Advance View
https://doi.org/10.3354/cr01638

CLIMATE RESEARCH
Clim Res

Available online:
May 27, 2021

Contribution to CR Special 'Sustainable management of renewable resources in a changing environment: an integrated approach across terrestrial, freshwater and marine ecosystems'

OPINION PIECE

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

Jarad Pope Mellard[1,*,#], John-André Henden[1,#], Åshild Ønvik Pedersen[2], Filippo Marolla[1], Sandra Hamel[3], Nigel Gilles Yoccoz[1], Rolf Anker Ims[1]

[1]University of Tromsø, The Arctic University of Norway, AMB, 9037 Tromsø, Norway
[2]Norwegian Polar Institute, 9296 Tromsø, Norway
[3]Département de biologie, Université Laval, Québec City, QC G1V 0A6, Canada

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

---

*Corresponding author: jarad.p.mellard@uit.no
#These authors contributed equally to this work.

Publisher: Inter-Research · www.int-res.com

al. 2013a). 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 biotrophic 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). Thus, we reduce complex maps of static food web structure (Fig. 2a,b) to what we consider the most relevant and responsive parts of 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 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*

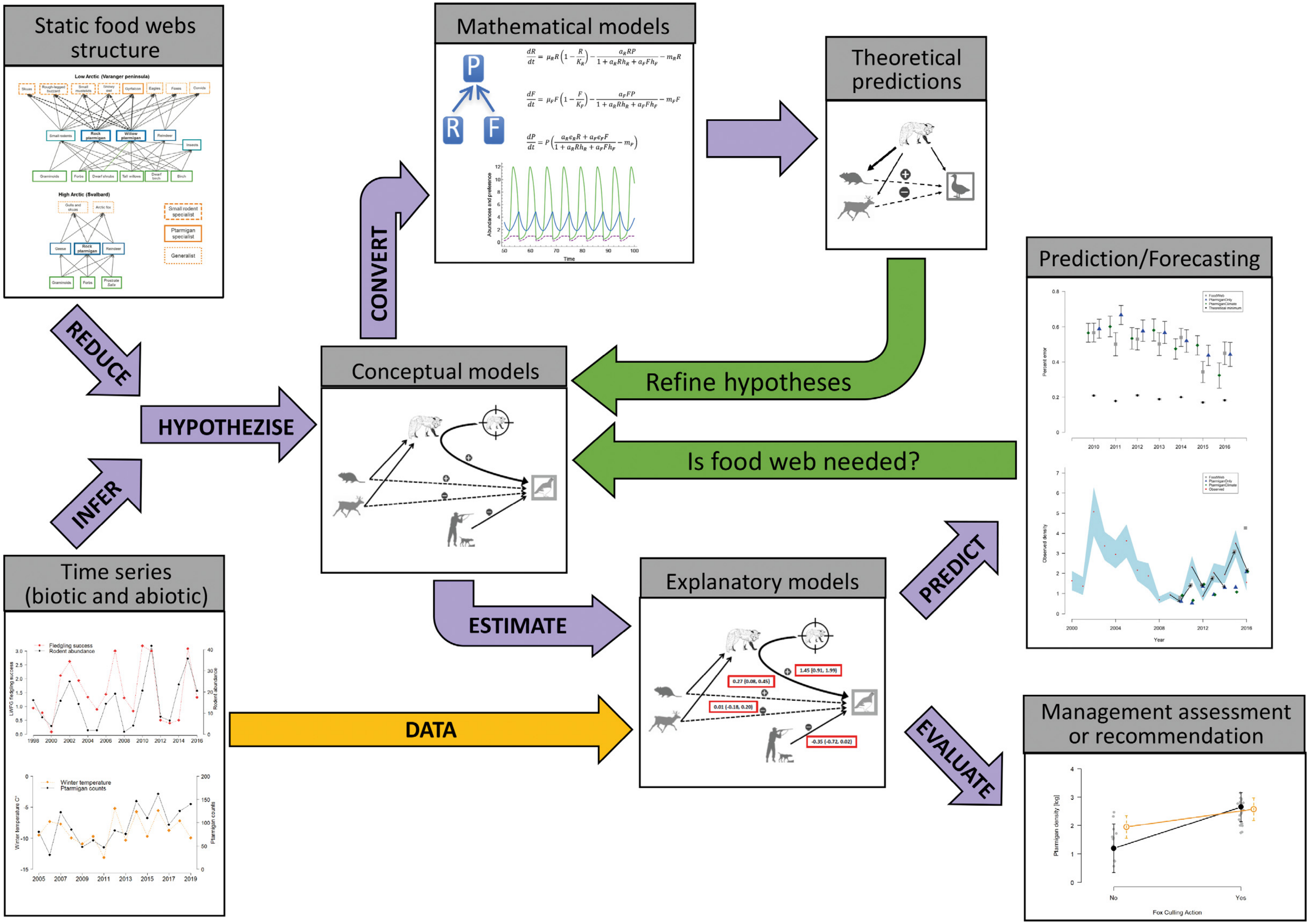


Fig. 1. The food web approach we present and have employed thus far is a composite, multidirectional (looped), and adaptive workflow that combines a number of qualitative and quantitative methods and results in deliverable end-user products in the form of understanding, predictions, assessments, and 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

