OPINION PIECE

Food web approach for managing Arctic wildlife populations in an era of rapid environmental change

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ABSTRACT: Scientists and wildlife managers implementing adaptive monitoring and management schemes, are tasked with providing predictions of population responses to harvest and environmental changes. Such predictions are useful not only to forecast direct effects of climate, productivity, land use, or habitat degradation, but also changes in the food web, such as expanding/increasing species that are predators, prey, and competitors of populations of concern. Explicit consideration of food webs and their dynamics in more complex models could provide better predictions of future changes, and allow us to better assess the influence of management actions. Here, we present our perspective on what we have learned from conducting a number of case studies using such a food web approach with a focus on climate and harvest impacts and their implications for management. We found empirical support for many of our hypothesized food web effects, and were able in some cases to obtain short-term forecasts with slightly lower prediction error using models that account for food web dynamics compared with simpler models. Predictions are the foundation of adaptive management because they allow quantitative assessment of the effects of management actions; however, evaluating predictions requires adequate and high-quality monitoring data. Results from our case studies show that a combination of long-term monitoring and different types of study designs coupled with models of adequate complexity are likely required to better understand populations’ responses to environmental changes and harvest, as well as the consequences for food webs.

KEY WORDS: Food web · Wildlife populations · Adaptive management · Climate change · Predictions

1. BACKGROUND

Food web ecology, with its long and rich tradition (Elton 1927), has seen many new applications and approaches. Although the suitability and relevance of food web approaches have been advocated (e.g. for Arctic ecosystems; Post et al. 2009), surprisingly few studies have applied such approaches in managing wildlife that is subjected to rapid climate change. In this study, we share some important experiences we have gained from different case studies in the Norwegian project SUSTAIN (www.sustain.uio.no).

In the terrestrial Arctic, climate has unarguably been the most important driver of species’ adaptation (Callaghan et al. 2004a) and the structure and functioning of tundra ecosystems (Post et al. 2009, Ims et
Due to short and cool summers, the structure and functioning of tundra ecosystems are mainly determined by low primary productivity, restricted plant growth, and metabolic activity from bacteria, fungi, and invertebrates (Bliss 1997, Callaghan et al. 2004a). Low primary productivity, in turn, limits secondary productivity (Oksanen et al. 1981, Oksanen & Oksanen 2000, Callaghan et al. 2004b). Thus, the biotic web (hereafter tundra food web) is usually considered to be composed of 3 major trophic levels: plants, herbivores, and predators (Krebs et al. 2003, Ims & Fuglei 2005). Despite their relatively low structural complexity, tundra food webs are often governed by strong and complex inter-specific interactions, especially between trophic levels (Ims & Fuglei 2005). Tundra food webs are bottom-up limited due to their low primary productivity; however, both herbivores and predators can exert a strong top-down control on lower trophic levels. For instance, reindeer and caribou are known to generate strong shifts in vegetation state (Ravolainen et al. 2020), while predators such as mustelids, birds of prey, and foxes can generate extensive fluctuations in small mammalian herbivores and ground-nesting birds (Ims et al. 2019, Marolla et al. 2019). When present, multi-annual population cycles of small rodent species (lemmings and voles) often lie at the basis of bottom-up and top-down interaction cycles (Ims & Fuglei 2005, Krebs 2011, Henden et al. 2020, 2021a) and are closely connected to the functioning of the whole ecosystem. These non-trivial fluctuation patterns show periods of transience, with shifts in occurrence, periodicity, and amplitude of population cycles (Moss & Watson 2001, Henden et al. 2009, Fuglei et al. 2020), which complicates the dynamics of tundra systems even further.

