



SYMPOSIUM

To Everything There Is a Season: Summer-to-Winter Food Webs and the Functional Traits of Keystone Species

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From the symposium “Evolutionary Impacts of Seasonality” presented at the annual meeting of the Society for Integrative and Comparative Biology, January 4–8, 2017 at New Orleans, Louisiana.

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Synopsis From a trophic perspective, a seasonal increase in air temperature and photoperiod propagates as bottom-up pulse of primary production by plants, secondary production by herbivores, and tertiary production by carnivores. However, food web seasonality reflects not only abiotic variation in temperature and photoperiod, but also the composition of the biotic community and their functional responses to this variation. Some plants and animals—here referred to as seasonal specialists—decouple from food webs in winter through migration or various forms of metabolic arrest (e.g., senescence, diapause, and hibernation), whereas some plants and resident animals—here referred to as seasonal generalists—remain present and trophically coupled in winter. The co-occurrence of species with divergent responses to winter introduces seasonal variation in interaction strengths, resulting in summer-to-winter differences in trophic organization. Autumn cooling and shortening day length arrests primary productivity and cues seasonal herbivores to decouple, leaving generalist carnivores to concentrate their predation on the few generalist herbivores that remain resident, active, and vulnerable to predation in winter, which themselves feed on the few generalist plant structures available in winter. Thus, what was a bottom-up pulse, spread among many species in summer, including highly productive seasonal specialists, reverses into strong top-down regulation in winter that is top-heavy, and concentrated among a small number of generalist herbivores and their winter foods. Intermediate-sized, generalist herbivores that remain active and vulnerable to predation in winter are likely to be keystone species in seasonal food webs because they provide the essential ecosystem service of turning summer primary productivity into winter food for carnivores. Empirical examination of terrestrial mammals and their seasonal trophic status in the boreal forest and across an arctic-to-tropics seasonality gradient indicates seasonal specialization is more common among herbivores, small body sizes, and in regions with intermediate seasonality, than among carnivores, large body size, and regions where summers are very short or very long. Better understanding of food webs in seasonal environments, including their vulnerability and resilience to climate change, requires a multi-season perspective.

Introduction

Seasonality is an annual cycle which, at high latitudes, is comprised of wave-like variation in photoperiod—short, then long, and then short again—and temperature—cold, then warm, and then cold again (Bridgman and Oliver 2006). Winters are characterized by short photoperiods, cool air temperatures, reduced or suspended primary production, and reduced or suspended activity of many animals (Williams et al. 2015). Summers are characterized by long photoperiods, warm air temperatures, elevated primary production, and increased animal activity including reproduction.

From a trophic perspective, the annual sine wave in air temperature and primary production propagates, from bottom-to-top, into a seasonal wave of secondary production by herbivores, and a seasonal wave of tertiary production by carnivores (Elton 1927; Ostfeld and Keesing 2001). Because interacting species present in the same environment experience climate conditions simultaneously, shared and synchronizing responses to climate forcing may reinforce seasonal cycles initiated by a bottom-up pulse (Liebhold et al. 2004). Alternatively, physiological, behavioral, and ecological diversification of animals

may cause seasonal variation to manifest quite differently in different parts of the food web (Humphries and Umbanhowar 2007). The amplitude of the seasonal wave likely diminishes from the base to the top of the food web because only a small fraction of consumption at one level gets converted into biomass at the next level (McCann 2012) and because higher trophic levels may be capable of buffering environmental variation through behavioral flexibility (McNamara and Houston 2008), energy storage (Varpe et al. 2009), and ecological storage effects (Warner and Chesson 1985).

Thus, whether climate forcing propagates as a bottom-up wave of synchronization across multiple trophic levels or contributes to food web desynchronization and differentiation depends on the diversity of seasonal energetic strategies present within a food web and the impact of these differentiated seasonal phenophases on ecological dynamics (McMeans et al. 2015; Ruddell et al. 2016). Seasonality has long been recognized to affect organisms in very general ways (Seeger 1962), but less explored is how this seasonal ubiquity can lead to either trophic synchrony or decoupling depending on the nature and extent of abiotic variation in temperature and photoperiod, as well as the composition of the biotic community and their functional responses to seasonality (McGill et al. 2006).

In this article, we present some ideas and some data pertaining to the seasonality of food web structure. The ideas presented here may be quite general and possibly relevant to food web organization wherever seasonal environments occur, including terrestrial and aquatic ecosystems and seasonality defined by variation in temperature, precipitation, or photoperiod. The data presented here are illustrative examples from a much more restricted taxonomic and geographic perspective, focused first on several mammal species comprising one well-studied boreal food web in northern Canada and focused second on North American mammals in general, their functional traits, and their co-occurrence across a gradient of seasonality. This mammal, terrestrial, and North American focus reflects the happenstance that these are the systems with which we are most familiar and that the ideas we present here arose from our research and reading on them. In addition, North American mammal assemblages offer well-studied species and systems to an area of ecology with limited field data, especially regarding trophic interactions outside of the growing season. Mammals are also an informative group in that they are typically year-round residents, yet some hibernate and many others are active throughout winter, resulting in taxonomically-similar but seasonally-differentiated food web components.

Accordingly, we have divided the article in two sections. The first section focuses on general patterns, predictions, and a model food web, and is intended to speak to potential generalities by avoiding most taxonomic and system specificities. The second section focuses on terrestrial mammals and how they inform the general perspectives presented in the first section. We conclude the article by identifying the critical field data required to either advance or refute the ideas and trends presented here.

Some general ideas

Three fundamental axes of variation, and their prevalence among the plants and animals comprising the local community, will be particularly important in defining seasonal variation in terrestrial food web structure.

Trophic position and diet

The distinction between autotrophs (primary producers) and heterotrophs, and between herbivores (secondary producers) and carnivores (tertiary producers), is fundamental to food web organization (Elton 1927; Lindeman 1942; McCann 2012). Herbivores that consume vegetative structures (e.g., leaves, vegetative buds, and stems) are typically bulk feeders with enlarged digestive chambers hosting symbiotic microbes (Barboza et al. 2009). Other herbivores target energy- and nutrient-rich reproductive structures (e.g., seeds, berries, pollen, nectar, and flowers) and typically have specialized morphology and behavior that allows them to locate, access, and often store these less available, higher quality resources (Brown and Reichman 1979; Freed et al. 1994). Herbivores are generally easier to digest but harder to capture than plants, so carnivores tend to have simple guts, a high degree of encephalization, lean and muscular body composition, and fast and inflexible metabolic rates (Gittleman 1986; Aiello et al. 1995).

