CellPress

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.

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.

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

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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 IA). 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 IB) 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 IC). 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 IC, i; data adapted from [14]), forming the basis for asynchronized 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 IC, ii). Other generalist consumers, such as grazing gastropods [17], remain active and could temporally couple phytoplankton and detrital energy pathways (Figure IC, iii), or feed omnivorously on abundant, lower trophic level resources in summer and on higher trophic level prey in winter (Figure IC, iv), as occurs in some Arctic amphipods [20].

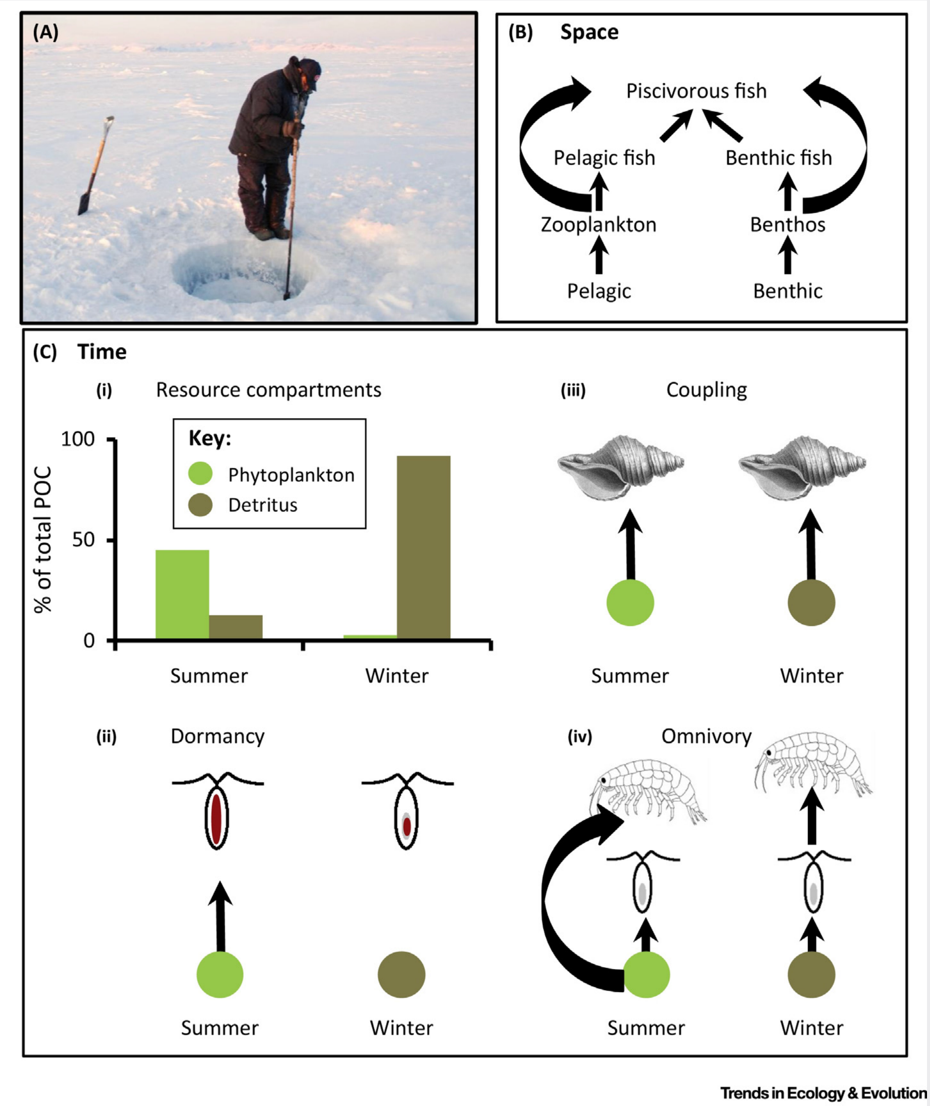

Figure I. Spatial and Temporal Shifts in Food Web Structure Could be Central to Sustained Function. (A) Climate-driven losses in sea ice threaten important ecosystem services (transportation, fishing, and hunting) and the food web interactions that maintain important functions (photo credit: Bailey McMeans). (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.