Many of these ‘regulatory functions’ in tundra food webs are now experiencing severe changes, of which several are linked (van der Wal & Stien 2014, Le Moullec et al. 2019). The most prominent impact of rapid climate change in the Arctic (Post et al. 2009) is represented by increased plant biomass due to increased primary productivity (especially of tall woody plants, e.g. Myers-Smith et al. 2015), a phenomenon known as ‘Arctic greening.’ Dampening and irregular small rodent cycles (Ims et al. 2008, Kausrud et al. 2008) and intensified outbreaks of insect herbivores in the tundra–boreal forest ecotone (Jepsen et al. 2011, 2013) have also been attributed to changes in climate. However, climate change interacts with changes in land use, which represent another emerging driver in the Arctic. Anthropogenic landscape-use and climate change in combination with extirpation of apex predators (Elmhagen et al. 2015) have changed predator communities. In particular, generalist mesopredators such as red fox Vulpes vulpes and corvids have increased in abundance and expanded their distribution ranges (Elmhagen et al. 2015, 2017, Sokolov et al. 2016, Gallant et al. 2020). This increase seems to be aided by higher availability of subsidies, such as reindeer Rangifer tarandus carrion (Stien et al. 2012, Hansen et al. 2013, Henden et al. 2014), marine resources (Roth 2003, Killengreen et al. 2011, Ims et al. 2017), anthropogenic resources (Gallant et al. 2020), and increasing populations of some migrant prey species like geese (Fox & Madsen 2017).

Increasing abundances of boreal and human commensal species may affect Arctic species through competition (Arctic fox; Henden et al. 2010, Hamel et al. 2013) or predation (ground-nesting birds; Kubelka et al. 2018, Ims et al. 2019, Marolla et al. 2019, Henden et al. 2021a). For instance, nest predation appears to have increased in the Arctic (Kubelka et al. 2018) and has been linked to the recent community-wide decline in arctic–alpine birds in northern Europe (Lehikoinen et al. 2014, 2019). In combination with changes in small rodent dynamics (Ims et al. 2008), the expansion of mesopredators may have weakened the link between the rodent cycle and the cycle of alternative prey populations. Hence, wildlife species that used to depend on predation relief in years of high abundance of small rodents may now experience more constant predation pressure (Ims et al. 2019), an effect also exacerbated by the increase in anthropogenic subsidies such as carrion from semi-domestic reindeer that attract and sustain mesopredators (Killengreen et al. 2011, 2012).

Anthropogenic changes impact Arctic ecosystems through changes in resource availability, species interactions, and food web structure (Post et al. 2009, Hansen et al. 2013, Ims et al. 2019). Investigating such impacts in rapidly changing systems is challenging because the direction and timing in the response of different species may vary between different pathways in the food web. It is therefore increasingly argued that understanding the consequences of environmental change warrants an understanding of direct and indirect processes that occur with time lags and across several trophic levels (Post et al. 2009, Evans et al. 2013, Urban et al. 2016). This is particularly important for management of species situated at intermediate trophic levels in food webs and therefore affected by both lower and higher trophic levels. Management interventions may therefore be confounded with other ecological drivers of the management target, drivers
that must be taken into account for robust assessment of management effectiveness (Underwood 1992, Hewitt et al. 2001).

Due to climate change and the emerging biodiversity crisis, the demand for anticipatory predictions (i.e., forecasting) in ecology to aid decision-making at the science–policy interface has grown (Clark et al. 2001, Mouquet et al. 2015, Petchey et al. 2015, Houlahan et al. 2017, Dietze et al. 2018). However, predictions in ecology often carry a mismatch between predictions that focus on climate change responses on very long timescales and the time horizon relevant for management decisions (Pouyat et al. 2010, Hobday et al. 2016). Short-term predictions matching the time horizon relevant for environmental decision-making have been proposed to solve this issue (Hobbs et al. 2015, Nichols et al. 2015, Dietze et al. 2018). Such near-term forecasts are iteratively updated and evaluated as more and new data become available on a relatively short time scale. Predictions on a time scale that is relevant for decision-making allows for scientific evidence to increase rapidly as knowledge is generated and, most importantly, management strategies to be tailored and evaluated simultaneously (Houlahan et al. 2017, Dietze et al. 2018).

This perspective paper draws on what we have learned from case studies of changing tundra food webs in both low- and high-Arctic environments, focusing on harvested and managed species. We present our food web approach in 4 themed sections (Sections 2–5) before we highlight remaining challenges and future research directions (Section 6).