Seasonal specialization

The contrast between generalists and specialists often focuses on the degree of dietary, habitat, or range specificity (Van Valen 1965; Futuyama and Moreno 1988; Machovsky-Capuska et al. 2016), but here we focus on the extent of seasonal specialization. We consider a seasonal specialist to be a species that concentrates accelerated growth and productivity during specific periods within the annual cycle then decouples from the local food web for the remainder of the year, and a seasonal generalist to be a species with a broader seasonal niche, a longer annual period of growth, productivity, and trophic

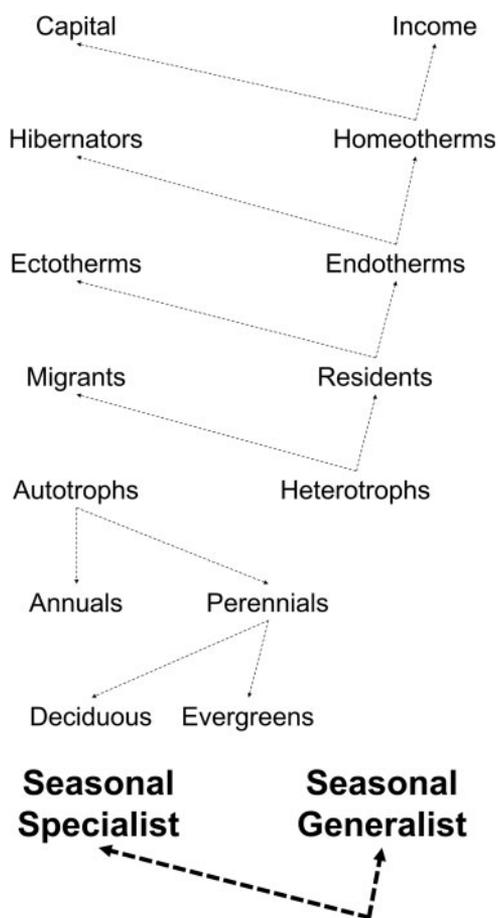


Fig. 1 The functional traits of seasonal specialists and seasonal generalists. Within autotrophs, annuals are more seasonal than perennials and deciduous trees are more seasonal than evergreen trees, as their growth is concentrated in summer months. Ectothermic heterotrophs are necessarily seasonal specialists at high latitudes because they are unable to be active at subzero temperatures. Endotherms have the potential to be seasonal generalists because their thermoregulatory capacity buffers them from ambient conditions, but functionally they can be positioned across the specialist–generalist continuum. Endothermic seasonal specialists include migrating and hibernating species, whereas resident endotherms that remain homeothermic, active, and tropically-coupled in winter are seasonal generalists. Intermediate strategies include daily heterotherms that express more torpor and feed less in winter than in summer, homeotherms that occupy refuges to avoid climate extremes and predators, and species that accumulate fat reserves or food hoards (i.e., capital) in preparation for winter.

coupling, and a dampened response to seasonal variation. Various functional categories position organisms closer to the seasonal specialist or seasonal generalist end of this continuum (Fig. 1). This is more a difference in degree, rather than in kind; seasonal generalists are still likely to express seasonal phenologies, including seasonal reproduction and a summer-to-winter reduction in growth rate, and seasonal specialists may retain varying extents of

functionality and coupling during their winter phenophase (Ruddell et al. 2016; Williams et al. 2017). The specialist–generalist trade-off is often framed as the relative advantages of doing one or a few things very well versus doing many things adequately (Wilson and Yoshimura 1994). Accordingly, when considering the co-existence of seasonal specialists and generalists, a reasonable expectation is that the relative performance of the two strategies (in terms of growth, survival, and overall biomass production) will vary by season, with seasonal specialists outperforming generalists in summer (or whenever their season of specialization occurs), but generalists outperforming specialists in winter (or at times of year other than the specialists’ season of specialization; e.g., Givnish 2002).

Body size

Body size is fundamental to trophic interactions because (i) large-bodied species have longer fasting endurance than small-bodied species (Lindstedt and Boyce 1985), (ii) small-bodied species can access spatial refuges that are inaccessible to larger bodied species (Huey et al. 2012), and (iii) large-bodied herbivores are difficult for small-bodied carnivores to kill (Owen-Smith and Mills 2008). As a result, large-bodied species are capable of buffering seasonal variation and are more likely to be seasonal generalists, whereas small body species are more likely to be seasonal specialists that spend most or all of the winter in refuges where they can simultaneously decouple from environmental stresses and predators. This small-bodied specialist, large-bodied generalist pattern may extend to aquatic systems and even autotrophs, if larger organisms generally have more buffering capacity and, as a result, are less responsive to seasonal scale variation than smaller, faster-responding organisms. Among heterotrophs, refuge occupation by small herbivores and predator invulnerability of large herbivores (except to the largest carnivores) should cause intermediate-sized herbivores, which are neither small enough nor large enough to avoid predation, to be a critical resource for most carnivores in winter.

These three axes of variation combine to define the seasonality of trophic structure. Autotrophs have a higher capacity for suspension of growth and metabolism in winter than at least some of the heterotrophs that are positioned above them in the food web (Hochachka and Guppy 1987). Furthermore, the functional attributes of carnivores (e.g., fast and inflexible metabolism, lean body composition, and larger body size) will cause them to be, in general,

Table 1 Predicted seasonal responses of food web attributes. Seasonal specialists are highly productive (in terms of growth, reproductive output, and overall biomass production) in summer and trophically-decoupled in winter, while seasonal generalists have dampened seasonal responses and remain coupled throughout the year

Attribute	Summer	Winter
1. Prevalence	Seasonal specialization declines with trophic position	Specialists decouple, generalists remain coupled
2. Productivity	Specialists are more productive than generalists	Generalists are more productive (or at least lose less) than specialists
3. Consumption (by heterotrophs)	Generalists and specialists consume productive specialists and less productive generalists	Generalists consume other generalists
4. Food web structure	Normal, with high primary production supporting secondary and tertiary production	Inverted, with arrested primary production, decoupling of many secondary producers, and largely unabated tertiary consumption
5. Trophic control	Bottom-up, distributed among many specialists and generalists	Top-down, concentrated among few generalists
6. Size structure	Dominated by smaller specialists	Dominated by larger generalists
7. Keystone species	Intermediate-sized generalist herbivores	

more seasonally-generalized than the herbivores they consume (Pond and Mattacks 1985; Lovegrove 2004; Muñoz-García and Williams 2005; Edmunds et al. 2016). Thus, the prevalence of seasonal specialization is likely to decline with trophic position (Table 1 Attribute 1), from near ubiquity at the bottom of the food web to rarity at the top of the food web. Given a specialist–generalist trade-off, specialists are likely to be more productive in summer than generalists (Attribute 2), and these highly productivity specialists are likely to be consumed by the generalists positioned above them in the food web (Attribute 3). Thus, in a general sense, seasonal food webs are likely to be characterized by a food web inversion in winter, with rates of consumption, growth, and metabolism remaining high at the top of the food web while the base of the food web enters a state of suspended animation (Attribute 4). As a result, the bottom-up trophic flow in summer (including links connecting highly productive seasonal plants and seasonal herbivores to year-round active carnivores), should reverse into strong top-down regulation in winter when the decoupling of specialist plants and herbivores forces generalist carnivores to concentrate their feeding on generalist herbivores (Attribute 5). Because large organisms have, relative to small organisms, an expanded dietary niche, prolonged fasting endurance, and reduced access to refuges, they are likely to be overall less seasonal than small organisms, with the potential consequence of a small to large size–structure transition from summer to winter food webs (Attribute 6). Finally, given the smallest herbivores are likely to be seasonal specialists that decouple in winter and the largest herbivores are invulnerable to predation

except by the largest predators, intermediate-sized herbivores that are present and active throughout the year are likely to experience the strongest top down regulation in winter and may represent keystone species in seasonal food webs (Attribute 7). Although these intermediate-sized, seasonally-generalized herbivores may be inessential food sources for carnivores in summer (when many productive specialists are also available), they are likely critical in defining food web structure throughout the year. In essence, they store summer primary productivity in a form that can be consumed by carnivores in winter (Warner and Chesson 1985), and in so doing, they maintain predators in the system.

