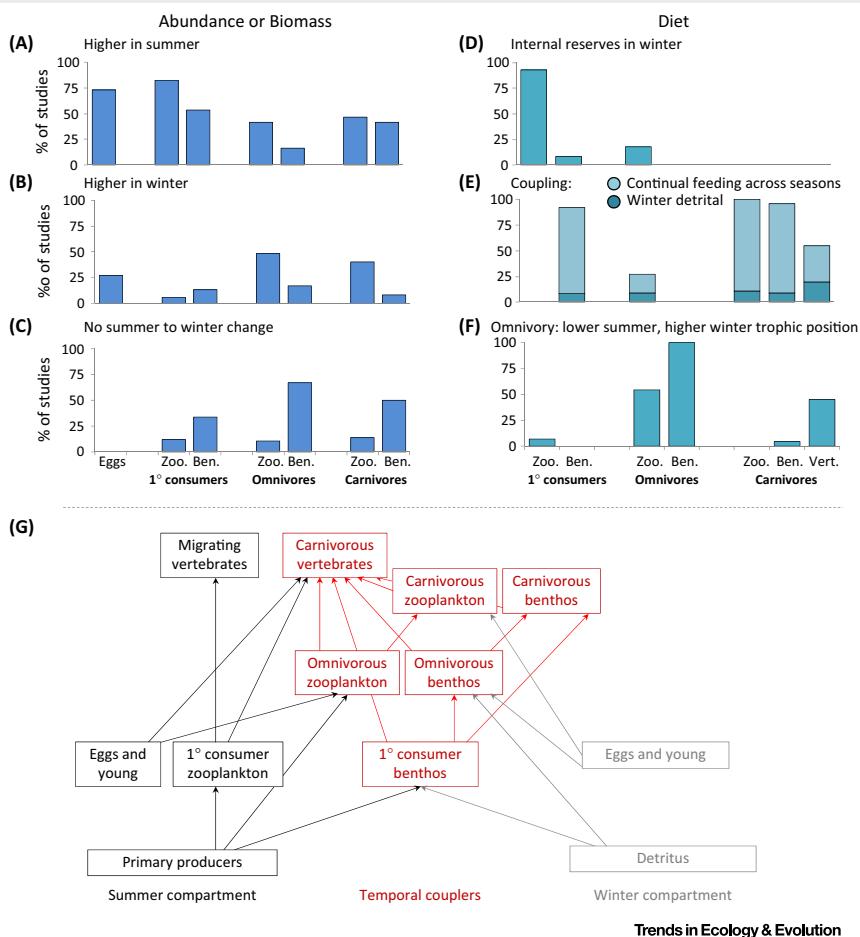
Based on existing information about summer to winter shifts in abundance and biomass synthesized from the literature, different functional groups either contribute to, and further set up, these distinct temporal compartments or act to integrate and couple across these compartments. **Primary consumers** contribute to the summer compartment because they tend to track variation in primary producers by exhibiting peak biomass in summer (Box 2), with reduced winter biomass being attributed to declines in growth and reproduction [14] or seasonal migration [16]. The reproductive products of invertebrates (eggs and young stages) could contribute to either the summer or winter compartment depending on the phenology of different species (Box 2, Table S1 in the supplemental information online). The remainder of functional groups would likely belong to both compartments because they maintain or even increase their presence from summer to winter (Box 2).

#### Evidence for Temporal Coupling and Omnivory

In response to seasonality in primary production, primary consuming zooplankton cease feeding on their declining resource base (i.e., **decoupling**) and overwinter on stored lipid reserves (Box 2). Migrating vertebrates that exit Arctic waters before ice cover sets in would also belong only to the summer compartment and effectively drop out of the food web in winter (Box 2).