2. OVERALL SCHEME

Studying entire food webs (Pimm 1982) is challenging due to the large number of species and trophic links, even in relatively simple ecosystems such as tundra food webs. Hence, many studies take into account only a single trophic interaction (e.g., predator–prey) as a basis for adaptive management (Johnson et al. 2019, Serrouya et al. 2019). In our food web approach (Fig. 1), we attempt to strike a balance between focusing on one interaction vs. the whole web (Hunter et al. 2018). We generally reduce the complexity by considering only a subset of focal species with key functional roles in the food web (Ims & Yoccoz 2017). In our food web approach, we attempt to strike a balance between focusing on one interaction vs. the whole web (Hunter et al. 2018). We generally reduce the complexity by considering only a subset of focal species with key functional roles in the food web (Ims & Yoccoz 2017), and infer the likely strong food web interactions from analyses of statistical models that are based on time series of species abundances and environmental drivers (simplified examples depicted in Fig. 2c,d). Hence, we target those key trophic interactions that we expect to change rapidly and exhibit the most pronounced effects.

Once key food web interactions are identified (Fig. 1), we generate hypotheses on likely direct and indirect pathways of climate and human impact on the target species and present them in the form of conceptual models (Figs. 1 & 3). The use of mathematical models gives insight into hypothesized conceptual mechanisms and helps to generate refined theoretical predictions (Box 1). We then use time series data in statistical models to estimate relationships and generate explanatory models. We use these explanatory models to generate short-term predictions or ‘forecasts’ (Fig. 4) and assess and recommend management actions (Fig. 5). Whenever possible, the steps are performed jointly with stakeholders through a structured involvement process (Henden et al. 2020, Hamel et al. 2021, this Special).

3. INCLUDING DIRECT AND INDIRECT INTERACTIONS

Many food webs have a reticulated topology with one or more predators on top and several alternative prey below (Figs. 1–3; Box 1; see Ims et al. 2013c, Legagneux et al. 2014, Henden et al. 2017). Predators can therefore be mediators of indirect food web interactions between alternative prey. This ‘looped’ topology differs from simpler food webs consisting of parallel chains (Wollrab et al. 2013) and can lead to complex responses to perturbations. For instance, increased abundance of one species due to climate change or management can translate to increases or decreases in the abundance of other species by acting through their shared predator. This mechanism is known as apparent competition (Holt 1977) or apparent mutualism/facilitation (Holt 1977, Abrams et al. 1998), depending on the outcome, but the conditions that should give rise to one or the other remain slippery in practice.

Which of the 2 patterns we observe in tundra food webs differs across systems (Ims et al. 2011, Kleiven et al. 2018, Marolla et al. 2019, Henden et al. 2020). Although prediction in this realm is difficult, we are beginning to understand some of the likely mechanisms in tundra food webs through a combination of accumulated case studies, previous theoretical studies, and current modeling. In a case study focusing on the lesser white-fronted goose Anser erythropus...
Fig. 1. The food web approach we present and have employed thus far is a composite, multidirectional (looped), and adaptive workflow that combines a number of qualitative and quantitative methods and results in deliverable end-user products in the form of understanding, predictions, assessments, and recommendations. We use known trophic relationships and static food web maps (see Fig. 2a,b; figures after Henden et al. 2017) and combine them with time series of those biotic variables along with relevant abiotic variables (see Fig. 2c,d; figures after Marolla et al. 2019, 2021) to form hypotheses on likely strong interactions in the food web and tightly linked abiotic/biotic components. We convert these hypothesized relationships to conceptual models (see Fig. 3; figures after Henden et al. 2021a) that represent simplified food webs impacted by climate and management. We use mathematical models (figure after Marolla et al. 2019) to confirm the logic in the conceptual models, gain insight, and refine theoretical predictions (figure after Marolla et al. 2019). We convert the conceptual models to competing statistical models to quantify the relationships between the food web components and build explanatory models (see Fig. 5a; Henden et al. 2021a). We then use these explanatory models to generate predictions and use short-term forecasts to compare the abilities of different models for making predictions/forecasting (see Fig. 4; Henden et al. 2020). The explanatory models are also used to evaluate management actions to provide management assessments or recommendations (Henden et al. 2021a). Chart and model thumbnails presented here are intended only to illustrate the information type; refer to the actual figs/boxes for further information.
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(Marolla et al. 2019), for instance, it was not clear which type of indirect interaction should be expected regarding the effect of different prey types on predation. Thus, we built mathematical models to make theory-based predictions (Box 1), which were then compared/assessed with long-term monitoring data. Overall, our studies support the notion that predation plays an important role in Arctic food webs (Ims et al. 2013b, 2019). However, predation remains quantitatively a poorly known interaction due to a paucity of direct data on predator abundances, movements, and foraging behavior in the food webs we study. The exact functional response of predators is vital information for predicting apparent competition or mutualism. In the few cases where functional responses have been estimated for Arctic predators (e.g. Gilg et al. 2003, Therrien et al. 2014), these functions have not been used to analyze dynamics in the context of food web management options.