A simple three-trophic-level food web comprised of seasonal specialists, seasonal generalists, and an intermediate category illustrates the predicted seasonal trophic structure. We construct the food web (see Supplementary Material) by assuming seasonal specialists predominate among plants are as common as generalists among herbivores, and are uncommon among carnivores. Further, we assume that specialists are more productive than generalists in summer, and that higher trophic levels consume lower trophic levels in proportion to their abundance and productivity. Based only on these three assumptions, the summer food web becomes dominated by bottom-up flows between seasonally-specialized plants and specialist and generalist herbivores, as well as between seasonally-specialized herbivores and seasonally-generalized carnivores (Fig. 2A). In winter, when seasonal specialists decouple and interactions become concentrated among the remaining generalists and intermediates, the strongest trophic link is between seasonally-generalized carnivores and seasonally-generalized herbivores (Fig. 2B).

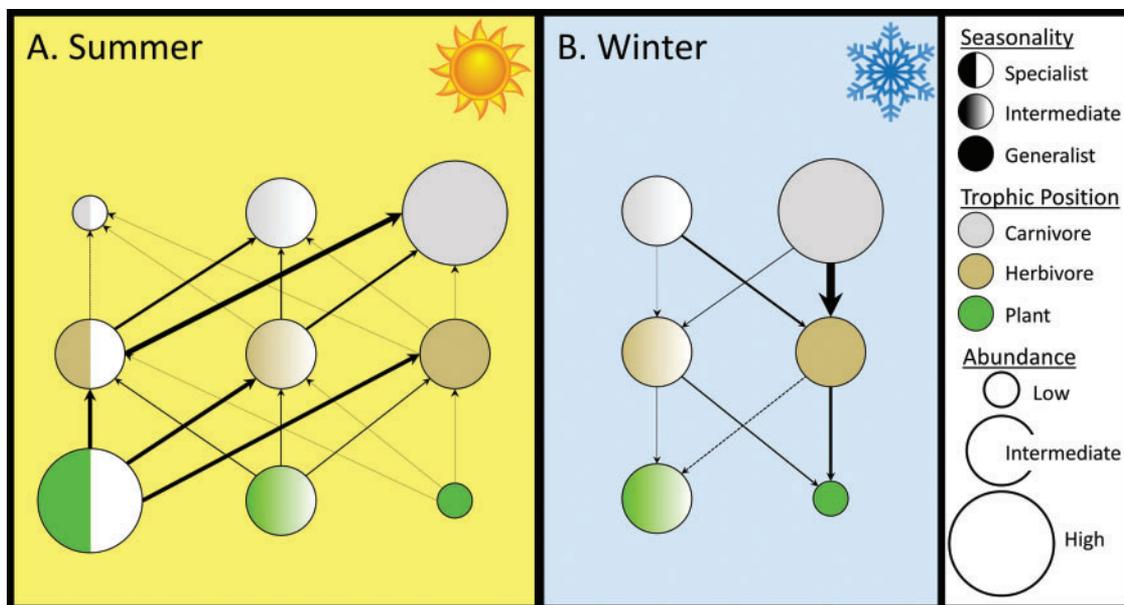


Fig. 2 A three trophic-level food web composed of seasonal specialists, seasonal generalists, and an intermediate category. The food web model, interaction strengths, and assumed parameters are described more fully in the Supplementary Material. But, briefly, circle size indicates biomass abundance and line thickness indicates interaction strength presented as total biomass flux. Assuming (i) seasonal specialists predominate among plants, are as common as generalists among herbivores, and are rare among carnivores, (ii) specialists are more productive than generalists in summer, and (iii) higher trophic levels consume lower trophic levels in proportion to their abundance and productivity, generates a food web with bottom-up flows in summer connecting seasonal specialized plants and herbivores to seasonally-generalized carnivores, which, following decoupling of seasonal specialists, transitions into a winter food web characterized by strong top down regulation of generalist and intermediate herbivores by generalist carnivores. Note that, for clarity of presentation, the asymmetrical interaction strength of carnivores on herbivores versus herbivores on carnivores is not presented as two separate lines, but in all seasons the top to bottom arrow (shown in winter) is $1/e$ times stronger than the bottom to top arrow (shown in summer), where e is the conversion efficiency of the predator.

Terrestrial mammals and the seasonality of their trophic interactions

A boreal food web example

The boreal forest is the world's most seasonal environment and its largest terrestrial biome, with broadly similar community composition and structure across its northern Eurasian and North American expanse. The boreal vertebrate food web has been particularly well-characterized in the Kluane Region of southwestern Yukon, Canada, through the long-term monitoring and large-scale field experiments described by Krebs et al. (2001). This research highlights the importance of snowshoe hares (*Lepus americanus*) as a keystone species, and the importance of the 10-year snowshoe hare and lynx (*Lynx canadensis*) population cycle that influences the abundance and trophic interactions of many other vertebrate species present in the system. Consideration of temporal variation in the structure of this food web has focused primarily on multi-annual variation associated with the highs and lows of the 10-year lynx-hare cycle. Here we focus on

temporal variation in Kluane food web structure shaped by seasonal variation between summer and winter conditions and the trophic interactions of seasonal specialists and generalists (recalling that here the specialist vs. generalist contrast focuses on the seasonality of activity and trophic coupling, not dietary niche breadth). We focus on the four most abundant mammal herbivores in this system, including a seasonal specialist (arctic ground squirrel, *Spermophilus parryi*), two seasonal generalists (hares and moose, *Alces alces*), and a seasonal intermediate (red squirrel, *Tamiasciurus hudsonicus*), and their trophic interactions with three broad categories of vegetation (seasonally specialized grasses, forbs, and berries; seasonal specialized deciduous shrubs and trees including mainly *Salix* spp. and trembling aspen, *Populus tremuloides*; and seasonally generalized evergreens represented by white spruce, *Picea glauca*) and three major mammalian predators (coyotes, *Canis latrans*, lynx, and wolves, *Canis lupus* all of which are seasonal generalists).

In summer, Kluane has a diffuse food web structure with many weak and few strong interactions