**Box 2. Responses to Seasonal Variation Differ among Arctic Marine Functional Groups**

Existing reports for summer to winter shifts in abundance or biomass (Figure 1A–C) and diet (Figure 1D–F) were synthesized and are shown as the percentage (%) of total reports located for each functional group in each response category. See supplemental information for literature search details, individual reports, and study citations (Table S1, abundance and biomass shifts; Table S2, diet shifts). These synthesized literature findings (i) show that different Arctic marine functional groups respond differently to seasonal variation, and (ii) were used to generate a highly simplified conceptual model for a seasonal Arctic food web, based on a primary producer compartment in summer and detrital compartment in winter (Figure 1G). Based on these existing seasonal data: (i) the eggs and young stages of invertebrates ('eggs and young') can contribute to both summer and winter compartments (Figure 1G) because different species reproduce during different seasons (Figure 1A,B); (ii) primary consuming zooplankton belong to the summer compartment (Figure 1G) because their biomass tends to peak in summer (Figure 1A) and they cease feeding in winter (Figure 1D); and (iii) the other functional groups act to temporally couple both compartments (Figure 1G) because they can maintain (Figure 1C) or even increase their presence from summer to winter (Figure 1B) and forage on both primary producer- and detrital-based prey (Figure 1E) or on multiple trophic levels (Figure 1F). No biomass data were available for migrating vertebrates, but these species would belong to the summer compartment (Figure 1G) if they exit Arctic waters before sea ice forms.



**Figure 1. Previously Reported Summer to Winter Abundance or Biomass (A–C) and Dietary Responses (D–F) in Arctic Marine Functional Groups.** Abbreviations: Eggs, eggs and young stages of invertebrates; Zoo., zooplankton; Ben., benthos; Vert., vertebrates. Abundance or biomass responses were categorized as either higher in summer (A), higher in winter (B), or similar between summer and winter (C). Dietary responses were categorized as either a shift towards reliance on internal reserves in winter (D), coupling primary producer and detrital compartments (via either foraging as generalists on available resources across seasons or by actively switching towards detrital prey in winter; E), or foraging on different trophic levels between summer and winter (i.e., omnivory; F). The number of reports for each of these response categories in each functional group was summed and is shown on all y-axes as a % of the total number of reports located for each functional group (see Tables S1 and S2 for individual reports). A conceptual food web model was generated from these seasonal responses (G).

Benthic primary consumers primarily act as temporal couplers by flexibly consuming available carbon sources as they vary seasonally (Box 2). This includes consuming phytoplankton or macroalgae in summer, and phytodetritus [14] or macroalgae-derived detritus [17] in winter. A lack of observable diet switching (i.e., reports of species consuming similar prey all year) can also be taken as evidence of temporal coupling even if this behavior is not apparent from stomach contents or stable isotope data (potential limitations of which are discussed in the subsequent section). This is because the available carbon source base switches from primary producers in summer to detritus in winter (Box 1) [14,15]. Aquatic primary consumers are widely recognized to couple primary production and detrital resource pathways [13], and this behavior seems reasonable in systems like the Arctic where primary production is incredibly seasonal. Other evidence that supports the putative shift from primary producers to detrital reliance by Arctic consumers includes the observation that fresh chlorophyll *a* is relatively more available than degraded matter during the open-water period [18], and that a detrital sediment food bank supports Antarctic benthos in the absence of fresh material [19]. Even **carnivores** that maintain a varied and generalist diet all year, in addition to actively switching to benthic and/or detrital sources (Box 2), would act as temporal couplers because their prey (primary consumers) would themselves be supported by different carbon sources through time.

Finally, zooplankton and benthic **omnivores** exhibit seasonal omnivory by feeding on abundant primary producers in summer and higher trophic position prey in winter (Box 2). Recognized winter energy sources for these omnivores include zooplankton and their reproductive products [15]. Some vertebrate predators also act as seasonal omnivores by consuming invertebrate diets in summer and more fish-based diets in winter (Table S2 in the supplemental information online).

It is important to mention that while some invertebrate and vertebrate predators maintain or even increase their activity levels in winter [20], cold temperatures typically drive reduced growth, respiration, or feeding rates and increased reliance on stored reserves of some Arctic marine species [21]. This ‘slowing down’ of species in winter might serve as an additional mechanism to dormancy, coupling and omnivory by which consumers decouple from their declining resource base. Further, while variation was present within each functional group in their response to seasonality (Box 2), which warrants further attention considering that environmental change could impact species-level biodiversity [22], Arctic marine food webs appear to broadly exhibit seasonal resource asynchrony, coupling, and omnivory.