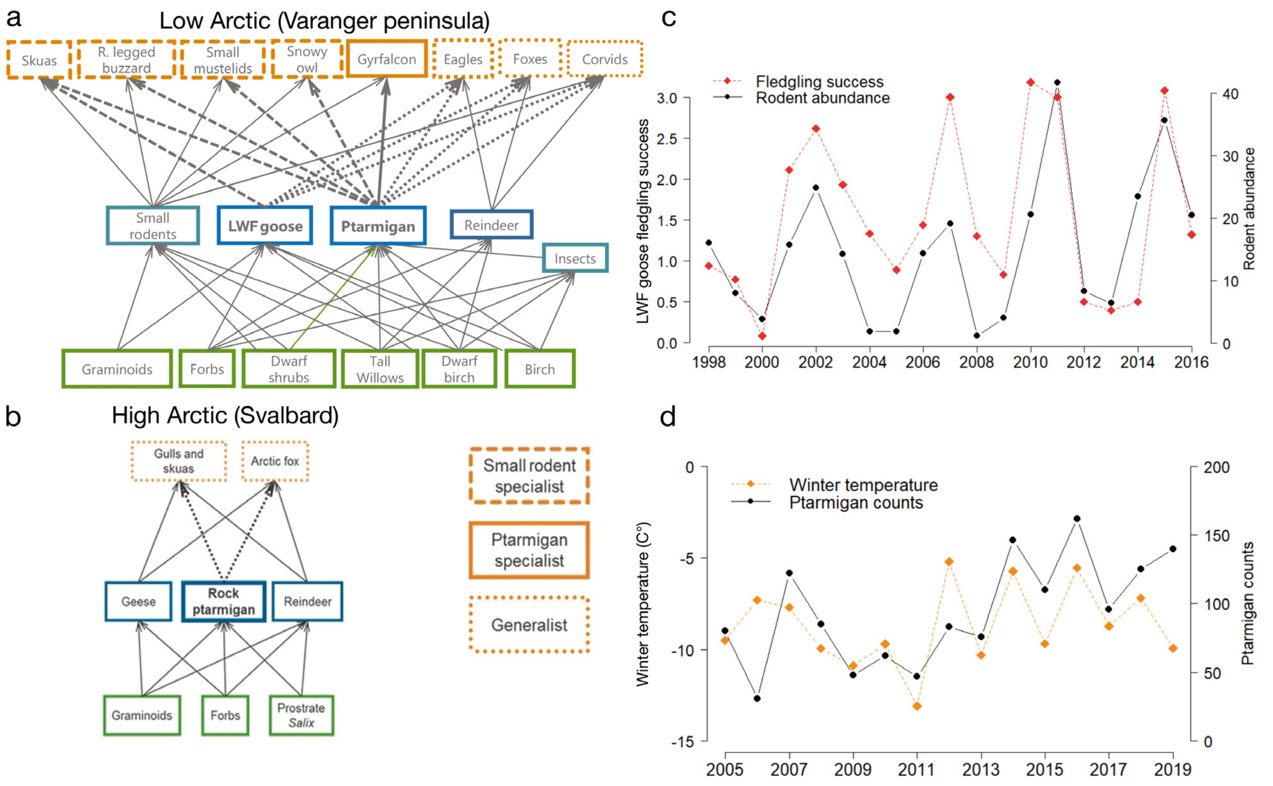


Fig. 2. Static food web maps of (a) low-Arctic and (b) high-Arctic ecosystems and example dynamics (time series) of strong drivers within each for the (c) low Arctic and (d) high Arctic. R. legged buzzard: rough-legged buzzard; LWF: lesser white-fronted. (c) Time series of LWF goose breeding success (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 km^2 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)