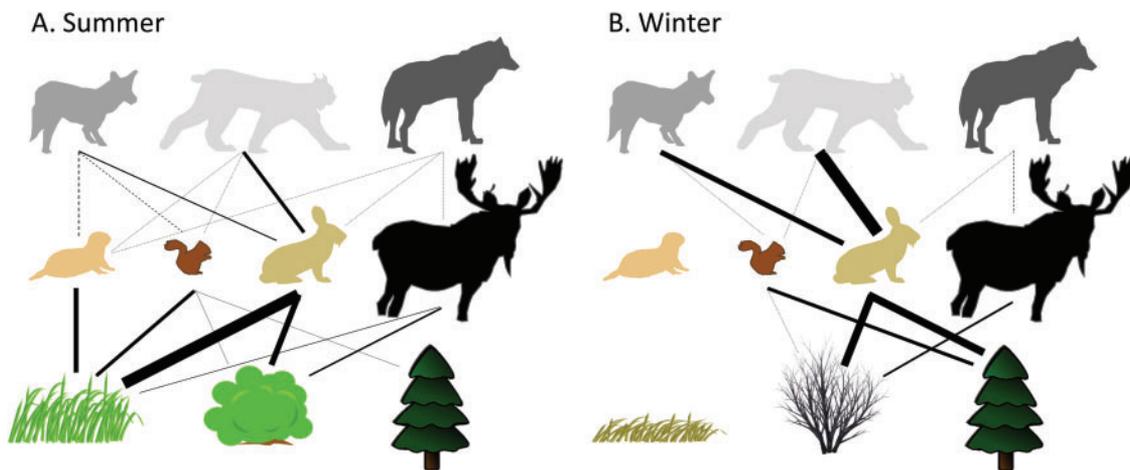


Fig. 3 Changes in interaction strength of the Kluane food web from (A) summer, when there are strong flows connecting seasonally-available plants, seasonally-available herbivores including ground squirrels (left) and red squirrels (left middle), and year-round carnivores including coyotes (left), lynx (middle), and wolves (right) to (B) winter, when interaction strengths become concentrated among year-round carnivores and any readily accessible herbivores and plant parts. Year-round activity of snowshoe hares (middle right) causes them to be vulnerable to predation year-round, whereas moose (right) and red squirrels, whose large body size or arboreality and reduced activity in winter, respectively, render them less vulnerable in winter. Interaction strengths, indicated by line thickness and reflective of total biomass flow, are based on estimated biomass density (kg/km^2) and dietary fractions (see Supplementary Material). Plant symbols indicate, from left to right, grasses–forbs–berries, shrubs–aspen, and white spruce.

(Fig. 3A). The strongest interaction is between snowshoe hares and seasonally-available plants and plant parts including graminoids, forbs, leaves, and new growth. Ground squirrels and red squirrels are also most strongly connected to these seasonally-available plants and plant parts. Coyotes and lynx, the two most abundant carnivores in the system, consume snowshoe hares, but also ground squirrels and red squirrels. Wolf diets have not been well quantified in the Kluane region, but across the boreal, wolves are thought to rely heavily on ungulates during the summer, including young-of-the-year calves, but to also kill snowshoe hares when abundant as well as seasonally-available prey like beaver and ground squirrels.

In winter, Kluane has a simplified and intensified food web structure that is dominated by a few strong interactions (Fig. 3B). Annual plants decline markedly in abundance, while deciduous shrubs and trees decline in biomass, accessibility, and forage quality, leaving really only the woody twigs of shrubs and conifer trees as exploitable resources at the base of the terrestrial food web. The decoupling of these seasonal specialist herbivores shifts predation pressure to the remaining seasonal generalists that do not reduce their activity in winter. At Kluane, snowshoe hares, spruce grouse (*Falci pennis canadensis*), and moose are all seasonal generalists that browse on shrubs, aspen, and occasionally spruce. However, the large body size of moose renders them invulnerable to predators smaller than wolves, whereas grouse, like red squirrels, can at least

use trees to evade terrestrial predators. Small mammals like mice and voles are active throughout winter, but tend to be most active in subnivean space where hard and deep snow pack offers at least partial protection from predators (Gese et al. 1996). Thus, for abundant resident predators like lynx and coyotes, snowshoe hares are the only constantly vulnerable herbivore available in winter.

The Kluane food web, thus, changes from summer—when there are many and more diffuse interactions including strong flows connecting seasonally-available plants, seasonally-available herbivores, and year-round carnivores—to winter—when interaction strengths become concentrated among year-round carnivores and any still accessible herbivores and plant parts. The year-round activity of snowshoe hares and their year-round vulnerability to all predators may cause hares to experience the strongest top down interactions in winter.

Functional traits and seasonal trophic structure of North American mammals

Here we move beyond our boreal food web example to consider the functional traits and seasonal trophic structure of North American Mammals. Based on a sample of 237 mammal species present at (one or more of) 50 localities spread across the continent, we quantify the prevalence of seasonally-specialized and seasonally-generalized mammal species and how this prevalence varies with trophic position, diet, and

body size. Based on the general ideas presented in the first section, we hypothesize that, within North American mammals, the prevalence of seasonal specialization will decrease with trophic position, body size, and year-round access to primary food sources.

In addition, we consider how the composition of the mammal community and their functional responses to seasonality varies from high latitudes, where summer growing seasons are short and winters are long and cold, to lower latitudes, where summers are long and seasonal differences are less extreme. As seasonality varies, we hypothesize that the composition of large versus small species and generalists versus specialists will also vary, with concomitant impacts on the seasonality of trophic interactions. In particular, we predict seasonal specialist strategies are likely to be most prevalent in regions where winter and summer are vastly different in environmental conditions but roughly similar in durations. Short, mild winters are predicted to promote seasonal generalization if winters are too ephemeral and too similar to summer conditions to select for seasonal specialization. Very long winters are predicted to promote either (i) extreme seasonal specialization, with concentrated growth and reproduction during a very short summer season followed by an extended period of decoupling, or (ii) seasonal generalization, if the gains achievable during a short summer season cannot equal or exceed the losses sustained during a long winter season. In this latter case, very long winters will favor seasonal generalists that can continue to forage and minimize energy losses during winter, which, at least for mammals, may favor larger-bodied generalists because larger mammals lose less heat and are better able to digest low quality diets. Thus, we hypothesized that seasonal specialization would be most common where season lengths were intermediate and least common where either summer or winter conditions prevailed for most of the year. We also hypothesized that body size would be largest in the localities with the longest winters, particularly among seasonal generalists.

Methods

We used growing season length to define a latitudinal gradient in seasonality because it is a well-quantified indicator of seasonality that exerts a strong control on ecosystem function (White et al. 1999; Steltzer and Post 2009). Although growing season length is affected by multiple meteorological, photoperiod, soil, and vegetative metrics (Euskirchen et al. 2006), it can and is often operationally approximated as the number of

frost free days, starting on the first spring day and ending on the last autumn day when average minimum temperature exceeds 0 °C (Natural Resources Canada and Government of Canada 1995). Accordingly, we use frost-free-days to define growing season length in the following analysis. Across North America, from the Canadian high Arctic to the US–Mexico border, from high elevations to low, and from maritime to continental climates, growing season length varies from less than 20 days to more than 240 days (Bonsal et al. 2001; Easterling 2002). Across this continental gradient, we identified 10 seasonality zones (0–20, 20–40, 40–60, 60–80, 80–100, 100–120, 120–160, 160–200, 200–240, >240 days) and selected five localities within each zone, generating 50 sites total (5 replicate sites for 10 seasonal zones; Supplementary Table S1). Replicate sites were situated as distant as possible from each other to maximize beta diversity across the five replicates, but nevertheless wide ranging species occurred at multiple sites within zones and across multiple zones (see Supplementary Table S1).

For all 50 sites, we used the map search function within Smithsonian Mammals of North America (Smithsonian n.d.) to obtain the list of mammal species present at each site, based on species range distributions. Species range maps are a coarse approach for predicting local patterns of species occurrence and co-occurrence, because they provide no information about scarcity or relative abundance, are inaccurate around range margins, and do not reflect habitat-specific occurrences that are important at local scales (Rondinini et al. 2006). However, in using this approach, we do not intend to recreate the exact community assemblages present in a specific locality, but rather seek to inform a continental-scale comparison by identifying the trophic niche characteristics of mammals present within a particular zone of seasonality. Having five replicate sites per seasonal zone is a further attempt to counter the site-specific idiosyncrasies of inferring assemblages based on over-lapping range distributions.

