Ecological resilience of Arctic marine food webs to climate change

Gary P. Griffith [1*], Haakon Hop[1,2], Mikko Vihtakari [3], Anette Wold[1], Kjersti Kalhagen [1] and Geir Wing Gabrielsen[1,4,5]

How real-world marine food webs absorb change, recover and adapt (that is, ecological resilience) to climate change remains problematic. Here we apply a novel approach to show how the complex changes in resilience of food webs can be understood with a small core set of self-organizing configurations that represent different simultaneously nested and multiple-species interactions. We identified a recent emergent pattern of an improving but possibly short-lived resilience of a highly observed Arctic marine food web (2004–2016), considered a harbinger of future Arctic change. The changes can be explained by continuing subsidiary inputs of Atlantic species that repair (self-organize) interactions within some configurations. Despite significant environmental perturbation, we found that the core ecological processes are maintained. We conclude that Arctic marine food webs can absorb and begin to adapt to ongoing climate change.

The resilience of marine food webs to ongoing climate change depends on the collective interplay of multiple simultaneous species interactions[1]. Unprecedented changes in the composition of Arctic food webs are resulting in novel interactions between incoming boreal species and resident Arctic species[2–4]. Observed changes in this region may therefore provide a 'road map' of the long-term sustainability of marine food webs and the human communities that depend on them[5,6]. To date, there is evidence of a reconfiguration of interactions[3,4] and possible regime shifts[7] within specific communities, in particular fish. The changes have both potential risks (for example, loss of biodiversity) and benefits (for example, commercially important fish)[5,8]. Of particular concern is that novel changes in individual species interactions may produce collective effects on food-web resilience that facilitates ecosystem-wide regime shifts and collapses[8,9]. However, it has remained difficult to elucidate how resilient the whole food web is to emerging changing species interactions. To arrive at a more fundamental understanding beyond a limited part of the food web, we can draw on the perspective of complex adaptive systems[1].

Food webs represent complex adaptive systems composed of species and trophic interactions that link the community together. Complexity theory assumes that the structure of food webs emerges from the dynamic self-organization of small-scale interactions[1]. Most complex systems are controlled by a limited number of small-scale interactions[9]. Consequently the whole system response may be understood through a core set of these processes[1,9]. Here we applied a complex adaptive systems[1] perspective to identify changes in the ecological resilience of a glacial fjord in the Arctic (Kongsfjorden, 79° N, 12° E (Supplementary Fig. 1)) subject to ocean warming, decreasing sea ice and increasing influx of Atlantic species[10]. We defined ecological resilience as the capacity of a food web to absorb, recover and adapt to changing conditions by the self-organization of core ecological processes[9]. To illustrate the changes in ecological resilience, we analysed observed food-web data with a new analytical approach based on exponential random graph models

(ERGMs)[11] that statistically find the core set of combinations of configurations of different simultaneous self-organizing species interaction processes that best explain the observed food web structure (Fig. 1). Configurations represent a new interpretation of subsets of species that interact more frequently among themselves than with other members of the food web, defined in the scientific literature as networks motifs[12] or trophic modules[13]. In contrast to previous interpretations of resilience based on the compartmentalization of subsets of species[14], configurations do not assume a low connectivity between the networks of species interactions. Rather, configurations describe patterns of more complex multiple and nested processes that operate simultaneously.

We first determined the core set of configurations that account for the different ecological processes that best represent the observed data from Arctic and Atlantic food webs as our null hypotheses of the representative structures of an Arctic or Atlantic marine ecosystem. We then identified the core set of configurations that best explained each annual food web (2004–2016) of the Kongsfjorden marine system. We identified the configurations with a new Bayesian analytical approach applied to ERGMs[15]. The previous study that applied this approach to real-world marine food webs showed two important limitations[16]. First, the analysis requires sufficient observational data to allow the connections between species to simultaneously self-organize into the set of configurations that can best explain the observed data. Second, the difficulty in some cases of the classical inferential methods using the Markov Chain Monte Carlo maximum likelihood (MCMC) or maximum pseudo-likelihood estimation (MPLE) to generate graph models that closely resemble the observed graph[11,15]. Practically, this means that the model may be unable to generate a set of configurations that can statistically reproduce the complex structural characteristics of the observed food-web data.