### Importance for Stability and Ubiquity of Seasonal Food Web Shifts

Two general structures are important for food web stability based on spatial theory: (i) the existence of multiple resource compartments that vary out of phase with one another (i.e., asynchronously), and (ii) consumers that increase foraging on abundant resource compartments and decrease foraging on less abundant resource compartments [10,12]. We argue that these characteristics also arise in time and likely promote food web stability for the same reasons they do in space. Asynchronized availability of distinct resources provides a constant food source to primary consumers and omnivores. Differential responses among consumer functional groups (e.g., some peaking in summer and others in winter) further set up temporal resource compartments and provide a constant food source to higher trophic levels. Dormancy, migration, and flexible foraging behavior (coupling and omnivory), although clearly distinct strategies, should all promote food web stability by allowing species to forage on abundant and decouple from declining resource compartments, which ensures consumer populations persist when the availability of a single resource declines and that no single resource becomes dominant (consumers dampen abundant resources) or extremely rare (consumers release rare resources).

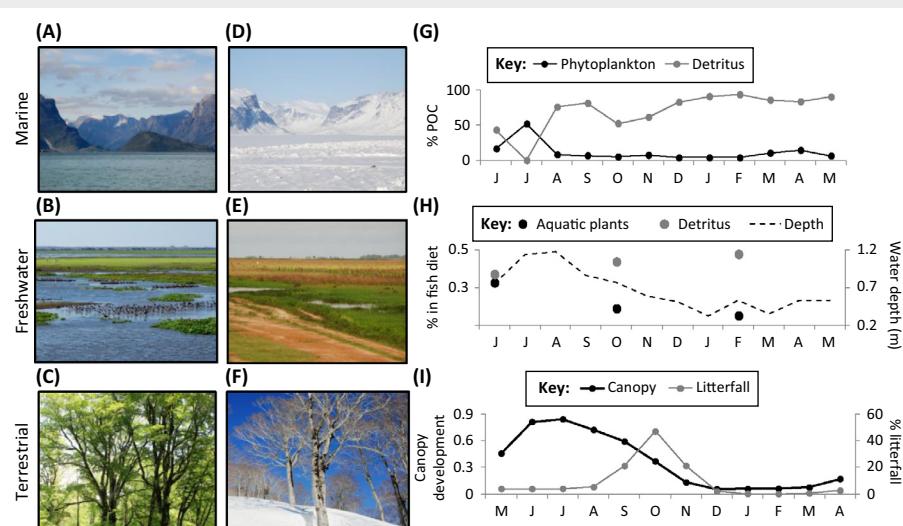
Given the near ubiquity of seasonal variation in Earth’s ecosystems, asynchronized temporal resource compartments arising within a single year are potentially widespread. While tropical

environments may not be subject to the temperature oscillations experienced by temperate and polar regions, among-season variation in precipitation represents another strong seasonal signal experienced by tropical species. The flood pulse concept, for example, is based on the lateral movement and expansion of water that provides increased access to floodplain habitats and production sources during the wet season, which is rapidly decomposed into detritus as waters recede in the dry season [3,23]. It seems likely that such temporal compartments based on primary producers and detritus are prevalent in nature because many ecosystems can be grossly characterized as having a productive and less productive season (Box 3). Organic matter produced during times of high light, nutrient, or water availability could later contribute to a continually available detrital pool that becomes increasingly important to consumers when conditions for primary production decline (Box 3). This includes autochthonous [17] and allochthonous sources of detritus [24]. The quality of detritus can be lower than freshly produced organic material, but still appears sufficient to subsidize consumers and support some secondary production when preferred resources decline in quantity and/or quality [24].

Of course, the relative length of productive and less productive seasons will vary latitudinally and be predominately driven by temperature, day length, and snow melt in temperate and polar latitudes and more so by precipitation in the tropics [25–27]. However, even ecosystems with

#### Box 3. Temporal Compartments Based on Primary Producers and Detritus Could Be Widespread

Many ecosystems can be broadly categorized as having seasons of higher (Figure 1A–C) and lower primary production (Figure 1D–F). Living organic material produced during productive times could die later in the year and enter into a detrital pool that subsidizes consumers during less productive times. This detrital pool could be continually available, but might become increasingly important as living resources decline in their relative availability during certain times of the year. For example, in Arctic seas detritus dominates total POC flux in winter after phytoplankton production ceases (Figure 1G; redrawn from [14]). In freshwater floodplains, aquatic macrophyte contribution to fish diet peaks in the wet season, with macrophyte-derived detritus becoming an important resource in the dry season (Figure 1H; redrawn from [39]). On land, canopy development in deciduous forests reaches a maximum in spring and summer, followed in autumn by peak leaf fall (Figure 1I; redrawn from [57] and [58], respectively).