Body size, seasonality, and diet are, to a certain degree, plastic and individually-variable within a species, but, at the broadest levels of variation, can also be treated as a functional attribute of a species (McGill et al. 2006). For the 237 mammals species present in one or more of our 50 sampling sites, we determined four species-level traits that helped to characterize their seasonal trophic status—body size, trophic position, diet, and degree of seasonal specialization. We obtained data on adult body mass and diet from Wilman et al. (2014), which includes dietary percentages across five carnivorous food types (invertebrates, vertebrate endotherms, vertebrate

ectotherms, fish, unknown vertebrates, scavenging) and four herbivorous food types (fruit, nectar, seed, plant). We classified species as carnivores if the sum of the five carnivorous food types comprised $\geq 50\%$ of their diet and as herbivores if the sum of the four herbivorous food types comprised $>50\%$ of their diet. Diet categories were based on the same data, with carnivore diets classified as either carnivore-vertebrate (c-ver) or carnivore-invertebrate (c-inv) and herbivore diets classified as either herbivore-vegetative (h-veg) or herbivore-reproductive (h-rep); see Supplementary Table S1 caption for details.

As described in more detail in the Supplementary Material, our classification of seasonal generalists (-gen) versus specialists (-spe) focuses on whether year-round resident species are active and foraging at all times of the year (seasonal generalists) or whether they feed, grow, and are active only during the growing season, then, outside of the growing season, decouple from food webs via inactivity, fasting, and refuge occupation (seasonal specialists). We focus our mammal classification of seasonal specialists and generalists according to whether or not they hibernate. In this context, we are interested in hibernation as an ecological trait focused on the tendency to spend winter in an inactive, non-feeding state.

Our restricted focus on hibernation causes us to exclude other potentially important forms of winter decoupling. Migration is widespread and well-documented form of seasonal specialization but, unlike birds, terrestrial mammals do not migrate long enough distances to avoid winter conditions. However mammals are characterized by more subtle and species-specific forms of winter decoupling, including the protection of beaver and muskrats by ice cover (Lancia et al. 1982) or the partial protection of many small mammals by snow cover (Korslund and Steen 2006). These more subtle forms of decoupling are widespread and known to be crucially important to ecological seasonality (Penczykowski et al. 2017), but were not considered here because they are difficult to classify at a species level and as binary categories. Thus, our review focuses on a rather distinct and obvious form of winter decoupling (though classification of mammalian hibernation has its own inherent complexities and limitations; see Supplementary Material and Discussion), yet beyond this hibernation focus, there are many additional forms of winter decoupling that warrant more attention.

Results

Seasonal specialization is more common in herbivores than carnivores, and is most common among

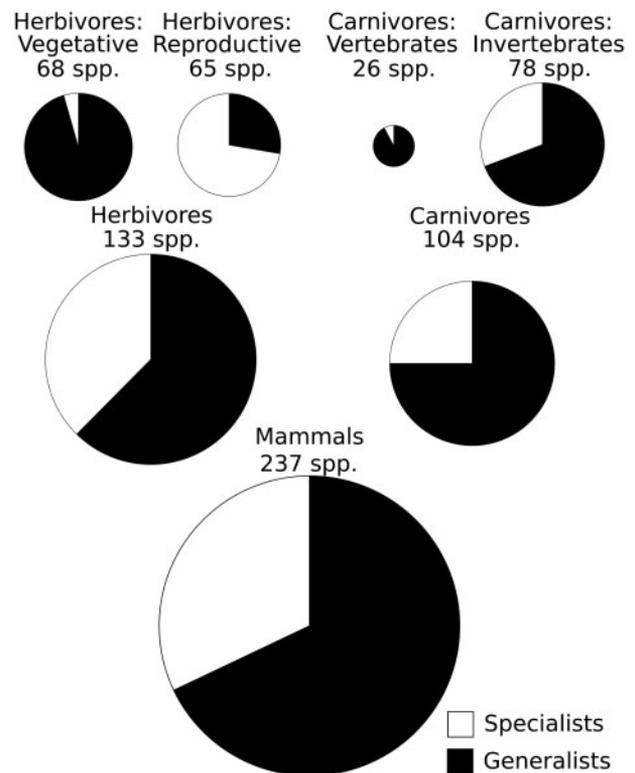


Fig. 4 Prevalence of seasonal specialists and seasonal generalists among 237 mammal species present at 50 localities distributed across the North American seasonality gradient. Pie charts indicate number of species belonging to each category among all species, among carnivores and herbivores, and among dietary subcategories of carnivores and herbivores.

herbivores that feed on the reproductive structures of plants and carnivores that feed on invertebrate prey. Among our sample of 237 mammal species, one-third (76 spp., 32%) were classified as seasonal specialists (i.e., hibernators) and two-thirds (161 spp., 68%) as seasonal generalists (i.e., non-hibernators). Among 133 herbivorous species (diets comprised $>50\%$ of plant matter), 38% (50 spp.) were seasonal specialists and 62% (83 spp.) were seasonal generalists (Fig. 4). However, 96% of herbivores consuming vegetative portions of plants (i.e., leaves, twigs, and stems) were seasonal generalists, whereas 72% of herbivores consuming reproductive plant parts (i.e., seeds, fruit, nectar, and pollen) were seasonal specialists. Among 104 carnivore species (diets comprised $>50\%$ of animal matter), 25% (26 spp.) were specialists and 75% (78 spp.) were generalists (Fig. 4). However, 92% of the specialist carnivores were insectivorous bats. Thus, among North American mammals, seasonal specialization is generally less common among carnivores than herbivores. Further, almost all seasonal specialists are herbivores that feed on reproductive plant structures or carnivores that feed on invertebrates, whereas seasonal

generalization predominates among herbivores that feed on vegetative plant structures and carnivores that specialize on vertebrate prey.

Seasonal specialists are smaller-bodied than generalists. Among the 161 species in our sample that were seasonal generalists, median body size was 84 g (range 2.4 g to 579 kg), whereas among the 76 seasonal specialists, median body size was 24 g (range 3.7 g to 181 kg). The prevalence of seasonal species is highest among the smallest mammals and lowest among the largest mammals (Fig. 5A). For example, among mammals weighing <1 kg, 36% of species are specialists (Fig. 5B), whereas among those that weigh >1 kg only 18% are specialists. The only very large seasonal specialists in our sample are black bears (100 kg) and brown bears (181 kg). However, within a given diet category, specialist species were not consistently smaller-bodied than generalist species (Fig. 5B). Thus, specialists are, in general, smaller than generalists because the diet categories in which specialists are most common (i.e., h-rep and c-inv) are smaller-bodied than the diet categories in which specialists are least common (i.e., h-veg and c-ver). Thus, although seasonal specialists range in size from small bats to big bears, and specialists are not necessarily smaller than their generalist counterparts, seasonal specialization is much more prevalent among small-bodied than large-bodied mammals.