We have investigated and quantified previously suspected but undocumented processes in food web dynamics that are ultimately linked to climate/weather (Marolla et al. 2019, 2021, Henden et al. 2020). Many of these processes concern scavenging-driven predation (Mellard et al. 2021), where carrion links target species indirectly through shared predators. We observe that target species in our food webs can have a negative, or apparent competition, relationship to carrion availability (Marolla et al. 2019, 2021) or a positive, or apparent mutualism, relationship to carrion availability (Henden et al. 2020), mediated by shared predators. A candidate explanation for the contrasting effect of this subsidy is the difference in timing of reproduction between target ground-nesting bird species. Birds that are present year-round and also breed during a peak carrion subsidy may have a positive relationship with carrion availability (Henden et al. 2020), while the same relationship may be negative for migrating birds that are present and breed later in the season (Marolla et al. 2019). Moreover, different predator identities between studies, different geographical sites, and different temporal data resolution (e.g. year range and sub-annual carrion abundance) may be responsible.

Fig. 2. Static food web maps of (a) low-Arctic and (b) high-Arctic ecosystems and example dynamics (time series) of strong drivers within each for the (c) low Arctic and (d) high Arctic. R. legged buzzard: rough-legged buzzard; LWF: lesser white-fronted. (c) Time series of LWF goose breeding success (fledgling success, i.e. number of fledglings per breeding pair) and rodent abundance (average catches per grid). (d) Time series showing counts of Svalbard rock ptarmigan performed in a study area of ca. 1200 km² in Svalbard, and average winter temperature (December–March) calculated using data from the Svalbard airport weather station. Note that the scale of the 2 y-axes differs in both c and d. Figure panels after (a,b) Henden et al. (2017), (c,d) Marolla et al. (2019, 2021)
for these contrasting patterns. Consequently, more studies are needed to confirm these patterns.

The permanence of indirect interactions in tundra food webs is evident from evolved life-history traits to cyclic interactions in several species (e.g. Andersson 1981, Tannerfeldt & Angerbjörn 1998). As some of these interactions are now changing rapidly, ignoring food web interactions has consequences for understanding and predicting what will happen to managed populations (Trijoulet et al. 2020).

4. SHORT-TERM PREDICTIONS

We performed a near-term forecasting approach, based on explanatory statistical food web models, to case studies of harvested populations of low-Arctic willow ptarmigan *Lagopus lagopus* (Henden et al. 2020) and Svalbard rock ptarmigan *L. muta hyperborea* (Marolla et al. 2021). A key goal was to inform stakeholders about the near-future state of the population, information to be used as a basis for adaptive management of ptarmigan. An additional goal was to assess whether the predictive ability of the statistical models improved by including food web interactions in contrast with simpler models (i.e. a multi-model approach; cf. Henden et al. 2020, Marolla et al. 2021).

Our food web models highlighted several environmental drivers explaining ptarmigan population growth and thereby the recent changes in ptarmigan populations. For the willow ptarmigan case, delayed winter start, increased precipitation around hatching, and intensified moth outbreaks had a negative influence on ptarmigan population growth. For the Svalbard case, increased temperatures during winter had the strongest positive effect on ptarmigan population growth, likely because it reduced the energy needed for thermoregulation during winter. Hence, our mod-
We briefly describe an alternative prey model (see graphic at bottom of this Box) after Marolla et al. (2019) where the probability $a_R$ for a predator $P$ to attack an alternative resource $R$ (rodents or carrion or other non-focal prey in our food webs) depends on the density of the alternative preferred resource $R$ so that

$$a_R(R) = \frac{R^b}{1 + b_R R^b}$$

where $b$ is a shape parameter and $b_R$ is the handling time of that alternative resource. We include this probability of attack $a_R$ in the multispecies disc equation (MacArthur & Pianka 1966, Charnov 1976, Fryxell & Lundberg 1994), which determines the predation rate on the focal prey item (i.e. the prey). Predation rate on the focal prey item is then defined as