(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

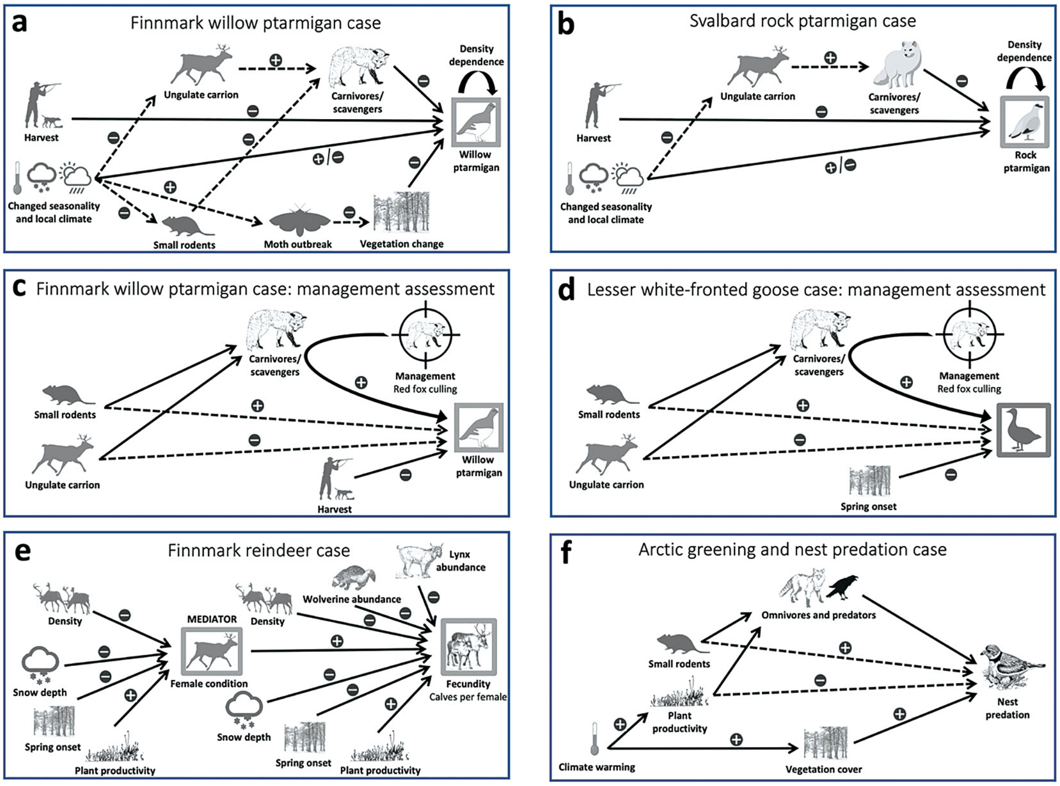


Fig. 3. Conceptual models of 6 food web case studies (see references to original studies below). The models depict expected interactions between the components of the food web and the target species. Solid arrows represent direct effects, dashed arrows represent indirect effects or paths. Each conceptual model was tailored to a specific study case, therefore the meaning of the arrows can change slightly among diagrams. For example, dashed arrows in (a), (b) and (e) show the entire indirect path through the food web (e.g. in panel a, environmental change that affects small rodents, which in turn affects carnivores/scavengers until the effect becomes direct). However, in panels c, d, and f, dashed arrows connect the target species with species at the same trophic level or environmental factors that exert an indirect effect through the main predator, and the expectation (i.e. +/−) is placed on the dashed arrow, highlighting the predicted direction of the relationship that is actually tested. References to original studies: (a) Henden et al. (2020), (b) Marolla et al. (2021), (c) Henden et al. (2021a), (d) Marolla et al. (2019), (e) Henden et al. (2021b), (f) Ims et al. (2019)

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-

Box 1. Predator functional response and alternative prey cycles

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

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

where b is a shape parameter and h_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

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

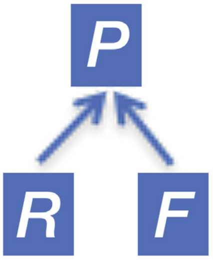
where a_F is the probability for attacking prey F and h_R is the handling time of prey F. Thus, what drives the change in predation rate is largely a function of attack $a_R(R)$ on the preferred alternative prey, abundance of alternative prey, and abundance of predators. We define the rate of change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

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

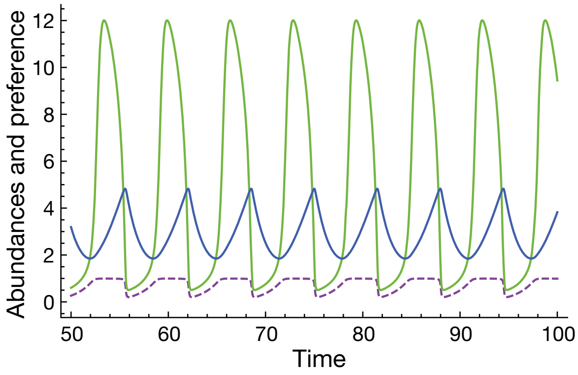
where m_P is the mortality rate, and e is the energy conversion of prey species into predators.

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.



Food web module of predator P, focal prey item F, and alternative resource R



Numerical simulation of the alternative prey model illustrating the cycles of the alternative prey R (green line), predator P (dark blue line), and probability of attack on the alternative prey $aR(R)$ (purple dashed line)

eling approach has widened the scope for potential mitigating actions, by highlighting novel drivers of ptarmigan population dynamics, including manageable drivers such as management-enhanced forest regrowth after moth outbreaks (Henden et al. 2020, Marolla et al. 2021). Interestingly, our results indicate that protection against hunting or reduced hunting quotas would have limited effects on population state because current harvest was not among the key drivers of ptarmigan population dynamics of either Svalbard rock ptarmigan or willow ptarmigan (see also Sandercock et al. 2011).

Concerning near-term forecasting, the predictive performance of all models generally increased (i.e. the prediction error diminished) with increasing length of the time series used to parameterize the models, as expected (Henden et al. 2020, Marolla et al. 2021). In both case studies, however, the more complex models did not perform markedly better than the simpler models. Therefore, whether including food web inter-