**Figure 1.** Examples of Productive (A–C) and Less Productive Seasons (D–F) and Associated Asynchrony in the Relative Availability of Different Resources (G–I). Photos (A,B) by Bailey McMeans; Photo (C) by Fernando Flores, licensed under CC BY-SA 3.0 via Wikimedia Commons; Photo (D) by Laura De Oliveira, licensed under CC BY-SA 3.0 via Wikimedia Commons; Photos (E,F) by Alpsdake, licensed under CC BY-SA 3.0 via Wikimedia Commons.

relatively brief nonproductive periods could still support food webs that are temporally compartmentalized if an alternative resource subsidizes consumers when a preferred resource becomes less available. Further work is required to address this idea. Other examples of asynchronized compartments in time include pelagic versus benthic resource use in oceans [28] and lakes [29], and in aquatic versus terrestrial prey consumption [30–32].

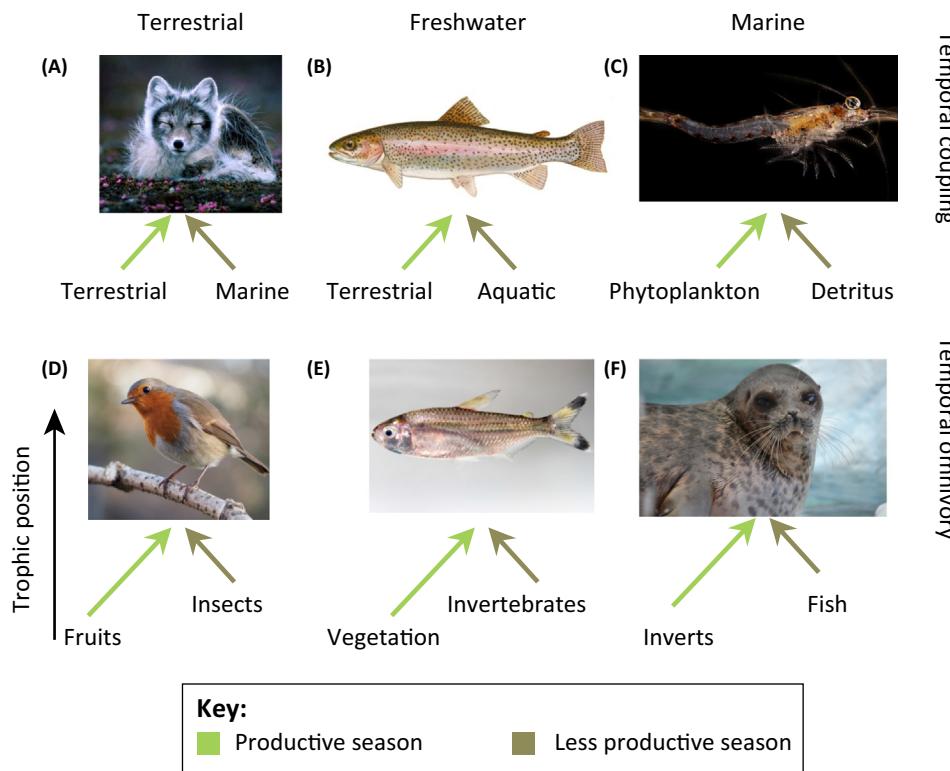
The observed seasonal responses exhibited by Arctic consumers also appear widespread. Many aquatic and terrestrial taxa, for example, possess physiological adaptations that permit reduced maintenance energy requirements during periods of resource shortage [33], which include the production of resting stages in aquatic invertebrates [34]. Latitudinal variation in the type of strategy employed (e.g., consumers either tolerating brief periods of low resource availability or entering full dormancy) appears likely in various taxa (zooplankton [35], mammals [36]) and warrants further attention (see Outstanding Questions). Seasonal migration is also a widespread strategy employed by many birds in terrestrial ecosystems [37]. In the Serengeti, ungulates also show differential migratory responses to seasonal variation in rainfall and soil nutrients [38]. In tropical river–floodplain systems, some aquatic plants and invertebrates survive the dry season by producing dormant stages, whereas fishes can migrate out of the floodplain or switch their diet as waters recede [23]. Although few additional studies have actively gathered data for temporal coupling and omnivory, several examples located in the literature suggest that these foraging behaviors also occur in diverse ecosystem types (Figure 1).