$$\text{Predation}(F) = \frac{a_F P F}{1 + a_R h_R + a_F h_F}$$

where $a_F$ is the probability for attacking prey $F$ and $h_R$ is the handling time of prey $F$. Thus, what drives the change in predation rate is largely a function of attack $a_R(R)$ on the preferred alternative prey, abundance of alternative prey, and abundance of predators. We define the rate of change of predators $P$ to be governed by

$$\frac{dP}{dt} = p \left( \frac{a_F e_R R + a_F e_F F}{1 + a_R h_R + a_F h_F} - m_P \right)$$

where $m_P$ is the mortality rate, and $e$ is the energy conversion of prey species into predators.

We can observe predator–prey cycles with this model if prey have a non-linear growth rate. Under conditions where we observed cycles, we found the alternative prey can have a positive impact on the focal prey population (apparent mutualism), in agreement with previous predictions on the impact of predator switching (Abrams & Matsuda 1996). This positive impact occurs for at least part of the alternative prey cycle. However, during the part of the cycle when the alternative prey is in low abundance, predation can be high on the focal prey species. For parameters where we did not observe cycles, we found the alternative prey can have a negative influence on the focal prey (apparent competition), as observed previously (Holt & Bonsall 2017).

We find that predator mortality rate is a very important parameter in this model (where there is always non-linear functional responses and preferred prey), as it can control whether cycles are observed, which also determines whether one can expect to have apparent competition or apparent mutualism between the prey. Thus, a management action such as predator control that increases predator mortality may influence cycles and outcomes. In our models, we consider alternative resources to act independently of one another on the focal prey in the model, but future work could look at the interactive effect of several alternative prey species because they may act in concert, and in opposition to what increasing predator mortality does to increase cycles. For example, an additional alternative prey species could change the vital rates of the predator (reduce mortality) that then dampen the predator-prey cycles.
actions substantially improves our ability to forecast climate-induced effects on ptarmigan populations remains unclear. However, some caution is warranted. The case studies were based on relatively short time series (15 and 17 yr) and low quality and spatial resolution of the variables representing local climate (e.g. Svalbard case) and food web interactions. Better predictions could be gained by improving spatial matching of ptarmigan data and predictor variables and by modeling more mechanistic variables and relations that could account for nonlinear dynamics due to predator functional responses (Box 1).

While more complex models did not perform distinctly better in the short term, they may be better on a timescale of 10 to 20 yr, as these systems may not be stationary, and some inertia of climate change impacts is expected. A theoretical dynamical systems approach may help give insights into longer-term behavior. As more and better data is incorporated in the predictions in the coming years, in particular due to application of new technologies and methodologies in ecosystem-based monitoring (Ims & Yoccoz 2017), confidence will rise in the better-performing models. Such probabilistic evidence can be further examined alongside mechanistic evidence (Luján & Todt 2020) from food web and other studies. This may allow for more precise and useful predictions with respect to the most important drivers of population dynamics and trends (Nichols et al. 2007, 2019).

5. ASSESSING MANAGEMENT ACTIONS

Among the actions implemented for species that are conservation targets, mesopredator culling actions have been implemented in many places, including Fennoscandia (Angerbjörn et al. 2013, Ims et al. 2017). However, the success of such actions is rarely assessed, and when the actions are assessed, they are often deemed unsuccessful (Salo et al. 2010, Kämmerle & Storch 2019, Marolla et al. 2019, Henden et al. 2021a). This is partly because proper experimental designs to assess the efficacy of large-scale predator control actions (e.g. spatial scale, temporal and spatial controls of actions) are often difficult or even
impossible to implement (Taylor et al. 2017). Accordingly, it has been suggested that accounting for potential confounding drivers of natural dynamics (e.g. food web interactions) may alleviate these constraints and improve the accuracy of impact assessments (Stewart-Oaten et al. 1986, 1992). We describe 2 case studies that targeted the lesser white-fronted goose and the willow ptarmigan to illustrate different themes regarding management action assessments. Both focal species are locally red listed, and the anthropogenically driven expansion/increase in red fox abundance in Arctic ecosystems (Elmhagen et al. 2017) is one of the suspected causes for their red list status. Consequently, the common management action implemented in these cases was red fox culling to decrease population abundance.