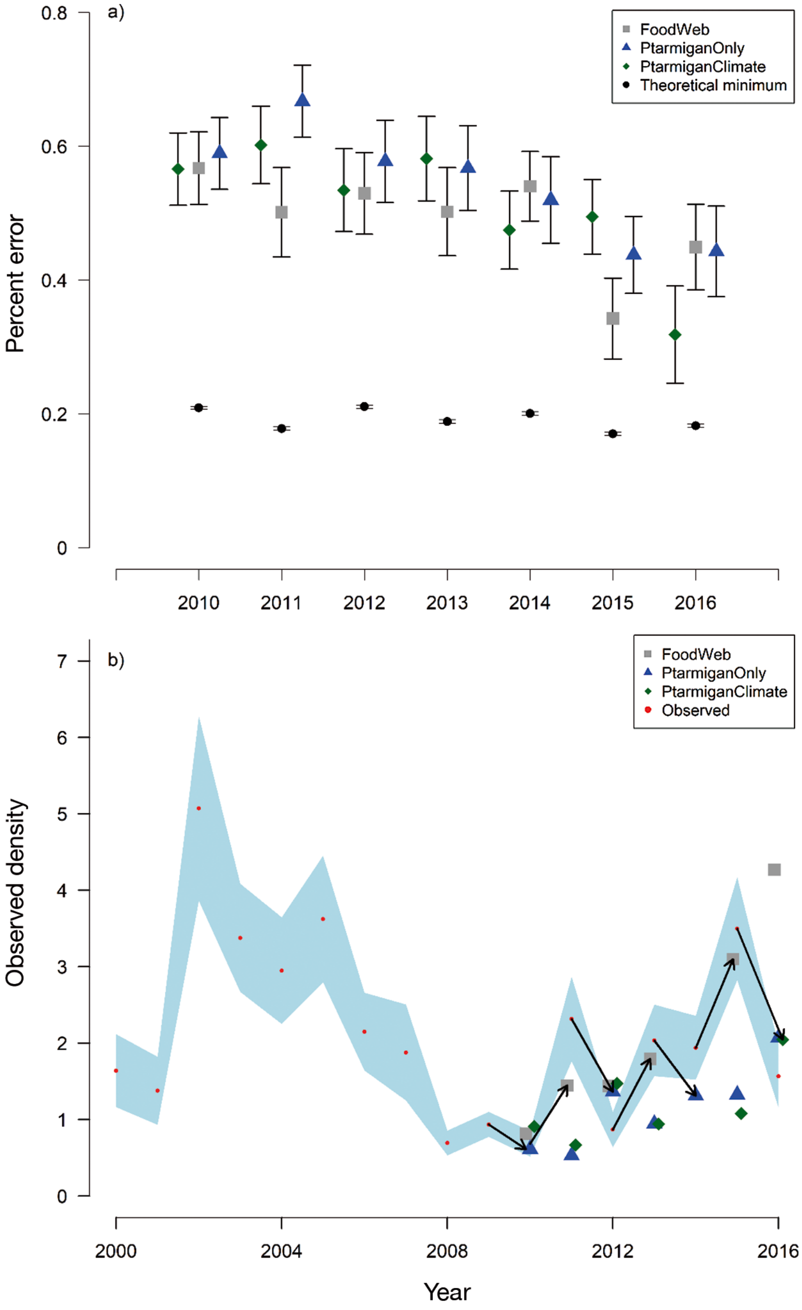


Fig. 4. Prediction error and near-term prediction of line-transect survey counts of low-Arctic willow ptarmigan populations (see Fig. 3a; Henden et al. 2020). (a) Iterative percent (percent/100) prediction error for the 3 candidate models, where error bars indicate confidence intervals. (b) Abilities of 3 candidate models to predict next year's mean observed density (counts/sampling area). Arrows point to the model that is best each year at predicting next year's observed density, and blue-shaded area indicates the confidence envelope. Figure panels after Henden et al. (2020)

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 non-linear 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

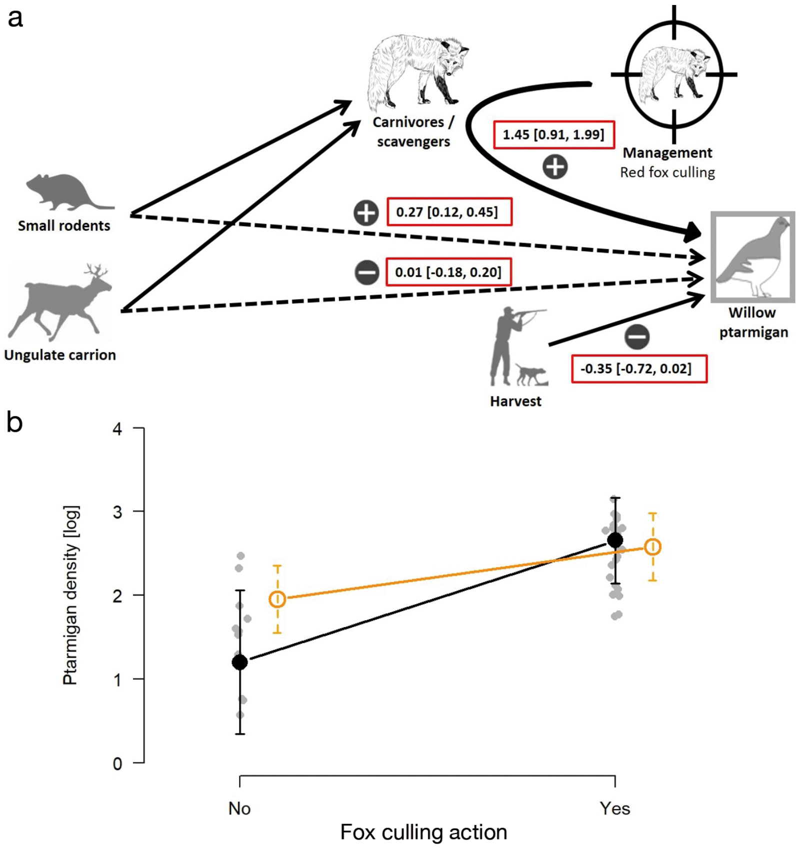


Fig. 5. (a) Explanatory model denoting the main food web and management drivers of willow ptarmigan density, where values with red boxes denote estimated coefficients of the covariates/predictor with 95% confidence interval. Solid arrows denote direct effects, while dashed arrows denote indirect effects of different drivers on ptarmigan population density. Also indicated are expected signs (+/−) of driver effects from the conceptual model (see Fig. 1). (b) Management action assessment. Estimated impact of the red fox culling action on ptarmigan population density (log-scale), adjusted for the influence of food web covariates (black line and filled symbols). For comparison, dark orange line and open circles denote the unadjusted estimates from a before–after–control–impact–paired–series model. Figure panels after Henden et al. (2021a)

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 tradeoffs 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-pairwise) mechanisms, i.e. trait-mediated indirect interactions (Levine et al. 2017); such hidden interactions may underlie nonlinearities. 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;

Box 2. Statistical and mathematical models of trophic interaction

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 (Asparouhov & 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.

Acknowledgements. This study was supported by the Norwegian Research Council (project SUSTAIN), the terrestrial flagship of FRAM – High North Research Centre for Climate and the Environment, the Climate-Ecological Observatory for Arctic Tundra (COAT), and the Norwegian Polar Institute. Moreover, COAT (UiT and Fram Centre grants) and the Norwegian Polar Institute have funded most of the time series used in this study. We thank all participants of the Strategic Foresight Process within the different modules of SUSTAIN for their contribution to the studies conducted within the project.