### Studying Seasonal Food Webs

The massive effort involved in studying food webs repeatedly through time using traditional, stomach content analysis (e.g., [39]) could explain the paucity of seasonal or temporal food web data in general. Of the existing suite of available ecological tracers and tools, stable isotopes are perhaps the most promising because they are capable of elucidating major energy flow pathways, including coupling and omnivory, with much less time and effort than traditional means (see [40] for a detailed review). Several limitations warrant mention, however, that researchers should keep in mind when planning and carrying out temporal food web studies based on stable isotopes.

In addition to the possible impacts of physiology (e.g., starvation) and environmentally-driven (as opposed to dietary-driven) variation in stable isotope signatures [40–42], researchers must pay special attention to the time required for isotope levels to equilibrate with dietary signatures [43]. Specifically, isotope turnover time must be sufficiently rapid to reflect the temporal dietary window of interest. Because isotope turnover time is longer in animals with larger body sizes and in ectotherms than endotherms [43], capturing intra-annual diet switches in large vertebrate ectotherms can require sampling of tissues with more rapid isotope turnover. For example, using the allometric equations provided by [43], full isotope turnover of a 2-kg vertebrate ectotherm is 3.4, 3.9, and 8.7 months for plasma, organs, and muscle, respectively. Plasma and organs would therefore allow for triannual sampling. In endotherms, tissues such as feathers and hair have also proven effective for studying seasonal diet shifts, even in very large vertebrates, where hair stable isotopes captured a shift from C<sub>4</sub> lowland plants to C<sub>3</sub> forest resources between rainy and dry seasons in elephants [44].

Recognition of the above limitations at the study design stage can ensure that proper stable isotope baselines [41,42] and tissues [43] are sampled at the appropriate intervals to capture temporal diet shifts. Complementary analyses of stomach contents can also provide valuable support to stable isotope data. We hope that recognition of both the potential applications and limitation of stable isotopes motivates researchers to pursue temporal food web studies, which are especially pressing considering the myriad of anthropogenic threats to existing environmental conditions.



Trends in Ecology &amp; Evolution

**Figure 1. Examples of Temporal Coupling (A–C) and Omnivory (D–F) by Consumers in Different Ecosystem Types.** Temporal coupling involves foraging on different carbon sources and temporal omnivory on different trophic positions during different time periods (e.g., seasons). (A) *Vulpes lagopus* forage on terrestrial prey in summer and marine prey in winter [32]. (B) *Oncorhynchus mykiss* in streams switch from abundant terrestrial insects during forest leafing periods and to aquatic invertebrates during the defoliation period [30]. (C) Crustaceans, such as Mysids, in the Beaufort Sea consume phytoplankton in summer and macrophyte detritus in winter [17]. (D) *Erithacus rubecula* switch from lower (fruit) to higher trophic position prey (insects) as these prey reach peak availability during different seasons [54]. (E) Omnivores, such as *Moenkhausia dichroura*, in the Pantanal wetland, Brazil, exhibit herbivory in the wet season and shift towards carnivory as water levels recede and restrict access to vegetative resources in the floodplain [59]. (F) *Pusa hispida* can increase the proportion of higher trophic position fish such as Arctic cod (*Boreogadus saida*) in their diet during winter [60]. All photos licensed under CC BY-SA 3.0 via Wikimedia Commons. Photo credits are as follows: (A) Mr Per Harald Olsen; (B) Raver, Duane; (C) Per Harald Olsen; (D) Francis C. Franklin; (E) Clinton & Charles Robertson; (F) Kingfisher.

### Seasonally Structured Food Webs in a Globally Changing Environment

The above examples argue that temporal resource compartments and dormancy, migration, coupling, and omnivory are potentially widespread mechanisms by which species respond to temporal variation and help sustain energy flow through food webs. This general framework is highly simplified and leaves many remaining questions (see Outstanding Questions) but could help shed light on the consequences of environmental change on ecosystem function. Specifically, any factor which (i) drives resources to become synchronized through time, or (ii) alters or inhibits the capacity of species to decouple from declining and forage on abundant resources would be predicted to destabilize food webs.

