



Novel feeding interactions amplify the impact of species redistribution on an Arctic food web

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Abstract

Species are redistributing globally in response to climate warming, impacting ecosystem functions and services. In the Barents Sea, poleward expansion of boreal species and a decreased abundance of Arctic species are causing a rapid borealization of the Arctic communities. This borealization might have profound consequences on the Arctic food web by creating novel feeding interactions between previously non co-occurring species. An early identification of new feeding links is crucial to predict their ecological impact. However, detection by traditional approaches, including stomach content and isotope analyses, although fundamental, cannot cope with the speed of change observed in the region, nor with the urgency of understanding the consequences of species redistribution for the marine ecosystem. In this study, we used an extensive food web (metaweb) with nearly 2,500 documented feeding links between 239 taxa coupled with a trait data set to predict novel feeding interactions and to quantify their potential impact on Arctic food web structure. We found that feeding interactions are largely determined by the body size of interacting species, although species foraging habitat and metabolic type are also important predictors. Further, we found that all boreal species will have at least one potential resource in the Arctic region should they redistribute therein. During 2014–2017, 11 boreal species were observed in the Arctic region of the Barents Sea. These incoming species, which are all generalists, change the structural properties of the Arctic food web by increasing connectance and decreasing modularity. In addition, these boreal species are predicted to initiate novel feeding interactions with the Arctic residents, which might amplify their impact on Arctic food web structure affecting ecosystem functioning and vulnerability. Under the ongoing species redistribution caused by environmental change, we propose merging a trait-based approach with ecological network analysis to efficiently predict the impacts of range-shifting species on food webs.

KEYWORDS

Arctic, Barents Sea, body size, borealization, ecological network, ecosystem vulnerability, food web structure, prediction of feeding interactions, trait-based approach

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1 | INTRODUCTION

Species are redistributing globally in response to ongoing environmental changes, impacting ecosystem functions and services (Pech et al., 2017; Poloczanska et al., 2013). As species redistribute, novel biotic interactions arise in the form of competition, mutualism or predation (Mitchell et al., 2006; Woodward et al., 2010). The successful establishment of a species in a new environment depends on its capacity to feed on a new prey pool and to escape predation. To maintain a sufficient food intake in a new ecosystem, a species will need to strengthen existing feeding interactions or initiate new ones within the local species pool (Lurgi, López, & Montoya, 2012). As species from different taxonomic and functional groups redistribute with varying pace and success (Lenoir et al., 2020; Poloczanska et al., 2013), ecosystems are likely to be composed of species that did not previously co-occur, which may result in novel feeding interactions and food web configurations (Bartley et al., 2019; Kortsch, Primicerio, Fossheim, Dolgov, & Aschan, 2015; Montoya & Raffaelli, 2010).

Successful feeding interactions between co-occurring species depend on several traits characterizing the consumer and the resource. Notable examples of consumer–resource trait matching are provided by co-evolved plants and pollinator species, where the bill length of a hummingbird or the tongue size of a bumblebee matches the corolla length of a flower (Harder, 1985; Ranta & Lundberg, 1980; Weinstein & Graham, 2017). In marine ecosystems, predators are generally larger than their prey (Brose et al., 2006), and the latter may evade or resist the attacks of predators by swimming faster or investing in protective structures, among other defensive strategies. However, whereas body size is a well-studied feature determining size-structured food webs in marine ecosystems (Andersen, 2019; Cohen, Pimm, Yodzis, & Saldana, 1993; Woodward et al., 2005), other traits such as movement type, metabolism and physical defence structures have received less attention in food web analyses. These traits can be important drivers of food web structure (Brose et al., 2019). The traits driving food web structure can be revealed through analyses of existing predator–prey interactions (Laigle et al., 2018). Analyses of existing trait-mediated interactions in food webs can also be used to infer potential feeding links between co-occurring species (Albouy et al., 2019; Pellissier et al., 2018). Furthermore, species traits may be used to predict feeding interactions among species that do not currently co-occur, but that are expected to co-occur in the future due to ongoing species range shift and redistribution (Albouy et al., 2014; Gravel, Poisot, Albouy, Velez, & Mouillot, 2013).

Climate warming is a main driver of species redistributions that may result in new feeding links and food web reconfigurations (Woodward et al., 2010). In marine ecosystems, some of the most rapid and extensive compositional reorganizations caused by climate-driven distributional shifts are taking place in the Arctic, as observed in the Barents Sea (Fossheim et al., 2015; Kortsch et al., 2015). The Barents Sea is a productive arcto-boreal marine

ecosystem that sustains economically important fish stocks and hosts unique and diverse biotas (ICES, 2019). The rate of sea temperature increase in the Arctic is twice the global average (Hoegh-Guldberg & Bruno, 2010), and the Barents Sea is experiencing some of the highest rates within the Arctic, now and in the future, with a warming trend of around 0.5°C/decade over the period 1976–2099 (Alexander et al., 2018). This warming resulted in a dramatic decrease in sea ice extent (Smedsrud et al., 2013; Stern & Laidre, 2016), and a decrease in salinity and stratification (Lind, Ingvaldsen, & Furevik, 2018). Increase in water temperature and decrease in sea ice have led to a northward distribution and weakening of the polar front (Lvshin, Trofimov, & Titov, 2019), which acts as a natural environmental barrier to the northward expansion of boreal species (Fossheim, Nilssen, & Aschan, 2006). These environmental alterations have triggered a reconfiguration of fish community composition through a northward shift of both boreal and Arctic communities, as well as the biomass increase of boreal species in the Arctic part of the Barents Sea (Fossheim et al., 2015). The Atlantic cod (*Gadus morhua*) is an example of a commercial boreal species that has benefitted from warmer water and higher primary productivity, with the Barents Sea cod stock reaching record high biomass levels (Kjesbu et al., 2014). Community alterations caused by environmental change have been documented in the region not only for fish, but also for benthos (Jørgensen et al., 2019; Kortsch et al., 2012), phytoplankton (Dalpadado et al., 2014) and zooplankton (Dalpadado et al., 2012).

This rapid borealization might have profound consequences for the structure and functioning of the Barents Sea ecosystem as the boreal species traits and life-history strategies differ from those of their Arctic counterparts. For example, Arctic fish communities are characterized by small benthivorous species whereas the incoming boreal species are characterized by large body size and a generalist diet (Frainer et al., 2017). Due to their broad diet, the incoming boreal species change the structure of the Arctic food web by increasing the number of feeding interactions and the connectivity between the benthic and pelagic compartments (Kortsch et al., 2015). However, the above assessment of food web structural change is constrained by the available empirical information on feeding links documented in the literature, and does not take into account potential novel feeding interactions between newly co-occurring species. Generalist species are more likely to create new feeding interactions when redistributing in an ecosystem where they were previously absent and, as they do, have the potential to rewire food webs (Bartley et al., 2019).