LITERATURE CITED

Aalen OO, Røysland K, Gran J, Kouyos R, Lange T (2016) Can we believe the DAGs? A comment on the relationship between causal DAGs and mechanisms. Stat Methods Med Res 25:2294–2314

Aalen OO, Røysland K, Gran JM, Stensrud MJ, Strohmaier S (2018) Feedback and mediation in causal inference illustrated by stochastic process models. Scand J Stat 45:62–86

Abrams PA, Matsuda H (1996) Positive indirect effects between prey species that share predators. Ecology 77: 610–616

Abrams PA, Holt RD, Roth JD (1998) Apparent competition or apparent mutualism? Shared predation when populations cycle. Ecology 79:201–212

Andersson M (1981) Reproductive tactics of the long-tailed skua *Stercorarius longicaudus*. Oikos 37:287–294

Angerbjörn A, Eide NE, Dalén L, Elmhagen B and others (2013) Carnivore conservation in practice: replicated management actions on a large spatial scale. J Appl Ecol 50:59–67

Asparouhov T, Muthén B (2019) Latent variable centering of predictors and mediators in multilevel and time-series models. Struct Equ Model 26:119–142

Asparouhov T, Hamaker EL, Muthén B (2018) Dynamic structural equation models. Struct Equ Model 25:359–388

Barraquand F, Louca S, Abbott KC, Cobbold CA and others (2017) Moving forward in circles: challenges and opportunities in modelling population cycles. Ecol Lett 20: 1074–1092

Beschta RL, Ripple WJ, Kauffman JB, Painter LE (2020) Bison limit ecosystem recovery in northern Yellowstone. Food Webs 23:e00142

Bjørnstad ON, Falck W, Stenseth NC (1995) A geographic gradient in small rodent density fluctuations: a statistical modelling approach. Proc R Soc B 262:127–133

Bliss L (1997) Arctic ecosystems of North America. In: Wielgolaski FE (ed) Ecosystems of the world. 3. Polar and alpine tundra. Elsevier, Amsterdam, p 211–310

Cade BS (2015) Model averaging and muddled multimodel inferences. Ecology 96:2370–2382

Callaghan TV, Björn LO, Chernov Y, Chapin T and others (2004a) Biodiversity, distributions and adaptations of Arctic species in the context of environmental change. Ambio 33:404–417

Callaghan TV, Björn LO, Chernov Y, Chapin T and others (2004b) Effects of changes in climate on landscape and regional processes, and feedbacks to the climate system. Ambio 33:459–468

Charnov EL (1976) Optimal foraging: attack strategy of a mantid. Am Nat 110:141–151

Cirillo P, Taleb NN (2020) Tail risk of contagious diseases. Nat Phys 16:606–613

Clark JS, Carpenter SR, Barber M, Collins S and others (2001) Ecological forecasts: an emerging imperative. Science 293:657–660

Dietze MC, Fox A, Beck-Johnson LM, Betancourt JL and others (2018) Iterative near-term ecological forecasting: needs, opportunities, and challenges. Proc Natl Acad Sci USA 115:1424–1432

Dormann CF, Calabrese JM, Guillera-Arroita G, Matechou E and others (2018) Model averaging in ecology: a review of Bayesian, information-theoretic, and tactical approaches for predictive inference. Ecol Monogr 88: 485–504

Elmhagen B, Kindberg J, Hellström P, Angerbjörn A (2015) A boreal invasion in response to climate change? Range shifts and community effects in the borderland between forest and tundra. Ambio 44:39–50

Elmhagen B, Berteaux D, Burgess RM, Ehrich D and others (2017) Homage to Hersteinsson and Macdonald: climate warming and resource subsidies cause red fox range expansion and Arctic fox decline. Polar Res 36:3

Elton CS (1924) Periodic fluctuations in the numbers of animals: their causes and effects. J Exp Biol 2:119–163

Elton CS (1927) Animal ecology. University of Chicago Press, Chicago, IL

Elton C, Nicholson M (1942) The ten-year cycle in numbers of the lynx in Canada. J Animal Ecol 11:215–244

Evans MR, Grimm V, Johst K, Knuuttila T and others (2013) Do simple models lead to generality in ecology? Trends Ecol Evol 28:578–583

Fox AD, Madsen J (2017) Threatened species to super-abundance: the unexpected international implications of successful goose conservation. Ambio 46:179–187

Fryxell JM, Lundberg P (1994) Diet choice and predator–prey dynamics. Evol Ecol 8:407–421

Fuglei E, Henden JA, Callahan CT, Gilg O and others (2020) Circumpolar status of Arctic ptarmigan: population dynamics and trends. Ambio 49:749–761

Gallant D, Lecomte N, Berteaux D (2020) Disentangling the relative influences of global drivers of change in biodiversity: a study of the twentieth-century red fox expansion into the Canadian Arctic. J Anim Ecol 89: 565–576

Gilg O, Hanski I, Sittler B (2003) Cyclic dynamics in a simple vertebrate predator–prey community. Science 302: 866–868

Grace JB, Irvine KM (2020) Scientist's guide to developing explanatory statistical models using causal analysis principles. Ecology 101:e02962

Griffith GP, Hop H, Vihtakari M, Wold A, Kalhagen K, Gabrielsen GW (2019) Ecological resilience of Arctic marine food webs to climate change. Nat Clim Change 9: 868–872

Hamel S, Killengreen ST, Henden JA, Yoccoz NG, Ims RA (2013) Disentangling the importance of interspecific competition, food availability, and habitat in species occupancy: recolonization of the endangered Fennoscandian arctic fox. Biol Conserv 160:114–120