The prevalence of seasonal specialists and generalists varies according to season length, with specialists most prevalent where winters and summers are approximately equal in duration and rare or absent where winters dominate the annual cycle. The median proportion of specialists (relative to all species in the assemblage) exceeded 30% where growing season length was between 100 and 240 days and reached a local maximum where the growing season and non-growing season had equal lengths (Fig. 6A). The prevalence of specialists declined to about 25% in regions with the longest growing season (>8 months, where site to site variability was also high) and declined to zero or near zero in regions with the shortest growing season (<1 month). These highest latitude, longest winter sites are dominated by seasonally-generalized herbivores feeding on vegetative structures (e.g., lemmings, *Dicrostonyx* and *Lemmus* spp., hares, *Lepus arcticus*, caribou, *Rangifer tarandus*, and muskox, *Ovibos moschatus*) and seasonally-generalized carnivores feeding on vertebrates (e.g., weasels, *Mustela erminea*, arctic foxes, *Vulpes lagopus*, and wolves; Fig. 6B). Moving southward along the gradient, away from the poles and toward longer summers, the first seasonal specialists to appear are herbivores feeding on reproductive parts of plants (e.g., ground squirrels, *Spermophilus* spp., marmots, *Marmota* spp., and bears, *Ursus* spp.), followed by, several climate zones

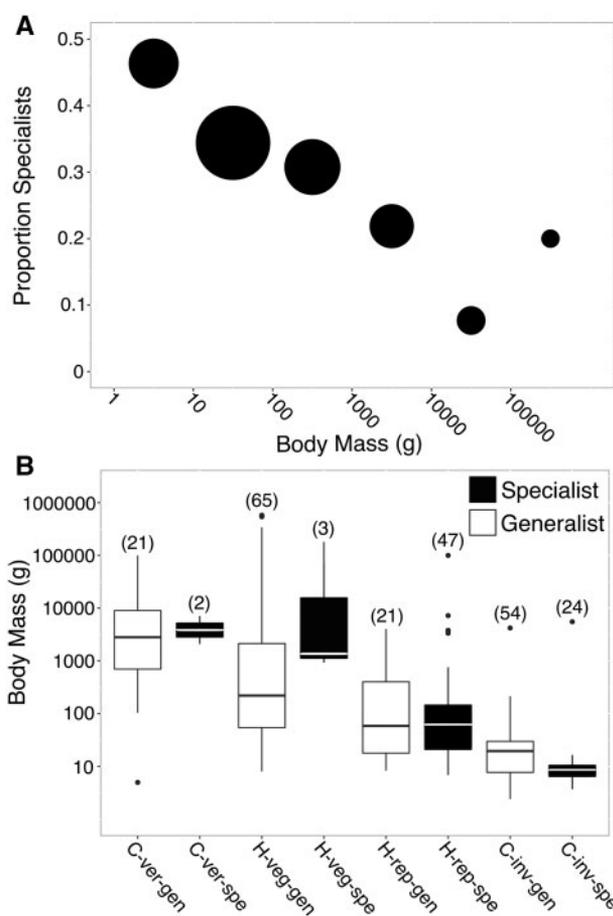


Fig. 5 The association between body mass and the prevalence of seasonal specialization. (A) The proportion of species that are seasonal specialists within six body mass categories (1–10 g, 10–100 g, 100 g–1 kg, 1–10 kg, 10–100 kg, and >100 kg) with the size of circles indicating the number of mammal species in each mass category (ranging from 5 species for the smallest circle, mass range >100 kg, to 95 species for the largest circle, mass range 10–100 g). (B) The body mass distribution of specialists and generalists within eight dietary clades (C, carnivore, H, herbivore, ver, vertebrate, inv, invertebrate, veg, vegetative, rep, reproductive, gen, seasonal generalist, spe, seasonal specialist). Central line indicates the median, boxes indicate the interquartile range, lines indicate 1.5 times the interquartile range, and dots are outliers beyond the lines. Numbers above each boxplot represent the number of species belonging to each category.

later, seasonally-specialized carnivores feeding on insects (e.g., vespertilionid bats). At the peak prevalence of specialists, where summer and winter are similar in length, five clades occur in roughly equal abundance, including three seasonally-generalized clades (h-veg-gen, h-rep-gen, and c-ver-gen) and two seasonally-specialized clades (h-rep-spe and c-inv-spe). The reduced prevalence of specialists in the most southerly, longest summer sites is due mainly to seasonally-specialized herbivores feeding on reproductive structures (h-rep-spe) being replaced by their seasonally-generalized counterparts (h-rep-gen; Fig. 6B).

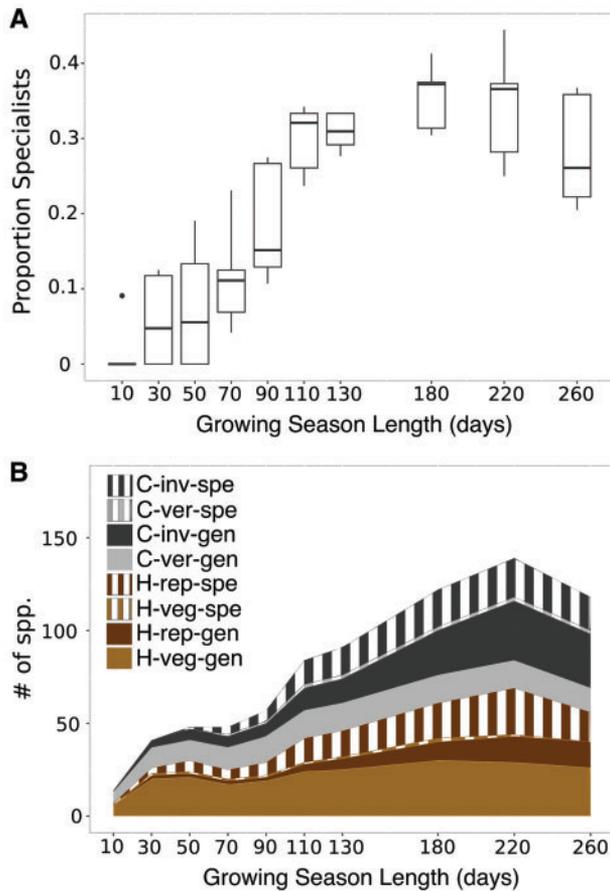


Fig. 6 The prevalence of seasonal specialists and generalists across a North American climate gradient in growing season length (number of frost free days). **(A)** Box plots illustrate how the proportion of specialists (relative to all species in the assemblage) varies across the five sites sampled per season length zone (with the bottom line indicating the site with the minimum prevalence, and the top line or point indicating the site with the maximum prevalence; five values are not always discernible per climate zone if the proportion of specialists was similar among sites). **(B)** The total number of species present across the gradients by dietary and seasonality category. See Fig. 5 caption for explanation of categories.