In this study, we use an extensive and spatio-temporally resolved food web of the Barents Sea marine ecosystem, coupled with a cross-organism trait database, to predict feeding interactions between species that might newly, or more frequently, co-occur under species redistribution. Based on a trait matching technique, we (a) identify which traits structure feeding interactions in the Barents Sea food web; (b) infer the most likely feeding interactions of incoming boreal species in the Arctic food web; and (c) quantify how this borealization and the emergence of potential new feeding

interactions, previously undocumented in the Barents Sea food web, affect the structural properties of the Arctic food web.

2 | MATERIALS AND METHODS

2.1 | Barents Sea food web

We used an extensive meta food web (metaweb) documenting 2,461 feeding links between 239 trophospecies that inhabit the Barents Sea (Planque et al., 2014), ranging from plankton, to benthic invertebrates, fish, birds and mammals. A trophospecies, hereafter referred simply as species, represents a set of one or more species that share the same resources and consumers (Yodzis & Winemiller, 1999). It can refer to biological entities that are described at different levels of taxonomic resolution, from species (e.g. *G. morhua*) to functional groups (e.g. phytoplankton). The feeding links were documented from peer reviewed literature, reports, personal communication with experts or inferred from taxonomically similar species, and spanned the period from 1927 to 2012 (Planque et al., 2014).

2.2 | Spatial occurrence

The Barents Sea metaweb does not represent a realized food web because not all species spatially co-occur. From the Barents Sea metaweb we subsampled regional food webs according to regional species composition. The spatial distribution of the 239 species was available from Kortsch et al. (2019), who allocated them to 25 different polygons following data from the Barents Sea ecosystem survey for the years 2004–2007 for megabenthos and fish species (Eriksen et al., 2018), and completed by expert knowledge and distribution maps for the species not surveyed (i.e. zooplankton, birds, mammals and meiofauna).

We further separated the Barents Sea into two regions according to their species composition, food web properties and environmental conditions: the boreal region, located in the south-western Barents Sea (regrouping 10 spatial polygons from Kortsch et al., 2019), and the Arctic region, located in the north-eastern Barents Sea (regrouping 3 spatial polygons from Kortsch et al., 2019; Figure 1). Compared to the boreal region, the Arctic region is characterized by colder and seasonally ice-covered waters, lower species richness and connectance and higher modularity (Kortsch et al., 2019). From the spatial information on species occurrence in the Barents Sea we derived (a) a list of species pairs that do not spatially overlap in any of the 25 spatial polygons; (b) two lists of all species present in each region; and (c) two lists of species that are present in only one region type (Figure 2; Table S1). A species was assigned to a region if it was occurring in at least one of the region polygons. A species was identified as present in only one region type, and thereafter referred as 'typical' Arctic or boreal, if it was present in one of the regions and had not been documented in the other region during the 2004–2007 period. The boreal and Arctic regions were inhabited by 222 and 165 species, respectively, out of the 239 species present in the Barents Sea metaweb. From these, 70 species were identified as 'typical' boreal and 13 as 'typical' Arctic (Table S1), whereas 152 species are common to the two regions (and four species from the metaweb are present in neither region).

2.3 | Temporal occurrence

We used the Barents Sea ecosystem survey data to assess whether some of the species that did not occur in the boreal or Arctic regions during the 2004–2007 period were observed in at least 2 years of a later period of warming 2014–2017. We assessed distributional changes for 46 of the 70 'typical' boreal species (fish, mega-benthos,

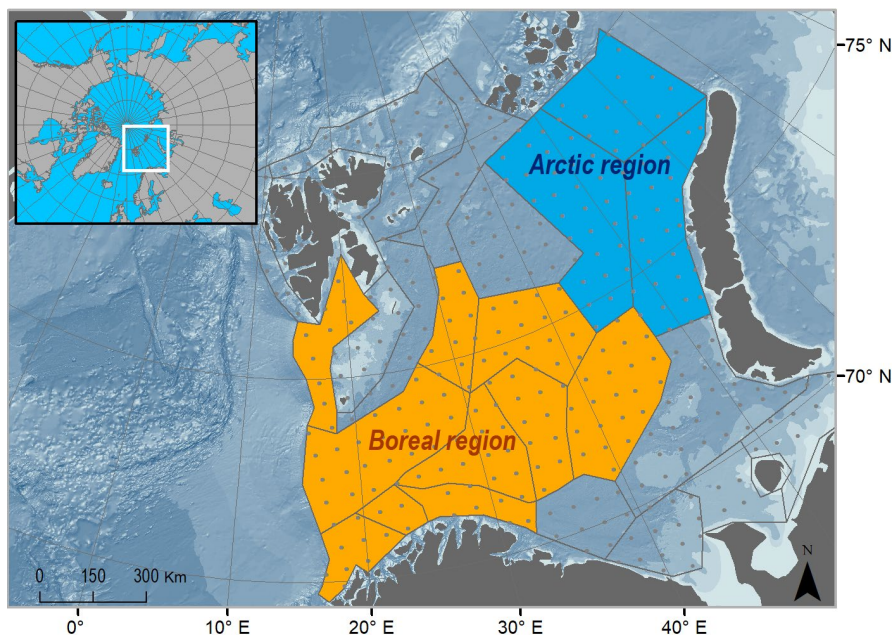


FIGURE 1 Map of the study area. The polygons dividing the Barents Sea are outlined with grey contour lines and the stations from the ecosystem survey with grey dots. The Arctic and Boreal regions were divided according to the polygons environmental conditions, species composition and food web properties following Kortsch et al. (2019). Compared to the boreal region, the Arctic region is characterized by colder and seasonally ice-covered waters, lower species richness and connectance and higher modularity (for more information, see Kortsch et al., 2019)