Hamel S, Ims RA, Yoccoz NG (2021) Challenges and opportunities when implementing strategic foresight: lessons learned when engaging stakeholders in climate-ecological research. Clim Res (in press) doi:10.3354/cr01653

Hansen BB, Grøtan V, Aanes R, Sæther BE and others (2013) Climate events synchronize the dynamics of a resident vertebrate community in the High Arctic. Science 339: 313–315

Hastings A, Abbott KC, Cuddington K, Francis T and others (2018) Transient phenomena in ecology. Science 361: eaat6412

Henden JA, Ims RA, Yoccoz NG (2009) Nonstationary spatio-temporal small rodent dynamics: evidence from long-term Norwegian fox bounty data. J Anim Ecol 78: 636–645

Henden JA, Ims RA, Yoccoz NG, Hellström P, Angerbjörn A (2010) Strength of asymmetric competition between predators in food webs ruled by fluctuating prey: the case of foxes in tundra. Oikos 119:27–34

Henden JA, Stien A, Bårdsen BJ, Yoccoz NG, Ims RA (2014) Community-wide mesocarnivore response to partial ungulate migration. J Appl Ecol 51:1525–1533

Henden JA, Ims RA, Fuglei E, Pedersen ÅØ (2017) Changed Arctic–alpine food web interactions under rapid climate warming: implication for ptarmigan research. Wildl Biol 2017:wlb.00240

Henden JA, Ims RA, Yoccoz NG, Asbjørnsen EJ and others (2020) End-user involvement to improve predictions and management of populations with complex dynamics and multiple drivers. Ecol Appl 30:e02120

Henden JA, Ehrich D, Soininen EM, Ims RA (2021a) Accounting for food web dynamics when assessing the impact of mesopredator control on declining prey populations. J Appl Ecol 58:104–113

Henden JA, Tveraa T, Stien A, Mellard JP, Marolla F, Ims RA, Yoccoz NG (2021b) Direct and indirect effects of environmental drivers on reindeer reproduction. Clim Res doi:10.3354/cr01630

Hewitt JE, Thrush SE, Cummings VJ (2001) Assessing environmental impacts: effects of spatial and temporal variability at likely impact scales. Ecol Appl 11:1502–1516

Hilde CH, Gamelon M, Sæther BE, Gaillard JM, Yoccoz NG, Pélabon C (2020) The demographic buffering hypothesis: evidence and challenges. Trends Ecol Evol 35: 523–538

Hobbs NT, Geremia C, Treanor J, Wallen R, White PJ, Hooten MB, Rhyan JC (2015) State–space modeling to support management of brucellosis in the Yellowstone bison population. Ecol Monogr 85:525–556

Hobday AJ, Spillman CM, Paige EJ, Hartog JR (2016) Seasonal forecasting for decision support in marine fisheries and aquaculture. Fish Oceanogr 25:45–56

Holt RD (1977) Predation, apparent competition, and structure of prey communities. Theor Popul Biol 12:197–229

Holt RD, Bonsall MB (2017) Apparent competition. Annu Rev Ecol Evol Syst 48:447–471

Houlahan JE, McKinney ST, Anderson TM, McGill BJ (2017) The priority of prediction in ecological understanding. Oikos 126:1–7

Hunter CE, Lauer M, Levine A, Holbrook S, Rassweiler A (2018) Maneuvering towards adaptive co-management in a coral reef fishery. Mar Policy 98:77–84

Ims RA, Fuglei E (2005) Trophic interaction cycles in tundra ecosystems and the impact of climate change. Bioscience 55:311–322

Ims RA, Yoccoz NG (2017) Ecosystem-based monitoring in the age of rapid climate change and new technologies. Curr Opin Environ Sustain 29:170–176

Ims RA, Henden JA, Killengreen ST (2008) Collapsing population cycles. Trends Ecol Evol 23:79–86

Ims RA, Yoccoz NG, Killengreen ST (2011) Determinants of lemming outbreaks. Proc Natl Acad Sci USA 108: 1970–1974

Ims RA, Ehrich D, Forbes BC, Huntley B and others (2013a) Terrestrial ecosystems. In: Meltofte H (ed) Arctic biodiversity assessment. Status and trends in Arctic biodiversity. Conservation of Arctic Flora and Fauna, Akureyri, p 384–441

Ims RA, Henden JA, Thingnes AV, Killengreen ST (2013b) Indirect food web interactions mediated by predator–rodent dynamics: relative roles of lemmings and voles. Biol Lett 9:20130802

Ims RA, Jepsen JU, Stien A, Yoccoz NG (2013c) Science plan for COAT: Climate-Ecological Observatory for Arctic Tundra. Fram Centre Report Series No. 1. https://www.coat.no/portals/coat/SciencePlanCOAT_web.pdf

Ims RA, Killengreen ST, Ehrich D, Flagstad Ø and others (2017) Ecosystem drivers of an Arctic fox population at the western fringe of the Eurasian Arctic. Polar Res 36:8

Ims RA, Henden JA, Strømeng MA, Thingnes AV, Garmo MJ, Jepsen JU (2019) Arctic greening and bird nest predation risk across tundra ecotones. Nat Clim Change 9: 607–610

Jepsen JU, Kapari L, Hagen SB, Schott T, Vindstad OPL, Nilssen AC, Ims RA (2011) Rapid northwards expansion of a forest insect pest attributed to spring phenology matching with sub-Arctic birch. Glob Change Biol 17: 2071–2083

Jepsen JU, Biuw M, Ims RA, Kapari L, Schott T, Vindstad OPL, Hagen SB (2013) Ecosystem impacts of a range expanding forest defoliator at the forest–tundra ecotone. Ecosystems 16:561–575