Body mass declines as growing season lengthens. There was a substantial decrease in median body mass from the highest latitude locations with the shortest growing seasons, where median body mass was 2.2 kg, to the lowest latitude locations with the longest growing seasons, where median body mass was 47 g (Fig. 7A). The two sites with the most extreme median body mass was a location where the growing season was 0–20 days long and median body mass was 17 kg and a location where the growing season was 200–240 days long and median body mass was 25 g. This change in median body mass from the poles to the tropics did not arise from substantial and consistent within-clade shifts in body mass (Fig. 7B) but rather from a gradual

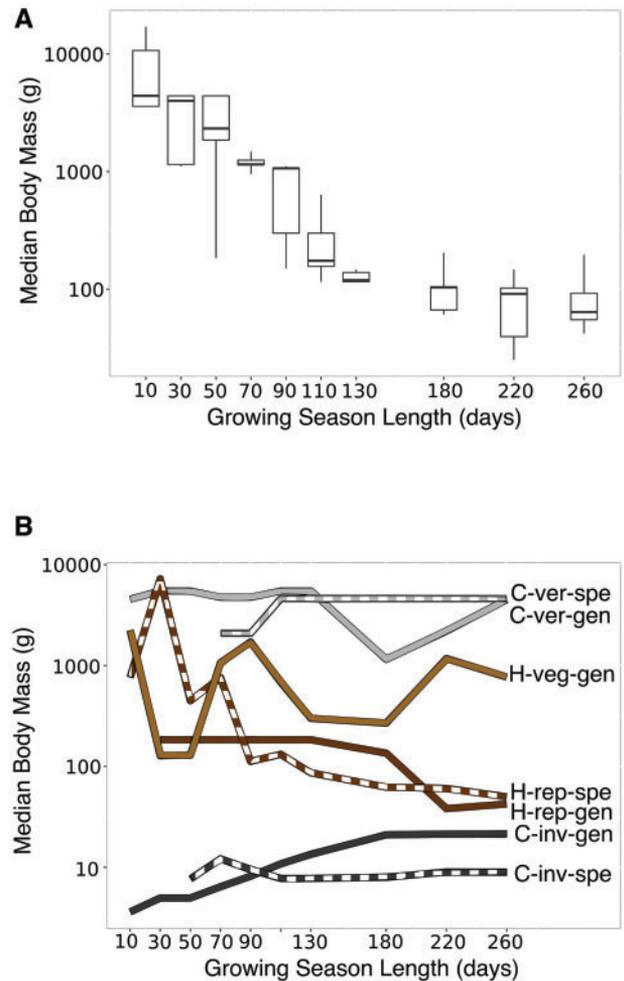


Fig. 7 The relationship between growing season length (number of frost free days) and the median body mass of North American mammal assemblages. **(A)** Box plot indicating the median mass of the mammal assemblage present at five localities sampled within each season length zone (with the bottom line indicating the median mass for the site with the lowest value, and the top line indicating the median mass for the site with the highest value; five values are not always discernible per climate zone if median masses were similar among sites). **(B)** Median mass trends within diet and seasonal specialization categories, with the value presented indicating the median mass of all species belonging to the category and present within the climate zone (i.e., five sites combined to generate a list of species per category per zone, and the median of that species group presented here). See Fig. 5 caption for explanation of categories.

reduction in the prevalence of larger bodied clades (i.e., c-ver-gen and h-veg-gen) and an increase in smaller-bodied clades (e.g., c-inv and h-rep; see also Figs. 5B and 6B).

Discussion

We propose the following general scenario of seasonality in food web structure as a testable hypothesis. Across a broad latitudinal range of seasonality,

seasonal specialists are highly productive during the summer growing season, generating a strong, bottom-up pulse of seasonal productivity. This seasonal pulse is consumed by seasonally-specialized and seasonally-generalized herbivores, which are in turn consumed by carnivores that are predominately seasonal generalists. Thus, the annual wave of seasonality—warm then cold then warm again—propagates as a bottom-up pulse into a seasonal wave of secondary production by herbivores and tertiary production by carnivores. For everything there is, indeed, a season. However, in autumn, seasonally-specialized clades decouple from local trophic interactions (via migration, senescence, diapause, and hibernation), whereas seasonally-generalized clades remain coupled throughout winter. Winter decoupling is more prevalent at the base of the food web (e.g., most primary production ceases in winter) than at the top (e.g., many top carnivores continue to consume and accumulate mass in winter). This causes the bottom-up summer productivity pulse to reverse into strong top-down regulation in winter, concentrated among numerous generalist carnivores feeding on less numerous generalist herbivores feeding on less-yet numerous generalized plant structures. Intermediate-sized generalist herbivores are the most likely to be consumed in winter because larger herbivores are invulnerable to predation except by the largest predators and smaller herbivores are more likely to be seasonal specialists and, even if they are seasonal generalists, are able to occupy refuges that are less accessible to larger herbivores and predators. As a result, these intermediate-sized, generalized herbivores, together with the plant parts that sustain them, are likely to be keystone species in seasonal food webs because they maintain predators in the system until the summer pulse returns.

In the boreal food web example we consider, this seasonal trophic structure manifests in summer as a bottom-up summer pulse connecting the primary productivity of annual sedges, grasses, and berries, deciduous shrubs to the secondary production of herbivores including seasonally-specialized ground squirrels, seasonally-generalized snowshoe hares and moose, and seasonally-intermediate red squirrels, which in turn support the tertiary production of seasonally-generalized carnivores including coyotes, lynx, and wolves. In autumn, when primary production ceases and snow cover blocks easy access to non-woody plants, ground squirrels decouple completely and red squirrels decouple partially, leaving snowshoe hares and moose as the primary generalist herbivores remaining available to predators. Moose are large enough to be invulnerable to

predation by lynx and coyotes, leaving hares to experience the strongest top-down pressure in winter. We suggest that this pattern in seasonal trophic structure may help to explain why snowshoe hares function as a keystone species in the boreal (Sinclair 2003; Krebs 2011) and why their average abundance and cyclicity appears to be decreasing with a warming climate despite an abundance of winter food (Krebs et al. 2017).

Our empirical analysis of the functional traits of North American mammal assemblages offers more general support for several patterns consistent with the above hypothesis, albeit from a still restricted taxonomic and geographic focus. First, for North American mammals in general, seasonal specialization is more common among mammalian herbivores than mammalian carnivores (despite both groups having access to seasonally-specialized and seasonally-generalized prey). Second, seasonally-specialized and seasonally-generalized herbivores co-occur across a broad North American gradient in seasonality and, in all these localities, the mammal carnivores that consume mammal herbivores are almost always seasonally-generalized. Identifying keystone species from multiple systems requires trophically-detailed cross-system comparisons, but it may be informative to consider the preferred prey of the 19 species of terrestrial carnivores specialized on endothermic vertebrates (i.e., mammals and birds) included in our seasonal gradient (Supplementary Table S2). The preferred prey of 16 of the 19 predators (85%) was from one of three taxonomic groups: lagomorphs (6 of 19, 32%), arvicoline rodents (6 of 19, 32%), or small artiodactylids (4 of 19, 21%). These preferred species differ in body size, taxonomy, and in many aspects of their ecology, yet notably almost all are intermediate-sized, seasonal generalists that feed on seasonally-generalized vegetation (h-veg-gen). These seasonally-generalized herbivores provide the essential ecosystem service of turning summer primary productivity into winter food for carnivores, which may at least partially explain why arctic lemmings, boreal hares, and temperate zone ungulates, all of which belong to the h-veg-gen category, often form keystone interactions within terrestrial vertebrate food webs (Sinclair 2003; Krebs 2011). Also important to consider is how these keystone species are able to persist in their respective systems, despite their year-round vulnerability to predation and their competition (both direct and indirect via shared predation) with smaller specialist and larger generalist herbivores that do not suffer such strong predation.