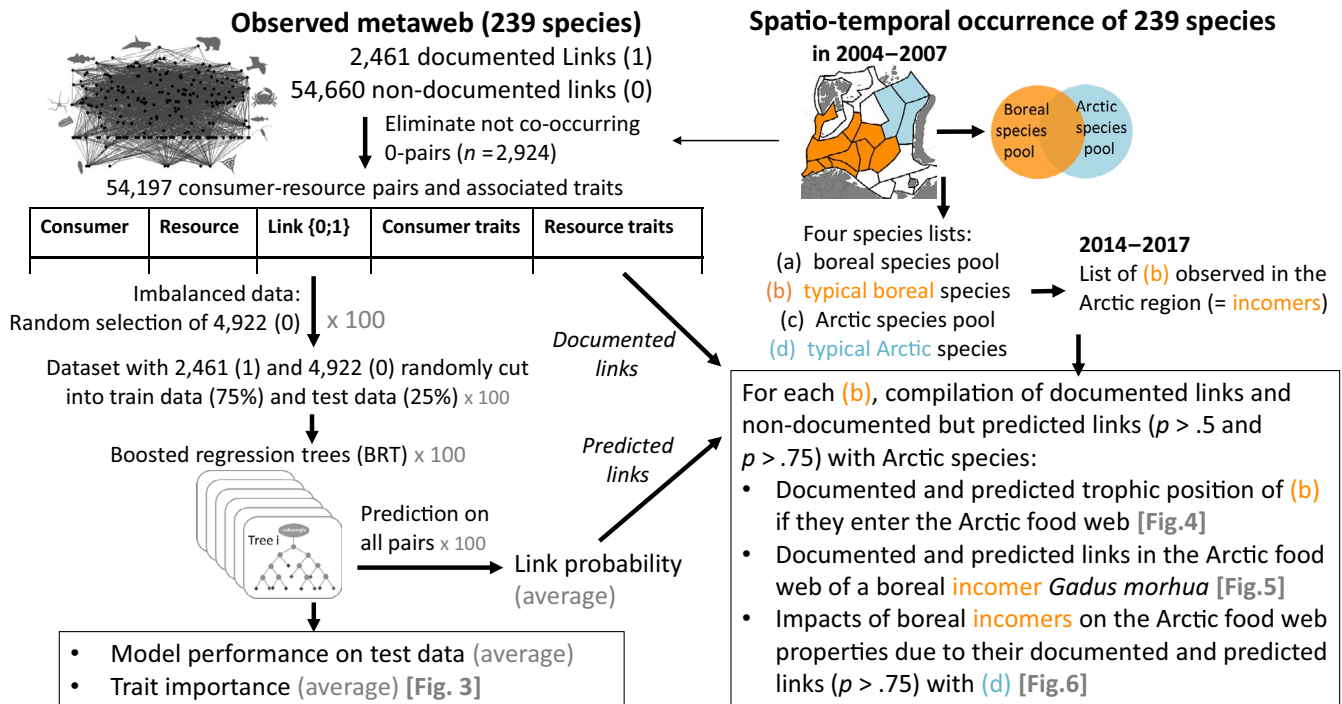


FIGURE 2 A schematic representation of the data prehandling, the different data sets used and the analyses performed in this study [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

marine mammals and birds), as the remaining species (predominantly zooplankton and meiofauna) could not be assessed due to unavailable spatio-temporal information (list of assessed species in Table S2). This species list is thus likely incomplete. Species spatial and temporal occurrences were indicative of their summer distribution, the food webs analysed here are thus representative of the summer season, when several boreal species are most likely to be found in the Arctic region.

2.4 | Trait information

For the 239 species present in the Barents Sea food web, we collected information on traits that are known to, or could, influence the consumer–resource feeding interactions (Cirtwill & Eklöf, 2018; Laigle et al., 2018). We selected traits that enabled the characterization of a large spectrum of organisms with very different feeding strategies and life histories, covering a large diversity of taxa from plankton to whales. The selected traits provided information on body size, metabolic type, feeding environment, mode of resource acquisition, feeding guild, feeding on living or dead resource, range of resource sizes, mobility, body toughness and sea-ice dependency, and are further described in Table 1. Trait categories were filled using a fuzzy coding approach (Chevenet, Doleadac, & Chessel, 1994), except for body size, metabolic type, body toughness and sea-ice dependency. The fuzzy coding approach indicates to which extent a species expresses each trait category from 0 to 3, with: 0, never or hardly ever expressed; 1, rarely expressed; 2, often expressed; 3, only this trait category is expressed. The set of traits used to model the consumer–resource interactions was different for the consumer

and the resource as they have opposite roles in the feeding interaction (eat or being eaten). Consumers were characterized by nine traits among which six were further subdivided into 17 fuzzy-coded categories, and the resources by six traits among which two were further subdivided into six fuzzy-coded categories.

2.5 | Modelling and predicting consumer–resource interactions

Modelling and prediction of consumer–resource interactions relied on the traits and metaweb data sets. The 239 species present in the metaweb have the potential to form 57,121 links (239×239 species). Of these, 2,461 are documented links (feeding interactions), whereas 54,660 are non-documented links. Non-documented links might be false-negatives, meaning that a feeding interaction between two species is possible, although it has never been observed. A feeding interaction could be possible but not observed due to, for example, low sampling effort, low or no co-occurrence, low abundance of one species or inadequate observation method. To account for the possibility that non-documented links might be due to low or no co-occurrence we eliminated from the data set all pairs of species that did not overlap spatially during the 2004–2007 period. This resulted in the elimination of 2,924 non-documented links. The final data set thus consisted of the 54,197 links between a consumer and a resource (2,461 documented links and 51,736 non-documented links) merged with the trait information of the resource and the consumer (Figure 2).

To predict feeding interactions in the Barents Sea ecosystem, we modelled the link occurrence as a function of the resource and

Traits characterizing consumer (C), resource (R) or both (C, R)	Trait types and categories
Body size (C, R)	Continuous, averaged total length in centimetres of the longest body axis of an adult individual of the species
Metabolic type (C, R)	Categorical, <i>Endotherm vertebrate, Ectotherm vertebrate, Ectotherm invertebrate, Basal species</i>
Feeding environment (C, R)	Categorical, fuzzy-coded: <i>Benthic, Benthic-pelagic, Pelagic</i> Foraging position in the water column
Mode of resource acquisition (C)	Categorical, fuzzy-coded: <i>Predator, Deposit Feeder, Filter feeder</i>
Feeding guild (C)	Categorical, fuzzy-coded: <i>Herbivore, Carnivore</i>
Feeding on living or dead (C)	Categorical, fuzzy-coded: <i>Living resource, Dead resource</i>
Range of resource sizes (C)	Categorical, fuzzy-coded: <i><1 mm, 1 mm–1 cm, 1 cm–10 cm, >10 cm</i>
Mobility (C, R)	Categorical, fuzzy-coded: <i>Sessile</i> (attached to a support), <i>Low mobility</i> (slow or current-drifter), <i>High mobility</i> (active movement)
Body toughness (R)	Ordered 0–3:0 endo- or hydrostatic skeleton, 1 exoskeleton—flexible extracellular matrix, cuticle, 2 exoskeleton—chitinous, 3 exoskeleton—hard shell, calcareous
Sea-ice dependency (C, R)	Binary: 0 not dependent; 1 dependent Whether any of the species life-stage is dependent on sea-ice (feeding, growing, reproduction)

TABLE 1 Consumer and resource traits used to model and predict feeding interactions

consumer traits using a boosted regression tree (BRT). This machine learning method uses an ensemble of decision trees to produce a prediction model by combining the decision tree algorithm (the link occurrence as a function of the traits is modelled by using recursive binary split) with the boosting method (the model predictive performance is improved by combining many weak models, adaptively, using a sequential approach, Elith, Leathwick, & Hastie, 2008). The BRT has several advantages, among others it can handle the different types of predictors, such as the continuous and binary traits used here. In addition, it can fit complex non-linear relationships, account for interaction effects between traits, is robust to outliers, and does not make assumptions on data distribution (Elith et al., 2008).