Johnson CJ, Mumma MA, St-Laurent MH (2019) Modeling multispecies predator–prey dynamics: predicting the outcomes of conservation actions for woodland caribou. Ecosphere 10:e02622

Kämmerle JL, Storch I (2019) Predation, predator control and grouse populations: a review. Wildl Biol 2019:1–12

Kausrud KL, Mysterud A, Steen H, Vik JO and others (2008) Linking climate change to lemming cycles. Nature 456: 93–97

Kempthorne O (1975) Fixed and mixed models in the analysis of variance. Biometrics 31:473–486

Killengreen ST, Lecomte N, Ehrich D, Schott T, Yoccoz NG, Ims RA (2011) The importance of marine vs. human-induced subsidies in the maintenance of an expanding mesocarnivore in the arctic tundra. J Anim Ecol 80: 1049–1060

Killengreen ST, Strømseng E, Yoccoz NG, Ims RA (2012) How ecological neighbourhoods influence the structure of the scavenger guild in low arctic tundra. Divers Distrib 18:563–574

Kleiven EF, Henden JA, Ims RA, Yoccoz NG (2018) Seasonal difference in temporal transferability of an ecological model: near-term predictions of lemming outbreak abundances. Sci Rep 8:15252

Krebs CJ (2011) Of lemmings and snowshoe hares: the ecology of northern Canada. Proc R Soc B 278:481–489

Krebs CJ, Danell K, Angerbjörn A, Agrell J and others (2003) Terrestrial trophic dynamics in the Canadian Arctic. Can J Zool 81:827–843

Kubelka V, Šálek M, Tomkovich P, Végvári Z, Robert P, Freckleton RP, Székely T (2018) Global pattern of nest predation is disrupted by climate change in shorebirds. Science 362:680–683

Le Moullec M, Pedersen ÅØ, Stien A, Rosvold J, Hansen BB (2019) A century of conservation: the ongoing recovery of Svalbard reindeer. J Wildl Manag 83:1676–1686

Legagneux P, Gauthier G, Lecomte N, Schmidt NM and others (2014) Arctic ecosystem structure and functioning shaped by climate and herbivore body size. Nat Clim Change 4:379–383

Lehikoinen A, Green M, Husby M, Kålås JA, Lindström Å (2014) Common montane birds are declining in northern Europe. J Avian Biol 45:3–14

Lehikoinen A, Brotons L, Calladine J, Campedelli T and others (2019) Declining population trends of European mountain birds. Glob Change Biol 25:577–588

Levine JM, Bascompte J, Adler PB, Allesina S (2017) Beyond pairwise mechanisms of species coexistence in complex communities. Nature 546:56–64

Lotka AJ (1920) Analytical note on certain rhythmic relations in organic systems. Proc Natl Acad Sci USA 6:410–415

Luján JL, Todt O (2020) Standards of evidence and causality in regulatory science: risk and benefit assessment. Stud Hist Philos Sci 80:82–89

MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. Am Nat 100:603–609

Marolla F (2020) Understanding and forecasting population dynamics in changing arctic ecosystems. PhD thesis, University of Tromsø

Marolla F, Aarvak T, Øien IJ, Mellard JP and others (2019) Assessing the effect of predator control on an endangered goose population subjected to predator-mediated food web dynamics. J Appl Ecol 56:1245–1255

Marolla F, Henden JA, Fuglei E, Pedersen ÅØ, Itkin M, Ims RA (2021) Iterative model predictions for wildlife populations impacted by rapid climate change. Glob Change Biol 27:1547–1559

McCann KS (2012) Food webs. Monographs in population biology 50. Princeton University Press, Princeton, NJ

Mellard JP, Hamel S, Henden JA, Ims RA, Stien A, Yoccoz N (2021) Effect of scavenging on predation in a food web. Ecol Evol 2021:1–24

Moss R, Watson A (2001) Population cycles in birds of the grouse family (Tetraonidae). Adv Ecol Res 32:53–111

Mouquet N, Lagadeuc Y, Devictor V, Doyen L and others (2015) REVIEW: Predictive ecology in a changing world. J Appl Ecol 52:1293–1310

Myers-Smith IH, Elmendorf SC, Beck PSA, Wilmking M and others (2015) Climate sensitivity of shrub growth across the tundra biome. Nat Clim Change 5:887–891

Mysterud A, Rivrud IM, Gundersen V, Rolandsen CM, Viljugrein H (2020) The unique spatial ecology of human hunters. Nat Hum Behav 4:694–701

Nichols JD, Runge MC, Johnson FA, Williams BK (2007) Adaptive harvest management of North American waterfowl populations: a brief history and future prospects. J Ornithol 148:343–349

Nichols JD, Johnson FA, Williams BK, Boomer GS (2015) On formally integrating science and policy: walking the walk. J Appl Ecol 52:539–543

Nichols JD, Kendall WL, Boomer GS (2019) Accumulating evidence in ecology: once is not enough. Ecol Evol 9: 13991–14004

Oedekoven CS, Elston DA, Harrison PJ, Brewer MJ and others (2017) Attributing changes in the distribution of species abundance to weather variables using the example of British breeding birds. Methods Ecol Evol 8:1690–1702

Oksanen L, Oksanen T (2000) The logic and realism of the hypothesis of exploitation ecosystems. Am Nat 155: 703–723

Oksanen L, Fretwell SD, Arruda J, Niemela P (1981) Exploitation ecosystems in gradients of primary productivity. Am Nat 118:240–261

Overland JE, Wang M, Walsh JE, Stroeve JC (2014) Future Arctic climate changes: adaptation and mitigation time scales. Earths Futur 2:68–74