We addressed the quality and length of observational data using results from the Norwegian BarEcoRe[17] project and the Norwegian Government Environmental Monitoring of Svalbard and Jan Mayen

[1]Norwegian Polar Institute, Fram Centre, Tromsø, Norway. [2]Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economics, UiT The Arctic University of Norway, Tromsø, Norway. [3]Institute of Marine Research, Fram Centre, Tromsø, Norway. [4]Department of Arctic Biology, University Centre in Svalbard, Longyearbyen, Norway. [5]Department of Arctic Technology, University Centre in Svalbard, Longyearbyen, Norway. *e-mail: gary.griffith@npolar.no

(http://www.mosj.no/en/)[18]. We constructed food webs of predator–prey feeding interactions as unweighted (presence/absence) and directed networks in which the link (solid arrows in Fig. 1) is the direction of energy transfer from prey to predator. This resulted in three food webs: (1) Atlantic food web of ~180 species, (2) Arctic food web of ~150 species and (3) annual (2004–2016) food webs of up to 161 species present in Kongsfjorden.

To circumvent the limitations of the classical ERGM approach, we applied a Bayesian approach based on the exchange algorithm[19,20]. We first searched for a statistical model that comprised an ensemble of the core set of configurations that could best reproduce the structural characteristics of each observed food web. Second, we tested how well each model estimated the observed frequencies of the configurations of each observed food web that was explicitly modelled. A well-fitting statistical model therefore represents a plausible theoretical hypothesis for the most probable core set of ecological processes that best explains the complex observed food web structure[16].

Seven out of a possible 39 configurations (Supplementary Table 3 and Supplementary Fig. 1) explained the observed food webs (Fig. 2). The configurations corresponded to the ecological processes: (1) generalists[4], species that feed on a wide variety of prey species, (2) keystone[21,22] species with the highest number of direct interactions to predators and prey, (3) highly predated, species shared by several predators, (4) omnivory[23], species that feed on more than one trophic level, (5) tritrophic[24], species interactions between lower trophic (for example, zooplankton), mid-trophic (for example, small pelagic fish), intra-trophic (for example, squid) and upper trophic (for example, marine mammals), (6) apparent competition[25], indirect interactions between two or more prey species that serve as prey to a predator and (7) intraguild predation[12], a configuration that includes omnivorous interactions and also upper trophic larger predators, such as seabirds and marine mammals.

Six of the configurations (generalist, keystone, highly predated, tritrophic, omnivory and apparent competition) correspond to those previously identified for the Baltic Sea using a conventional ERGM approach[16]. Applying Bayesian inference, we identified an additional configuration of intraguild predation previously identified in qualitative network models[12]. Intraguild predation represents predator–prey interactions that account for a large number of feedback loops that involve lower trophic (copepods and krill), mid-trophic (pelagic amphipods, ctenophores and little auk), intra-trophic (pelagic fishes) and upper-trophic levels (seabirds, seals, whales and polar bear). In pelagic Arctic marine ecosystems, intraguild predation is of particular importance[26].

We interpret system-wide ecological resilience as the overall capacity of the food web to self-organize (and repair) (positive values) or not (negative values) to maintain core ecological processes despite changing conditions. (Fig. 1c). System-wide resilience is measured as the most probable estimate (average and standard error of the Bayesian estimation of the posterior distributions[15]) of the set of configurations that explains the observed food-web structure. The Bayesian estimation of the posterior distributions is the probability of the configuration with the uncertainty of the configuration based on the observational data[15]. Both the Arctic and Atlantic food webs that represent our null hypothesis had similar positive system-wide resilience (Fig. 3). In comparison, since 2006 the Kongsfjorden food web showed a change from highly positive to negative system-wide resilience around year 2006 (Fig. 3)[25]. Between 2009 and 2013, the system-wide resilience remained negative. From 2013, the system-wide resilience improved but remained slightly negative.