Machine learning models such as the BRT are sensitive to imbalanced classes (Krawczyk, 2016), which is the case here where the ratio of non-documented to documented links is relatively high (~20:1). If all the non-documented links were included in the model, the algorithm would be biased towards this majority group (resulting in an over-prediction of zero-links; Krawczyk, 2016). Thus, to have more balanced classes we subsampled the non-documented links by randomly selecting 4,922 non-documented links, reaching a 2:1 ratio between non-documented and documented links. This ratio was selected following a sensitivity analysis of the model performance with respect to the number of documented links selected (Figure S1). We iterated 100 times the random sample of non-documented links to avoid influencing our results by a sampling bias. We thus obtained 100 data sets with

information on whether a link between a consumer and a resource is documented (2,461) or non-documented (4,922) and the associated consumer and resource traits. Each data set was separated into a training data set that was used to fit the models and a test data set that was used to assess the model performance. The training data set consisted of a random selection of 75% of the data and the test data set of the remaining 25% of the data. The BRT with a Bernoulli distribution was performed on the training data set with link occurrence (0;1) as the response variable, and consumer and resource traits as the predictor variables. To avoid overfitting, we pruned the total number of trees used to estimate the link probability based on the best number of trees using the 'cross-validation' technique (Ridgeway, 2019). We evaluated the model by predicting feeding interactions of the test data set and calculating performance metrics on the test data set confusion matrix (i.e. the table summarizing the prediction successes and errors). We calculated the model accuracy (total links classified correctly), sensitivity (proportion of documented links correctly predicted), specificity (proportion of non-documented links correctly predicted), and its true skill statistic (TSS, sensitivity + specificity - 1), which ranges between 1 (perfect prediction) and -1 (inverted prediction).

Finally, the 100 models built on the training data sets were used to predict the feeding interactions between all the metaweb species (57,121 potential links corresponding to the 239 × 239 species). We used the probability of feeding interactions between species pairs as prediction output instead of a simple binary classification, to

have an estimate of the likelihood of feeding interactions. For each consumer–resource pair in the metaweb (57,121), we estimated the probability of a feeding link by averaging the predicted probability from the 100 models. The BRT analysis was performed in R using the 'gbm' R package (Ridgeway, 2019).

2.6 | Traits structuring the Barents Sea food web

To assess which traits were most important for predicting consumer–resource interactions, we averaged the trait importance values obtained from the 100 models. In each model, the trait importance is calculated by averaging the number of times the trait is selected for splitting the data set into more homogeneous subsets, and is weighted by the squared improvement of the BRT model for each split (Ridgeway, 2019). The sum of the variable importance for all the variables present in the model adds up to 100.

2.7 | Potential new feeding interactions of boreal species incoming the Arctic region

We classified the feeding links of the 70 'typical' boreal species into documented links and non-documented but predicted links. For simplicity, we will hereafter refer to the non-documented but predicted links simply as predicted links (we will not analyse and discuss the links that are documented and predicted apart from when calculating the model performance). For the predicted links, we made a distinction between the links predicted with a probability higher than 0.5 ($p > .5$) and the links predicted with a probability higher than 0.75 ($p > .75$). We assessed the potential role of the 70 'typical' boreal species in the Arctic food web (2004–2007) by looking at their interactions with the 165 species present in the Arctic, and notably with the 13 'typical' Arctic species. We assessed the boreal species generality (number of resources) and their vulnerability (number of consumers) based on documented and non-documented but predicted links. For this analysis, we only looked at the interactions of each of the boreal species with the 165 species that were present in the Arctic in 2004–2007, and thus did not take into account that several boreal species might enter the Arctic simultaneously (i.e. not taking into account potential interactions between boreal species) and that some Arctic species might disappear from the Arctic. To illustrate the different link categories and the potential position of boreal species in the Arctic food, we represented the food web position of cod (*G. morhua*), a 'typical' boreal species extending its range into the Arctic.

2.8 | Potential impacts of incoming species on the Arctic food web properties

We assessed changes in the Arctic food web structure between the early period (2004–2007) and (a) the recent period (2014–2017) with the addition of the observed incoming boreal species and their documented

links; and (b) the recent period with the addition of the documented and the predicted links between the incoming boreal species and the 13 'typical' Arctic species. We calculated the food web properties of the three Arctic food web variants. Food web properties can be described through numerous metrics, but many are co-varying (Vermaat, Dunne, & Gilbert, 2009). We selected three metrics that describe different facets of food web properties, namely: number of links, connectance and modularity. Number of links is the sum of the feeding interactions in a food web and informs on food web complexity. Connectance is the proportion of realized links over the total number of possible links and has implications for food web robustness (Dunne, Williams, & Martinez, 2002a). Modularity measures the compartmentalization of the food web into clusters of species that interact more among themselves than with species from other clusters, and may influence the sensitivity of a food web to perturbation (Stouffer & Bascompte, 2011). Modularity was computed with the function 'cluster_spinglass' in the R package 'igraph' (Csárdi & Nepusz, 2006). The results presented here were calculated using the links predicted with a probability superior to 0.75, the results based on links with a probability threshold of 0.5 can be found in the supplementary material (Figure S6).

3 | RESULTS

The BRT models predicted consumer–resource interactions of the test data sets with an average accuracy of 0.87, sensitivity of 0.82 and specificity of 0.90, and with a TSS of 0.72. Body size was by far the most important trait structuring the Barents Sea food web, with consumer body size followed closely by resource body size (Figure 3). The third most important trait was the metabolic category of resources. Other relatively important traits were the habitat position of both consumers and resources (benthic, benthic-pelagic or pelagic), the preferred prey size range of consumers and body toughness of resources. Several traits had a negligible importance: resource acquisition mode, feeding guild, feeding on living or dead matter and ice dependency.