### 5.1. Lesser white-fronted goose

In the case of the Critically Endangered Fennoscandian lesser white-fronted goose population (Fig. 3d), the small size of the population only permitted a culling program where red foxes were removed from the breeding area, with no possibility for having a control area. We could therefore only assess the effect of fox culling using a before–after comparison. The culling action was assumed to work, since the population started to increase following the start of the culling. Nonetheless, when we accounted for important food web dynamics and local climate variables, we found no support for an effect of red fox culling on goose reproductive success (Marolla et al. 2019). Breeding success was mainly driven by the rodent cycle, showing a strong and temporally consistent synchrony, and was also affected by an anthropogenic food web driver, i.e. abundance of reindeer carrion. Our food web approach allowed us to include variables that confounded assessment of the culling action and evaluate its efficiency in absence of a proper experimental design. We further built upon these quantified food web relationships to investigate whether a slight increase in adult survival during the reproductive season, possibly fostered by the fox culling, contributed to the observed change in population growth rate after fox culling started. A full-cycle demographic analysis suggested that other demographic processes, e.g. winter survival of adult birds, may have been more important in driving the increase in the goose population than the culling action (Marolla 2020).

### 5.2. Willow ptarmigan

In the case of the willow ptarmigan (Fig. 3c), the fox-culling effort consisted of an action and a control area that was monitored both before (5 yr) and after the onset of the action (12 yr). In contrast to the goose case, the monitoring did not provide reliable data on the most important drivers of food web dynamics (i.e. rodents and reindeer) nor harvest levels prior to the
action (Henden et al. 2021a). A simple before−after−control−impact−paired−series analysis (Stewart-Oaten et al. 1992), without food web covariates, indicated that red fox culling slightly limited the decline of the willow ptarmigan population in the experimental area. Still, 3 food web drivers, namely small rodents, reindeer carrion, and ptarmigan harvest levels, showed large spatiotemporal variation. When these drivers were included as covariates in a linear mixed model using data only after the onset of culling, we found that the culling action actually resulted in ~40% higher ptarmigan population density (4.3 more ptarmigan km⁻²) in the action area. Similar to the goose case, this example illustrates the strength of using a food web approach to more reliably estimate the impact of management actions to preserve wildlife. These 2 cases show that management action assessments can benefit from long-term food web monitoring that yields time series of both the target species and influential food web drivers that may confound the impact assessment. This might be particularly important in food webs with strong spatio-temporal dynamics, such as boreal and arctic food webs governed by non-trivial interaction cycles.

As we mainly work with managed species or populations, our food web approach can lead to a wider set of management actions, that is, to manage more than one species in the food web. However, this wider set of actions can be more difficult to implement if managers must prioritize between different conservation targets (Beschta et al. 2020), take into consideration the interests of different stakeholder groups, or different agencies/groups are involved in the actions (see Hamel et al. 2021, this Special). Objective functions can make such trade-offs explicit (Runge & Walshe 2014). Thus, while our food web approach introduces other challenges, it also increases the opportunity for more holistic ecosystem-based monitoring and management (Ims & Yoccoz 2017).

6. REMAINING CHALLENGES AND FUTURE DIRECTIONS

We have uncovered a number of challenges while implementing our food web approach. While many issues arise from a lack of sufficient spatial and temporal food web data due to data collection challenges, other challenges remain for implementing our approach. We suggest future studies should try to address and resolve the following 4 challenges.

6.1. Challenge 1: Non-linear and hidden interactions in food webs

In our cases, we have mostly resorted to linear statistical analyses because these gave both reasonable fits to the data and short-term predictions that were close to observations. However, non-linearities in food web interactions can change theoretical predictions (Box 1) and can lead to abrupt shifts in the state of the system. Complex dynamics can give false impressions of the state of a system, especially when trying to predict mid- and long-term dynamics (Hastings et al. 2018). For example, ghost attractors in non-linear systems may cause patterns in time series that may be interpreted as stable, or as state shifts enforced by environmental change, when in fact they are not. Interactions may remain hidden because of lack of data on food web components, but also because of indirect and higher-order (non-pair-wise) mechanisms, i.e. trait-mediated indirect interactions (Levine et al. 2017); such hidden interactions may underlie non-linearities. Climate−harvest interactions, combined with other drivers, remain unresolved for all of our cases due to a lack of adequate data. In the future, harvester behavior and how that may change with environmental drivers should be modeled explicitly, as it differs from other predators (Mysterud et al. 2020) and may ultimately affect population responses.