Dams, which dampen the magnitude of natural flood cycles [3], are one obvious driver of increased resource synchrony. Climate change is another possible avenue by which resources could become more synchronized. For example, warmer temperatures could mean that otherwise brief but intense periods of phytoplankton production become more prolonged and damped (e.g., in lower latitude arctic seas [2]) or that bacterial production increases [45].

Environmental changes are also altering the nutritional quality of resources. Global climate change and eutrophication could, for example, extend periods of high rainfall and warm temperatures that facilitate low quality algal growth [46]. Environmental conditions can also interact with resource quality and consumer metabolism to impact secondary production [24,47]. Thus, climate-driven changes in the timing or quality of resource production could prevent consumers from taking advantage of resources when they are most abundant or of highest nutritional quality [4,48]. Invasive vertebrates can also outcompete and prevent native species from exploiting abundant resource subsidies [6]. Altered abiotic seasonal signals could also collapse the current spectrum of environmental variation upon which different species have set up their temporal niches, threatening coexistence [49] in addition to food web stability.

The conceptual framework outlined here provides a guide for scientists to obtain a general view of which species (i) act to set up temporal resource compartments via reproduction, dormancy, and migration; (ii) flexibly buffer resource variation as temporal couplers and omnivores; and (iii) might be most susceptible to the loss of single resources by belonging to only a single compartment (e.g., herbivorous zooplankton, **Box 2**). Ultimately, scientists could use this type of information to direct efforts towards conserving and monitoring for potential changes in these important food web structures. Predicting the consequences of rapidly changing environmental conditions for ecosystem functions will also greatly benefit, and perhaps depend upon, such knowledge of how food webs are structured upon existing environmental conditions.

### Beyond Seasonality: The Urgency of Prioritizing Temporal Food Web Studies

Historically, food web approaches have largely ignored how species trophic interactions change in the face of both abiotically- (e.g., season, El Niño Southern Oscillation) and biotically-driven temporal variation (e.g., seasonal and decadal insect outbreaks [50]). This is surprising considering that individuals, and indeed whole systems, appear to be structured around this regular temporal variation [23,50]. While we have focused largely on seasonal cycles, we maintain that studying the responses of food webs to temporal variation at a variety of scales will allow researchers to better understand how food webs, via species-level behavioral responses, adapt to existing environmental variation. For example, even in weakly seasonal environments, such as certain equatorial terrestrial ecosystems [27] and open oceans [25], food webs could be structured around inter-annual or decadal climate oscillations that are known to impact trophic interactions [51,52]. Static studies cannot capture these dynamic characteristics.

### Concluding Remarks

In short, environments are naturally variable, at a variety of scales, across the globe. Widespread environmental changes threaten these existing abiotic signals and, in turn, the biotic processes and functions that are built around them. Continuing to ignore how food webs respond to existing temporal variation not only constitutes a missed opportunity to better understand key components of ecosystem structure and function but could also be detrimental for attempts to anticipate and mediate the ecosystem-level consequences of rapidly changing global environments.

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### Supplemental Information

Supplemental Information associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.tree.2015.09.001>.

### Outstanding Questions

#### How does season interact with longer-term, multi-annual forms of periodicity?

Climate indices such as the El Niño Southern Oscillation and North Atlantic Oscillation are well known to impact aquatic and terrestrial populations. It therefore remains important to understand the consequences of multiple and interacting forms of periodicity on food web structure and function, which might be gained by both short- and long-term repeated sampling within single ecosystems.

#### What is the importance of spatial versus temporal variation for structuring food webs?

Temporal food web structuring might be less prevalent in systems with low seasonality, or might occur simultaneously with spatially asynchronous resources, coupling and omnivory (e.g., seasonal migrations represent temporally explicit use of different spatial habitat compartments). Sampling both intra-annually and spatially (e.g., across latitudinal gradients) could help better understand the importance of temporal versus spatial processes for structuring food webs and maintaining essential ecosystem functions.

#### How do temporal resource compartments arise at different ecological levels of organization?

Broad-scale primary producer and detrital compartments were the focus here, but seasonal asynchrony can also arise within single resource compartments (e.g., sea ice or microbial availability could be treated as distinct resources within the primary producer or detrital compartments). Because different resources can differ drastically in their nutritional quality and ability to support secondary production, and environmental changes might alter the quantity and quality of available resource pools (e.g., phytoplankton and bacterial production), exploring the consequences of both quantity and quality asynchrony among resource compartments at various levels remains important.

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