The BRT predicted 1,447 ($p > .75$) feeding interactions that were not documented in the Barents Sea metaweb. Generalist species (with many documented food resources) were the ones with most predicted links, whereas specialist species (with few documented resources) had comparatively few predicted links (Figure S2). The Barents Sea species with the highest absolute number of predicted resources ($p > .75$) were the fish *Amblyraja radiata* and *G. morhua*, whereas the fish *Arctozenus risso* and *Argentina* sp., the pelagic mollusc *Clione limacina* and the crustacean zooplankton *Metridia lucens* had the highest number of predicted resources relative to the number of their documented ones. (Figure S2). The species with the highest absolute number of predicted consumers were the basal species Diatoms and Phytoplankton (unidentified) and the pelagic krill *Thysanoessa raschii* and *T. longicauda*, and the species with highest relative number of predicted consumers were the fish *Squalus acanthias* and the crustacean zooplankton *Paraeuchaeta glacialis* (Figure S2).

Eleven of the 70 'typical' boreal species were observed in the Arctic region during at least 2 years of the period 2014–2017

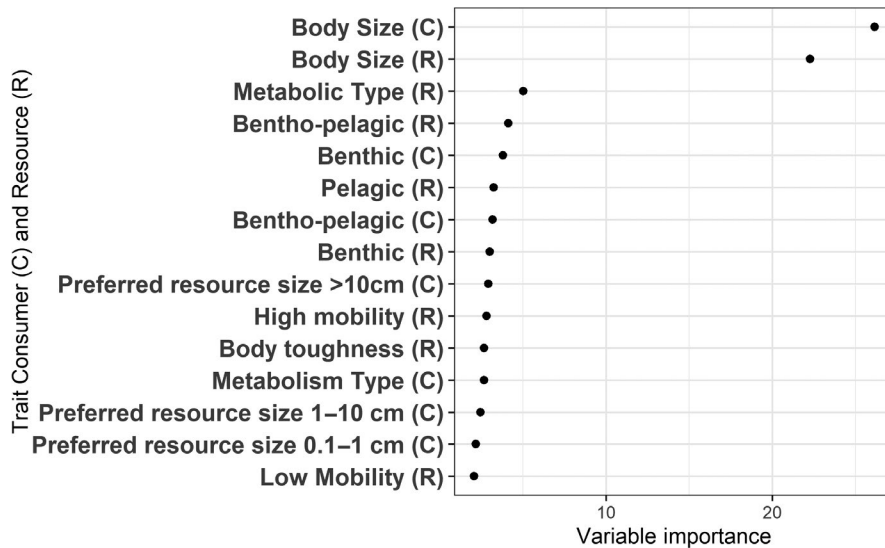


FIGURE 3 The most important traits of consumers (C) and resources (R) for predicting consumer–resource interactions in the Barents Sea food web, obtained by averaging the variable importance values from the 100 boosted regression trees (BRT) models. The variable importance is calculated by averaging the number of times the trait is selected to split the data set and is weighted by the squared improvement of the BRT model for each split. The sum of the variable importance for all the traits present in the model adds up to 100. For clarity, we only displayed here the 15 most important traits (complete set of traits in Figure S3)

(Figure 4). These species include 10 fish species and the benthic-pelagic krill *Meganctiphanes norvegica*. Several of these species are generalists (high generality Figure 4a): *Melanogrammus aeglefinus*, *G. morhua*, *Sebastes mentella* and *A. radiata* with, respectively, 67, 65, 40 and 31 documented resources in the Arctic food web. Other species constitute important resources (high vulnerability Figure 4b), for example, *M. norvegica*, *Clupea harengus*, and *G. morhua* with 17, 14 and 12 documented predators respectively. The average Arctic species (excluding basal species) has six documented resources, whereas the 11 incoming boreal species have high generality with 11 to 67 documented resources. In contrast, only five of the 11 boreal species have a higher vulnerability (number of documented consumers) than the average Arctic species. However, the addition of predicted links increases the boreal species' vulnerability and generality. For example, the ray *A. radiata* has no documented predators in the Arctic but was predicted to have three, whereas one boreal species (*A. risso*) has no documented resources in the Arctic but has thirteen predicted ones (Figure 4a).

With a total of 65 documented resources and 12 predators, cod is the boreal species with the highest number of documented links with species composing the Arctic food web. Another 40 potential resources were predicted by the BRT ($p > .75$; Figure 5). Among these, five were 'typical' Arctic (the fish *Arctogadus glacialis*, the zooplankton *Oikopleura vanhoeffeni*, the amphipods *Onisimus glacialis*, *Gammarus wilkitzkii* and *Apherusa glacialis*). An additional three predators of cod were predicted ($p > .75$), among which were the 'typical' Arctic marine mammals *Delphinapterus leucas* and *Monodon monoceros*.

The 2004–2007 Arctic food web contains 165 species that are connected through 926 documented feeding interactions (Figure 6). It has a connectance of 3.4% and a modularity of 0.343. Adding the 11 boreal species observed in the Arctic region in 2014–2017 to the Arctic food web, and based solely on their documented feeding interactions, increases the number of links to 1,365 and the connectance to 4.5%, whereas modularity decreases to 0.284. An additional 29 feeding links could be predicted