6.2. Challenge 2: Food web models

Because different types of models have different advantages, we suggest the way forward is to take multiple approaches to model building. Theoretical models of food webs (McCann 2012) have a long tradition in ecology and have been instrumental in developing important predictions for tundra food webs (Oksanen et al. 1981). Statistical models, and in particular dynamic structural equation models (SEMs) (cf. Henden et al. 2021b, this Special) that can incorporate direct and indirect effects, time-series dynamics, measurement errors, as well as proxies through the use of latent variables (Asparouhov et al. 2018), integrate detailed ecological knowledge about food webs in the analyses of empirical data. In SEMs, latent variables refer to variables that are not directly observed or measured, but inferred from other variables (i.e. indicators) that are directly measured (Spearman 1904; Box 2). While it is unclear how the theoretical and statistical approaches can be merged (Barraquand et al. 2017;
Ecology has a long tradition of mathematical modeling of trophic interactions, with models of plant–herbivore (Lotka 1920) and predator–prey (Volterra 1926) systems starting around the same time as early empirical works by Elton (e.g. Elton 1924, Elton & Nicholson 1942). More or less at the same time, Wright (1920) expanded multiple regression models to his path coefficients approach of analyzing direct and indirect effects. These 2 approaches developed more or less independently until the end of the last century, and it is only in recent decades that attempts have been made to integrate them, that is, putting the dynamical approach of models such as Lotka–Volterra in the statistical framework provided by structural equation models (SEMs) or causal models, the modern extension of Wright’s path coefficients.

Wootton pioneered different approaches for understanding direct and indirect ecological interactions, using a combination of classical community models (Wootton 1994a) and SEMs of experimental studies (Wootton 1994b). However, these early analyses were not integrated in the sense that SEMs were not dynamic or linked in parameters to community models. A related approach was to interpret models of single, linear food chains (predator–prey–vegetation) as delay-coordinates of the only component of the system that was observed (predator = lynx or prey = small rodents, depending on the system), and analyze it using statistical models for time series (Bjørnstad et al. 1995, Stenseth et al. 1997). The latter approach was limited in the sense that coefficients measuring direct and lagged effects could result from trophic interactions. However, without direct measurements, different interpretations were possible.

Recent years have seen considerable developments of SEMs and related approaches (e.g. instrumental variables), particularly in social sciences and epidemiology, but also increasingly in ecology (e.g. Grace & Irvine 2020). However, the use of dynamic SEMs (DSEMs; Asparouhov et al. 2018) is much rarer (this study) and, more importantly, such models are not related to the mathematical dynamical models developed to analyze trophic webs. Recent developments of DSEMs, however, provide a powerful approach, since they incorporate measurement error and site- and time-specific covariates (Asparouhov et al. 2018). Linking the 2 approaches implies that the mathematical models are discretized in a way that leads to models fitted on observed variables having interpretable and unbiased coefficients of underlying mechanisms, including processes occurring on different time scales (e.g. functional vs. numerical responses). Work done on survival models have shown that SEMs that are fit to discretized data may not reflect the underlying continuous mechanisms (Aalen et al. 2016, 2018). This is clearly an area where more work and data are needed.

Box 2), they should be seen as complementary tools to understand and predict food web dynamics, as well as suggest additional monitoring data and designs.

### 6.3. Challenge 3: Temporal and spatial scales

Within-year variability should be included explicitly because seasonal patterns are impacted by climate changes. Often, ‘shoulder seasons’ are ignored despite their large impact on vital rates and the sort of food web interactions that cause these impacts. Similarly, the consequences of spatial and temporal variability in climate drivers and food web components at different spatial and temporal scales need to be better understood (Box 3), particularly to disentangle short-term effects that could be mitigated (e.g. annual harvest) from the long-term impacts that are harder to mitigate (e.g. climate change).