Petchey OL, Pontarp M, Massie TM, Kéfi S and others (2015) The ecological forecast horizon, and examples of its uses and determinants. Ecol Lett 18:597–611

Pimm SL (1982) Food webs. Population and community biology. Springer, Dordrecht

Planque B (2016) Projecting the future state of marine ecosystems, 'la grande illusion'? ICES J Mar Sci 73:204–208

Post E, Forchhammer MC, Bret-Harte MS, Callaghan TV and others (2009) Ecological dynamics across the Arctic associated with recent climate change. Science 325: 1355–1358

Pouyat RV, Weathers KC, Hauber R, Lovett GM and others (2010) The role of federal agencies in the application of scientific knowledge. Front Ecol Environ 8:322–328

Ravolainen V, Soininen EM, Jónsdóttir IS, Eischeid I, Forchhammer M, van der Wal R, Pedersen ÅØ (2020) High Arctic ecosystem states: conceptual models of vegetation change to guide long-term monitoring and research. Ambio 49:666–677

Roth JD (2003) Variability in marine resources affects arctic fox population dynamics. J Anim Ecol 72:668–676

Runge MC, Walshe T (2014) Identifying objectives and alternative actions to frame a decision problem. In: Guntenspergen GR (ed) Application of threshold concepts in natural resource decision making. Springer, New York, NY, p 29–43

Salo P, Banks PB, Dickman CR, Korpimäki E (2010) Predator manipulation experiments: impacts on populations of terrestrial vertebrate prey. Ecol Monogr 80:531–546

Sandercock BK, Nilsen EB, Brøseth H, Pedersen HC (2011) Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of willow ptarmigan. J Anim Ecol 80:244–258

Serrouya R, Seip DR, Hervieux D, McLellan BN and others (2019) Saving endangered species using adaptive management. Proc Natl Acad Sci USA 116:6181–6186

Sokolov AA, Sokolova NA, Ims RA, Brucker L, Ehrich D (2016) Emergent rainy winter warm spells may promote boreal predator expansion into the Arctic. Arctic 69:121–129

Spearman C (1904) 'General intelligence', objectively determined and measured. Am J Psychol 15:201–292

Stenseth NC, Falck W, Bjørnstad ON, Krebs CJ (1997) Population regulation in snowshoe hare and Canadian lynx: asymmetric food web configurations between hare and lynx. Proc Natl Acad Sci USA 94:5147–5152

Stewart-Oaten A, Murdoch WW, Parker KR (1986) Environmental impact assessment: 'pseudoreplication' in time? Ecology 67:929–940

Stewart-Oaten A, Bence JR, Osenberg CW (1992) Assessing effects of unreplicated perturbations: no simple solutions. Ecology 73:1396–1404

Stien A, Ims RA, Albon SD, Fuglei E and others (2012) Congruent responses to weather variability in high arctic herbivores. Biol Lett 8:1002–1005

Tannerfeldt M, Angerbjörn A (1998) Fluctuating resources and the evolution of litter size in the arctic fox. Oikos 83: 545–559

Taylor G, Canessa S, Clarke RH, Ingwersen D, Armstrong DP, Seddon PJ, Ewen JG (2017) Is reintroduction biology an effective applied science? Trends Ecol Evol 32: 873–880

Therrien JF, Gauthier G, Korpimäki E, Bêty J (2014) Predation pressure by avian predators suggests summer limitation of small-mammal populations in the Canadian Arctic. Ecology 95:56–67

Thuiller W, Guéguen M, Renaud J, Karger DN, Zimmermann NE (2019) Uncertainty in ensembles of global biodiversity scenarios. Nat Commun 10:1446

Trijoulet V, Fay G, Miller TJ (2020) Performance of a state–space multispecies model: What are the consequences of ignoring predation and process errors in stock assessments? J Appl Ecol 57:121–135

Underwood AJ (1992) Beyond BACI: the detection of environmental impacts on populations in the real, but variable, world. J Exp Mar Biol Ecol 161:145–178

Urban MC, Bocedi G, Hendry AP, Mihoub JB and others (2016) Improving the forecast for biodiversity under climate change. Science 353:aad8466

van de Pol M, Jenouvrier S, Cornelissen JHC, Visser ME (2017) Behavioural, ecological and evolutionary responses to extreme climatic events: challenges and directions. Philos Trans R Soc B 372:20160134 van der Wal R, Stien A (2014) High-arctic plants like it hot: a long-term investigation of between-year variability in plant biomass. Ecology 95:3414–3427

Volterra V (1926) Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. Mem Acad Lincei Roma 2:31–113

Westneat DF, Araya-Ajoy YG, Allegue H, Class B and others (2020) Collision between biological process and statistical analysis revealed by mean centring. J Anim Ecol 89:2813–2824

Wollrab S, de Roos AM, Diehl S (2013) Ontogenetic diet shifts promote predator-mediated coexistence. Ecology 94:2886–2897

Wootton JT (1994a) Predicting direct and indirect effects: an integrated approach using experiments and path analysis. Ecology 75:151–165

Wootton JT (1994b) Putting the pieces together – testing the independence of interactions among organisms. Ecology 75:1544–1551

Wright S (1920) Correlation and causation. I. Method of path coefficients. J Agric Res 20:557–585

Yao Y, Vehtari A, Simpson D, Gelman A (2018) Using stacking to average Bayesian predictive distributions. Bayesian Anal 13:917–1007

Editorial responsibility: Tim Coulson (Guest Editor), Oxford, UK
Reviewed by: 2 anonymous referees

Submitted: August 26, 2020
Accepted: January 20, 2021
Proofs received from author(s): May 7, 2021