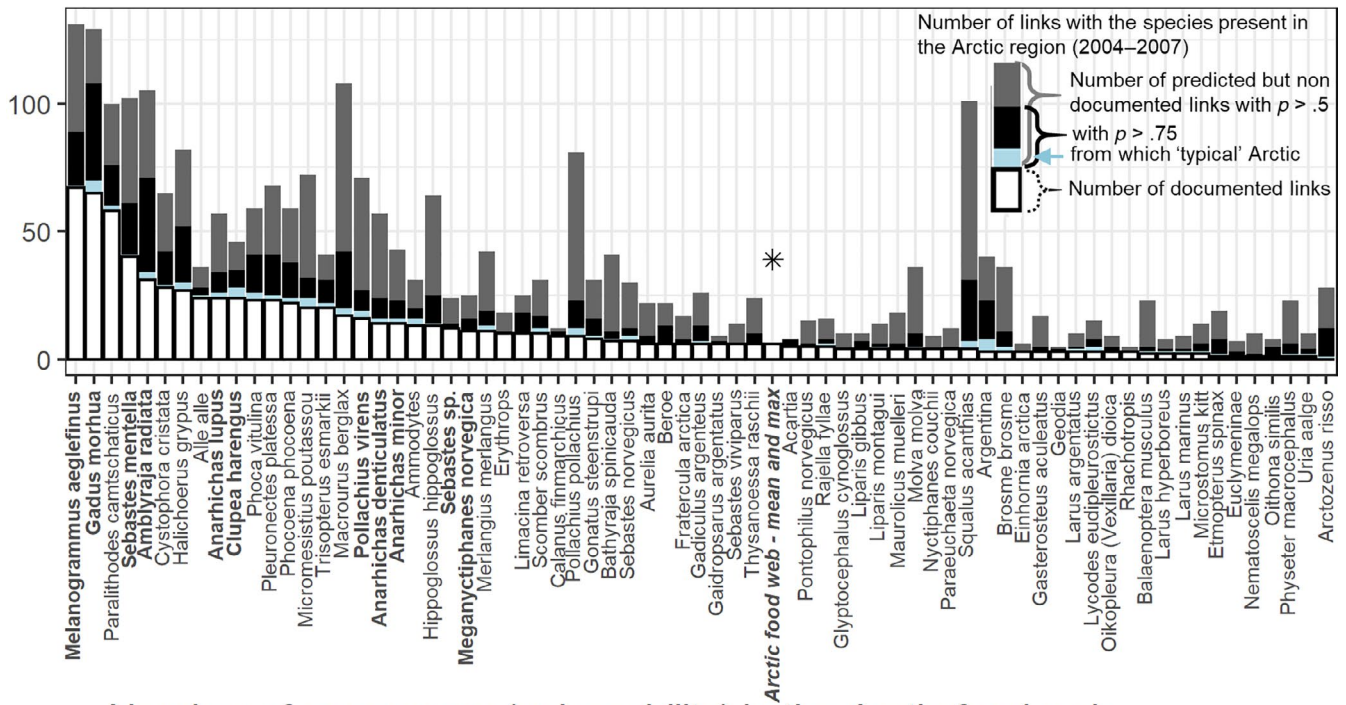
($p > .75$) between the incoming boreal species and the 13 'typical' Arctic species. These potential new feeding links between the incoming boreal species and the Arctic residents further increase the connectivity (4.6%) and decrease the modularity (0.278) of the Arctic food web.

4 | DISCUSSION

The Barents Sea is undergoing pronounced climate-driven environmental changes. The ecosystem is exposed to one of the highest rates of warming world-wide including an expansion of Atlantic water masses northwards, amplifying the 'Atlantification' of the Arctic region of the Barents Sea (Årthun, Eldevik, Smedsrud, Skagseth, & Ingvaldsen, 2012; Stern & Laidre, 2016). Many marine species appear to track these environmental changes by redistributing into the northern areas (Fossheim et al., 2015; Frainer et al., 2017), as well as extending their distribution in the whole Barents Sea (Jørgensen et al., 2019). The species that are most successful in entering the Arctic are generalist species (Frainer et al., 2017; Kortsch et al., 2015). In recent years (2014–2017), 11 boreal species were observed in the Arctic region. As species redistribute, and at distinct pace, it is important to account for the potential new interactions that might emerge when addressing the ecological implications of their range shifts.

Our results show that feeding interactions in the Barents Sea are largely structured by body size, a key trait known to shape marine food webs (Andersen et al., 2016; Cury, Shannon, & Shin, 2003; Eklöf et al., 2013). Consumer size was slightly more important than resource size for predicting interactions. As consumer size increases the size range of their resources increases, i.e. larger resources are added while smaller resources are kept in the diet. Several resource traits were also important, for example, the metabolic type of the resource was more informative than the consumer metabolic type. This might be due to a lower variability of metabolic type among the consumers or to

(a) Number of resources (generality) in the Arctic food web



(b) Number of consumers (vulnerability) in the Arctic food web

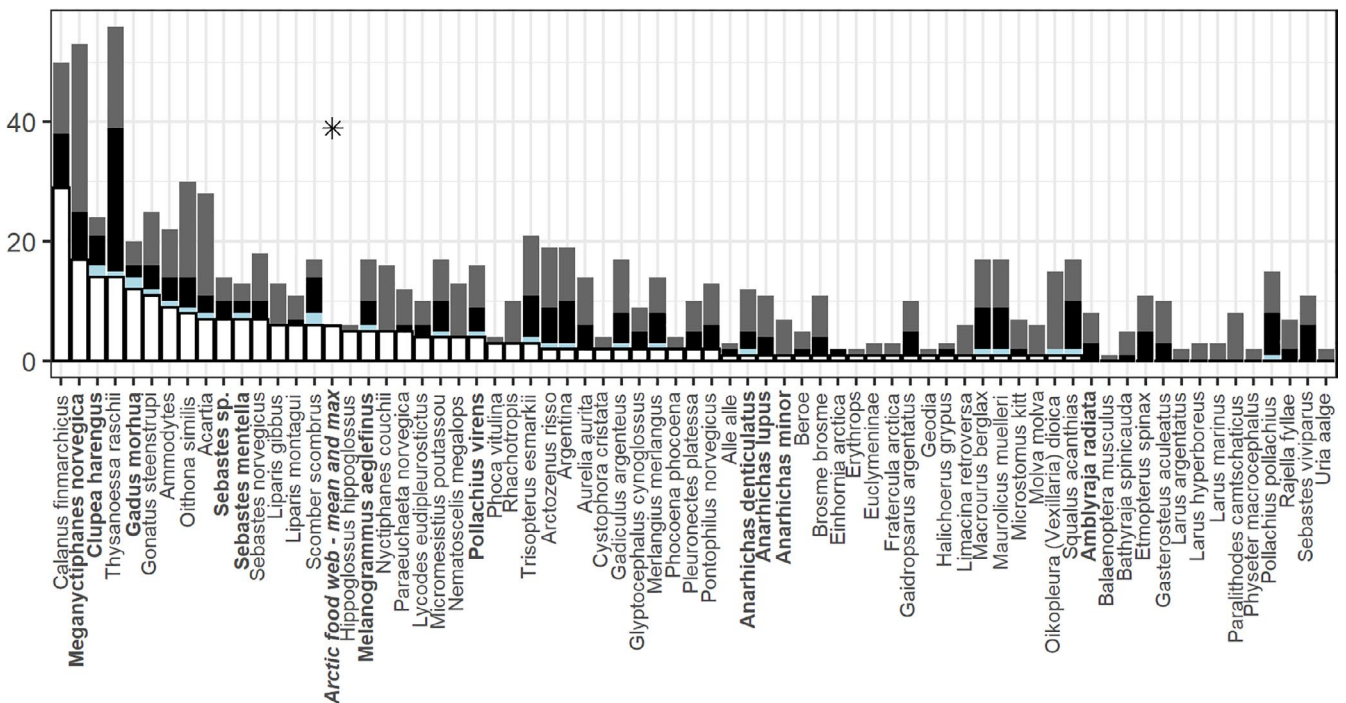


FIGURE 4 Potential trophic position of the boreal species in the Arctic food web in terms of (a) generality (number of resources) and (b) vulnerability (number of consumers) if they redistribute into the Arctic region. The number of resources and consumers is calculated based on their interactions with the 165 species present in the Arctic region in 2004–2007 (i.e. interactions between boreal species not taken into account). The species written in bold correspond to the 11 boreal species that have been observed in the Arctic ecosystem in the period 2014–2017. For comparison, we added the average and maximum (represented by an asterisk) number of resources and consumers of the non-basal species present in the Arctic food web