### 6.4. Challenge 4: Forecasts and predictions

In our case studies, we focused on providing short-term predictions (i.e. from months to a year). These have been deemed useful by stakeholders for harvested and red-listed species (Hamel et al. 2021, this Special). For now, we have comparatively little information on what happens to these food webs when they become rewired due to environmental changes (Griffith et al. 2019), and if indirect interactions stabilize them. Especially, considering that temperature may increase as much as 12°C in winter and 6°C in summer by the turn of the century (projection from CMIP5; cf. Overland et al. 2014), it is likely that the Arctic region without an arctic climate will eventually host completely novel food webs. Like Planque (2016), we think that our current understanding and data on food webs, as well as the occurrence of ‘black swan’ events associated with fatter distribution tails than often assumed (as illustrated for contagious diseases: Cirillo & Taleb 2020), lead to significantly higher uncertainties of long-term ecological forecasts than those given using standard biodiversity modeling (e.g. Thuiller et al. 2019). A proper understanding of risks associated with different management strategies indeed requires that the distribution of outcomes is approximately known, and not just its mean or variance (Cirillo & Taleb 2020).
Box 3. Weather vs. climate in food web models: disentangling short-term and direct vs. long-term and indirect effects

‘Climate is what you expect, weather is what you get.’
By definition, climate reflects long-term properties of weather, often focusing on the mean (‘expect’) but also on the variance and extremes (e.g. van de Pol et al. 2017, Hilde et al. 2020). Disentangling the effects of changes in weather and climate is difficult because those changes are not independent; for example, changing the mean will increase the severity of extreme events, and because organisms, as well as interactions between them, change because of short-term changes in weather (a rain-on-snow event leading to herbivore starvation) as well as long-term changes in climate (resulting in e.g. changes in habitats that affect predator–prey interactions).

Variation in weather can be decomposed into different components: temporal (averaging over space), spatial (averaging over time), and the residual (‘interaction time–space’; Oedekoven et al. 2017, Henden et al. 2020). The temporal average component can then be further decomposed into a smooth term (e.g. linear trend reflecting climate change) and year-to-year variation. These different components can then be included as predictors in causal models. This approach is straightforward when the environmental driver and causal links are well identified a priori, but it will lead to larger number of potential models if the drivers are not known, many links are plausible, and some form of model selection and averaging is used. ‘Blind’ model averaging (‘dredging’) should be avoided because of implausible model specifications, such as effects of residuals without the main temporal and spatial effects (Kempthorne 1975, Cade 2015). Interpretations of the effects can also be challenging, as centering and standardizing will be system specific and hard to compare among systems, or even lead to incorrect interpretations (Westneat et al. 2020). For making predictions, alternative approaches to model averaging such as model stacking may be more robust (Dormann et al. 2018, Yao et al. 2018).

What is less known, and to our knowledge has not been investigated in an ecological context, is how to extend such decomposition of the weather to food web components and trophic interactions. Species and interactions between species can be decomposed into spatial, temporal, and residual components that may affect other components of the food web, as well as being affected by different components of the weather. Obviously, this can lead to an overwhelming number of possible models, and knowledge of the food web and possible pathways is required to build a meaningful model set. Another issue is that components of food webs are often represented using latent variables, either because of measurement error or the use of indicators such as normalized difference vegetation index (NDVI) (Henden et al. 2021b, this Special). This affects how we incorporate temporal and spatial components, as work done on SEMs in social sciences have shown that averaging and scaling may lead to biased estimates of effects, because averages and standard deviations are estimated with varying degrees of uncertainty (Asparoukhov & Muthén 2019). Arctic tundra food webs may provide valuable testbeds for developing and understanding such models because they are characterized by relatively few components and interactions, and large variation in both drivers and individual components, thereby minimizing the consequences of measurement error on estimated effects.

7. CONCLUSIONS

The task of providing management guidance for target species is not insurmountable but does pose many challenges that are further magnified by rapid climate and other environmental changes. Our food web approach aims to address these challenges by modulating model complexity, while focusing on interactions that can affect target species or have considerable impacts on other parts of the food web. Although our approach succeeds in some areas, challenges remain. We will need to build more evidence, through the accumulation of case studies that verify mechanisms linking trophic interactions to managed populations, in order to determine whether this approach is significantly better than simpler approaches for supporting management decisions. Nevertheless, leaning on our experiences, we conclude that this approach remains promising as a valuable tool to provide answers to managers that are asked to plan for changing tundra ecosystems.

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