Our empirical analysis of the functional traits of North American mammals also provides some initial insight into how the composition of the biotic

community and their functional responses to seasonality varies across a large scale climatic gradient. At the highest latitudes, where summers are very short and winters very long, there are few seasonally-specialized mammals. Instead, assemblies are dominated by seasonally-generalized herbivores, like lemmings, hares, caribou, and muskox feeding on vegetative parts of plants, as well as seasonally-generalized carnivores, like ermine, arctic foxes, and wolves feeding primarily on mammalian prey. Although these species vary widely in body size, they tend to be larger than species found at lower latitudes. This decline in body mass from north to south along the latitudinal gradient is consistent with Bergmann's rule (Lindstedt and Boyce 1985; Blackburn et al. 1999; Ashton et al. 2000; Huston and Wolverton 2011), but yet is remarkable in the magnitude and consistency of the decline as well as the absence of any strong latitudinal trends in body mass within trophic levels and diet categories. Instead body size declines from high to low latitudes due only to the gradual reduction in the prevalence of larger bodied generalist clades and an increase in smaller-bodied clades comprised of specialists and generalists. We interpret the high latitude absence of seasonally-specialized mammals as resulting from, in a general sense, the specialists' season of relative advantage becoming too short and the generalists' season of relative advantage becoming too long. However, like all other phenological traits, the evolution and occurrence of seasonal specialization and generalization will depend on a host of other factors, including lifespan relative to season length, trade-offs, limits to plasticity, predator-prey co-evolution, and frequency dependent selection (Forrest and Miller-Rushing 2010; Williams et al. 2017).

Notably, the proportion of seasonal specialists incrementally increases with lengthening growing season, to reach a maximum when winter length and summer length are approximately equal, then declines again as the growing season begins to predominate the annual cycle. Understanding seasonal trophic structure at lower latitudes, where growing seasons are long and summer-to-winter contrasts in biotic conditions are more nuanced, requires going beyond the species-level functional classifications of potential seasonal niches we use here, to *in situ* observations of the realized seasonal niche of individuals and populations comprising local food webs. These *in situ* observations are important at all latitudes and within all food webs, but are a particular need for low latitude and low seasonality localities, where a broader range of winter activity patterns and energetic approaches is likely to be viable (Humphries et al. 2005).

We focus here (at least empirically) on North American mammals, but seasonal specialization is, of course, a functional characteristic of many organisms, from across the tree of life and from all seasonal environments on the planet. The patterns and consequences of seasonal specialization surely vary taxonomically and geographically. For example, although seasonal specialization is rare among arctic mammals (this study) and annual reproduction is exceedingly rare among arctic plants (Billings 1987), the arctic remains a highly seasonal place, abiotically and biotically, including seasonal perennials, invertebrates, and migratory birds (Pielou 2012). Although there are few seasonally-specialized mammals in the low latitude portions of North America, seasonal forms of endothermic heterothermy are more prevalent in other low latitude parts of the world (McKechnie and Mzilikazi 2011). Globally, after dormancy (e.g., hibernation and diapause), migration may be the next most common and ecologically-important form of seasonal-specialization. Because migration spatially separates reproductive and non-reproductive phases of the life cycle, migratory animals and their offspring offer a major seasonal food source and allochthonous input that is capitalized on by other migratory species as well as year-round residents (Giroux et al. 2012). Summer feeding by year-round residents on summer-only migrants will contribute to food web inversions in winter, because when migrants depart and decouple, the productivity they have supported stays behind and coupled. However, body size and trophic position appear to not be as strongly correlated with migration in birds, as hibernation is in mammals, so at least avian seasonal specialization does not appear to be as size-structured and trophic-position dependent as mammalian specialization.

The selective pressures that seasonal environments impart on organisms, and the genetic and life history constraints that shape responses to selection, are central to understanding the generalist-specialist composition of phylogenetic groups and community assemblies (Williams et al. 2017). The abiotic environment clearly drives the evolution of seasonal traits and seasonal traits clearly shape ecological outcomes, but so too will the ecology of trophic interactions influence the evolution of biological responses to seasonality. Better understanding of the biological and ecological impacts of seasonality awaits better integration of physiology, chronobiology, evolutionary ecology, and food web research (Williams et al. 2017), approached from a functional trait and community assembly framework (McGill et al. 2006).

Additional research is required to assess whether the seasonal trophic structures and keystone species characteristics that we describe here generalize across aquatic and terrestrial systems, distinct taxonomic groups, other regions, and varying forms of seasonality (McMeans et al. 2015). A recent analysis of a European temperate-forest food web, which considers seasonally-generalized and seasonally-specialized vertebrates in a manner similar to what we present here, concludes that seasonal changes of species interactions has regulating effects on community persistence (Saavedra et al. 2016). Similarly, research on insect communities in montane desert streams illustrates how distinct faunal assemblages can be maintained at the same sites through time-sharing of strong seasonal variation in abiotic conditions (Bogan and Lytle 2007). However, other research on the seasonality of food web structure, often in aquatic systems, has detected muted, spatially-inconsistent, and methodology-dependent summer-to-winter differences in interaction strength (Baird and Ulanowicz 1989; Winemiller 1990; Schoenly and Cohen 1991; Thompson and Townsend 1999).

Quantifying the extent and implications of seasonal variation in trophic structure requires integrated, multi-season environmental and biological monitoring that is, unfortunately, rather rare in recent and contemporary ecological research. Local environmental variation needs to be quantified throughout the annual cycle and over multiple years, including temperature, precipitation, and photoperiod, from above the canopy to below-ground in terrestrial systems and above the water surface to the benthos in aquatic systems, with particular attention paid to the hydrosphere, cryosphere, and subnivium wherever and whenever they are present (Douglas et al. 2005; Pauli et al. 2013; Tang et al. 2014). At the same time, the key taxa or functional groups that form strong interactions, either throughout the year or at specific times of the year, need to be identified, and their diet, energy intake, energy expenditure, growth, and reproduction need to be quantified over time and across changing environmental conditions (Power et al. 1995). Doing all of this is not likely to be easy, but it is also unlikely to be prohibitively difficult, at least among more accessible and tractable systems. However, a major hurdle that must be overcome does not involve what and where ecologists study, but rather when. For too long, research on ecological systems has focused too narrowly on the summer growing season and ignored too much about how systems function and organisms interact in the colder and darker months of the year (Campbell et al. 2005). Winter is, of

course, a critically important season (Ladwig et al. 2016; Sanders-DeMott and Templer 2017). Although many organisms may be harder to access and do less between autumn and spring than between spring and autumn, what they avoid, endure, and accomplish during winter, and the extent to which their seasonal response either integrates or differentiates them from other organisms experiencing the same environment, sets the stage for all that happens in spring. To everything there is a season, and no one season reveals everything. Better understanding of food webs in seasonal environments, including their vulnerability and resilience to climate change, requires a multi-season perspective (Williams et al. 2015).

Acknowledgments

We thank Manuelle Landry-Cuerrier for assistance with the literature, Juliana Balluffi-Fry for producing Supplementary Material, Kevin McCann and Bailey McMeans for advice and perspective related to quantifying interaction strengths and the seasonality of trophic interactions, and Caroline Williams and Gregory Ragland for organizing a seasonality symposium and especially for welcoming an ecological food web perspective into an evolutionary context.

Funding

This work was supported by a Natural Sciences and Engineering Council of Canada (NSERC, Canada) Discovery Grant and Institut Nordique du Quebec (INQ) Chair in Northern Research [to M.M.H.]; an NSERC Canada Graduate Scholarship [to E.K.S.]; and a Vanier Canada Graduate Scholarship [to A.K.M.].

Supplementary data

Supplementary data are available at *ICB* online.

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