consumers preferentially feeding on a specific taxonomic group (e.g. consumer feeding only on invertebrates). Traits relating to habitat use, notably species distribution along the water column,

also helped to predict feeding interactions, exemplifying forbidden links between species that are spatially segregated (Olesen et al., 2011). Some other traits not included here could further

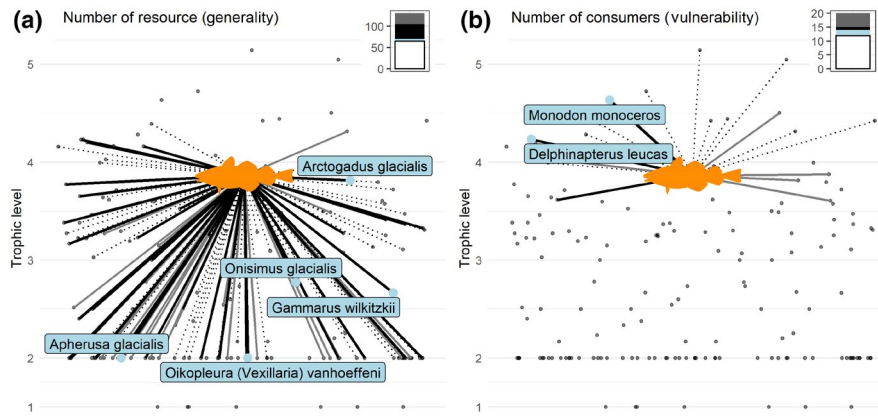


FIGURE 5 Example of trait-based feeding imputation for the boreal species cod *Gadus morhua*'s (a) generalism as a consumer and (b) vulnerability as prey. Lines indicate observed (dotted lines) and non-observed but predicted (solid lines) feeding links (with probability of $p > .5$ in grey and $p > .75$ in black). Each dot represents one of the 166 trophospecies present in the Arctic region. Labelled and highlighted in blue are the potential new feeding links ($p > .75$) that the incoming cod might form with the 'typical' Arctic species (i.e. species not found in the boreal region). The barplot inside the figures represents the cumulative number of links across the different categories (in white the number of observed links, in grey the non-documented but predicted among which $p > .75$ in black and the typical Arctic species in blue), see Figure 4 for the legend

determine the feeding interactions. For example, in addition to spatial uncoupling, phenological mismatch restricts species encounters and thus feeding interactions (Encinas-Viso, Revilla, & Etienne, 2012; Vizentin-Bugoni, Maruyama, & Sazima, 2014). Other predictors of feeding interactions could include trophic morphology (e.g. gape size), behavioural traits such as aggregation (Green & Côté, 2014) and migration.

Based solely on the documented diet information, seven boreal species would have only one or no resource in the Arctic food web, suggesting a food limitation to their establishment in the region. However, based on our trait matching analyses, we detected that all boreal species have probable resources present in the Arctic region. Some of these Arctic resources are already co-occurring with the boreal consumers, but trophic interactions have not been documented yet. The lack of documented feeding interactions in areas of co-occurrence might be due to boreal consumers having preferential alternative resources to feed on or to low abundances of the resource or consumer. When available, the integration of species abundance in network analyses could reveal important hidden features of food web structure (Olivier et al., 2019).

All boreal species had at least one potential resource in the Arctic region, therefore if they enter the Arctic ecosystem they can all possibly feed therein. Some of the predicted interactions between the Arctic species and incoming boreal species find support in recent literature. For example, the beluga (*D. leucas*), an Arctic marine mammal, is predicted to prey on several incoming boreal species and was indeed suggested to have started feeding on boreal prey (e.g. shift from polar cod to capelin; Vacquie-Garcia, Lydersen, Ims, & Kovacs, 2018). Another example is the boreal krill species *M. norvegica*, which was observed in the Arctic region in 2014–2017. Based on its traits, we predicted that this species could become a new resource for several species found in the Arctic. This is supported by

Eriksen et al. (2020) who found *M. norvegica* in the stomach of three Arctic fish species.

Food resources alone will not determine whether a boreal species can establish in the Arctic, as other factors can impede their success. For example, some boreal species might not survive in the Arctic if they are maladapted to the strong seasonal cycles at these high latitudes, such as the extreme light regimes (i.e. polar night and midnight sun) that can impede their feeding behaviour and success (Kaartvedt, 2008; Langbehn & Varpe, 2017). Other habitat properties could prevent the expansion of boreal species into the northern Barents Sea, such as water temperature, depth or sediment type (Husson, Certain, Filin, & Planque, 2020). In addition, just as the boreal species expand northward to track their environmental niche, some of the Arctic species studied here might also track their niche outside of the region and disappear locally. The latter is especially likely for ice-associated Arctic species whose abundances will decrease as the sea ice disappears under climate warming (Atkinson, Siegel, Pakhomov, & Rothery, 2004; Moore & Huntington, 2008). As a result of this spatial mismatch, some of the feeding interactions predicted here between boreal and Arctic species might never be realized.

Ten boreal fish species have been observed in the Arctic region in recent years (2014–2017). These boreal species have the characteristic of being generalists, with all of them having more documented resources present in the Arctic region than the average (non-basal) Arctic species. These species also have some of the highest number of documented Arctic resources among the boreal candidates to enter the Arctic (Figure 4). Larger and more generalist species, with a wide diet and habitat breadth, are in general more successful at invading and re-establishing in a native food web (Lurgi, Galiana, López, Joppa, & Montoya, 2014; Sunday et al., 2015), and are more likely to initiate novel feeding interactions in the local resource pool due to their resource flexibility (Ducatez, Clavel, & Lefebvre, 2015). On the contrary, specialist species may be more vulnerable to environmental

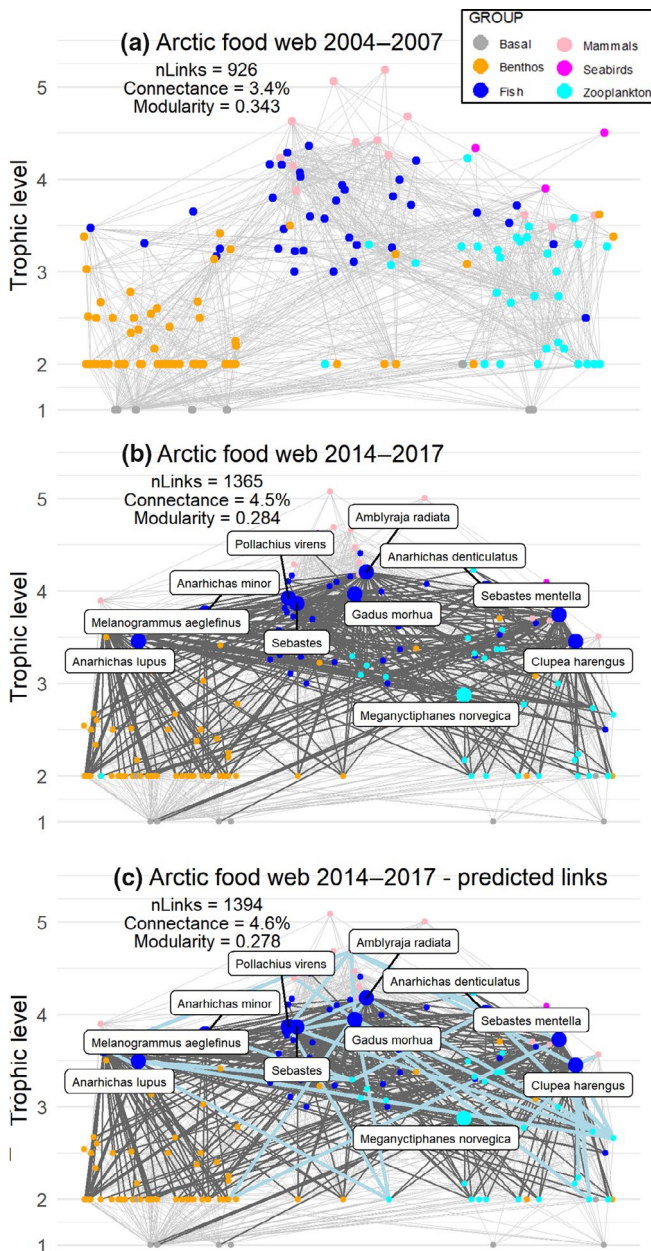


FIGURE 6 Changes in Arctic food web properties through the addition of documented and predicted new links associated with incoming boreal species. (a) Documented links (light grey lines) and properties of the Arctic food web representative of the 2004–2007 species composition (165 species) in the Arctic region. (b) Addition of 11 boreal species observed in the Arctic region in 2014–2017, represented by a larger dot and a name label, and their impact on the Arctic food web properties based on their documented links (dark grey lines). (c) Potential 29 new links (blue lines) could be initiated between the boreal and the ‘typical’ Arctic species and impact further the Arctic food web properties, based on the predicted ($p > .75$) but non-documented links obtained from the boosted regression trees models. nLinks refers to the total number of links. For visualization purposes the food web is organized around three species clusters (roughly corresponding from left to right to the benthic, benthopelagic and pelagic compartment) obtained by the function ‘cluster_springlass’ constrained to three clusters

change and the disappearance of their resources, resulting in a larger decline and extinction risk (Binzer et al., 2011; Lurgi et al., 2012). This increased abundance of generalist species, and the concurrent decline of specialist species have been observed in many ecosystems, and can result in large-scale homogenization of the communities (Clavel, Julliard, & Devictor, 2011; Ellingsen et al., 2020; Frainer et al., 2017; McKinney & Lockwood, 1999). This functional homogenization might impact ecosystem functioning (Tilman et al., 1997), and increase ecosystem vulnerability to further environmental disturbance (Olden, Poff, Douglas, Douglas, & Fausch, 2004).

The ability of the incoming generalist species to initiate feeding interactions with the Arctic residents might amplify their impact on the Arctic food web properties. Food web connectance influences food web topology and properties, with more connected food webs being more robust to perturbation (Dunne, Williams, & Martinez, 2002b). Here, the connectance of the Arctic food web increased due to the incoming boreal species, which could make the food web more robust to future perturbation. However, some of the incoming generalists feed on both pelagic and benthic resources, and thus connect more tightly the two compartments, decreasing food web modularity (Kortsch et al., 2015). Low food web modularity has been hypothesized to increase the vulnerability of a food web to perturbations (Stouffer & Bascompte, 2011). In a less modular Arctic food web, the effects of perturbations may spread more easily across modules with a greater overall impact on the ecosystem. The recent borealization of the Arctic ecosystem can be observed at the community level (Fosheim et al., 2015; Frainer et al., 2017), but also at the food web level, with the Arctic food web properties increasingly resembling those of the boreal food web (Kortsch et al., 2019). This borealization might drive a homogenization of regional food webs across the Barents Sea, which locally can increase ecosystem diversity and resilience, but regionally come at the expense of the overall food web diversity being lost.

In a time of rapid global change that causes extensive species redistributions, it is crucial to predict emerging feeding interactions that reorganize food webs and influence community dynamics and ecosystem functioning. Here, we used a machine learning model, trained on a metaweb of observed feeding interactions and associated resource-consumer traits, to predict the potential interactions between boreal and Arctic species. By predicting the probability of feeding interactions, our trait-based approach allows assessing and forecasting the effects of range shifts on food web ecology based on a few traits. Our study illustrates that species moving to a new ecosystem have the possibility to initiate feeding interactions with the local residents, and by doing so impact food web properties. Several studies have used trait-based modelling to predict species interactions under climate change (e.g. Albouy et al., 2014; Hattab et al., 2016), the novelty here resides in combining a regional empirical metaweb with a multi-trait modelling approach. Detection of feeding interactions by traditional approaches such as stomach content and isotope analyses, although fundamental, is cumbersome and cannot cope with the speed of global change, nor with the urgency of

understanding the consequences of species redistribution for the structure and functioning of marine ecosystems. We argue that merging a trait-based approach with ecological network analysis can be used to infer feeding interactions before they are realized and observed in situ, helping to predict the impact of range-shifting species on food web properties.

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DATA AVAILABILITY STATEMENT

The food web and trait data sets that support the findings of this study and the R code used to produce all findings will be made available in the Dryad Digital Repository.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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