Next, we interpreted the changes in ecological resilience within each configuration as changes in local resilience, measured as the capacity of individual ecological processes to self-organize (repair) to maintain species interactions under changing conditions (Fig. 1d). Local resilience is measured as the most probable estimate
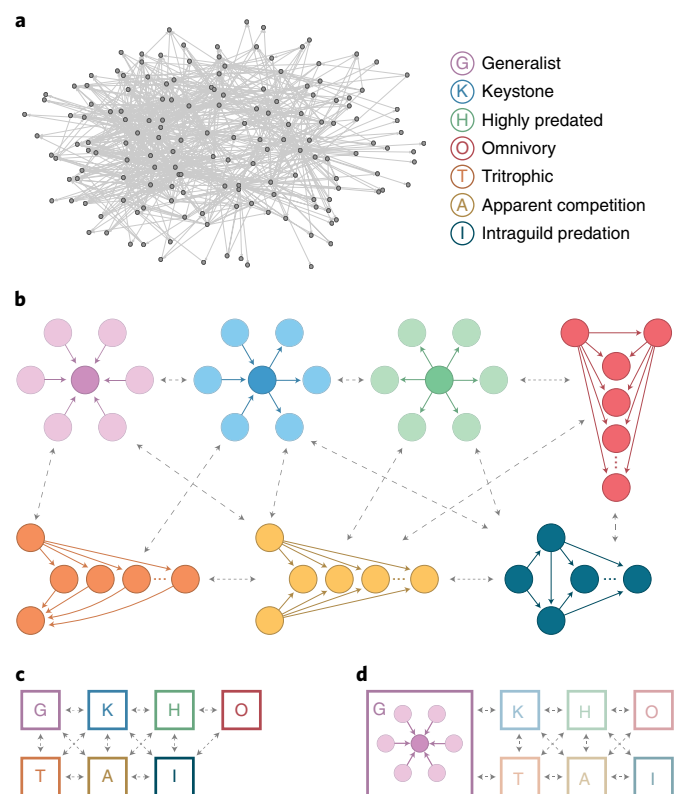
Fig. 1 | Conceptual framework of ecological resilience. a, Observed food web (Arctic) composed as an unweighted and directed network based on predator–prey interactions. The direction of energy transfer is from prey to predator (solid arrows). **b**, The core set of configurations that best explains the observed food web. Configurations represent different types of multiple and nested species interaction processes. **c**, System-wide ecological resilience results from the self-organization within and between all configurations to maintain the observed food web (dashed arrows). **d**, Local resilience results from the self-organization of species interactions within a configuration, given the presence of all other configurations.

(average and standard error of the Bayesian estimation of the posterior distributions[15]) of each individual configuration within the model to explain the observed food-web structure. Four of the configurations (generalist, keystone, key prey and intraguild predation) showed up to three transitions (positive to negative or negative to positive) in their capacity to self-organize. Keystone species interactions had the largest change, shifting from a significantly positive to a significantly negative local resilience. After 2012, local resilience within the keystone compartment showed a positive trend. Omnivory had a significantly positive local resilience, whereas apparent competition and tritrophic species interactions had a significantly negative resilience.
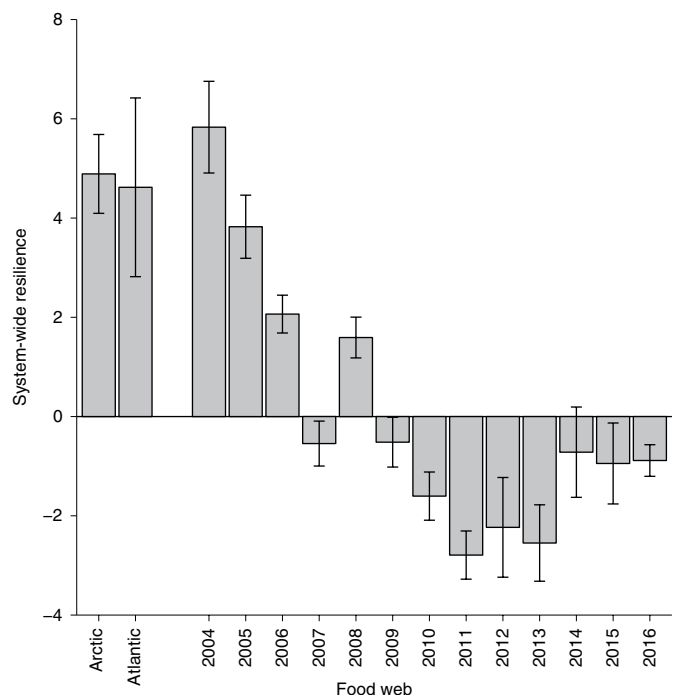
The consistency in the number and type of configurations, despite changes in species composition across all the marine food webs (Arctic, Atlantic and Kongsfjorden) was surprising. In particular, all the observed Kongsfjorden food webs could be explained by seven configurations of the core species interaction processes despite significant environmental changes and annual changes in species composition. That is, the response of system-wide predator–prey feeding interactions to the climate change effects was insufficient to transform the food web from being maintained by one set of mutually reinforcing functional ecological processes and structures to a different set of ecological processes and structures. A system-wide
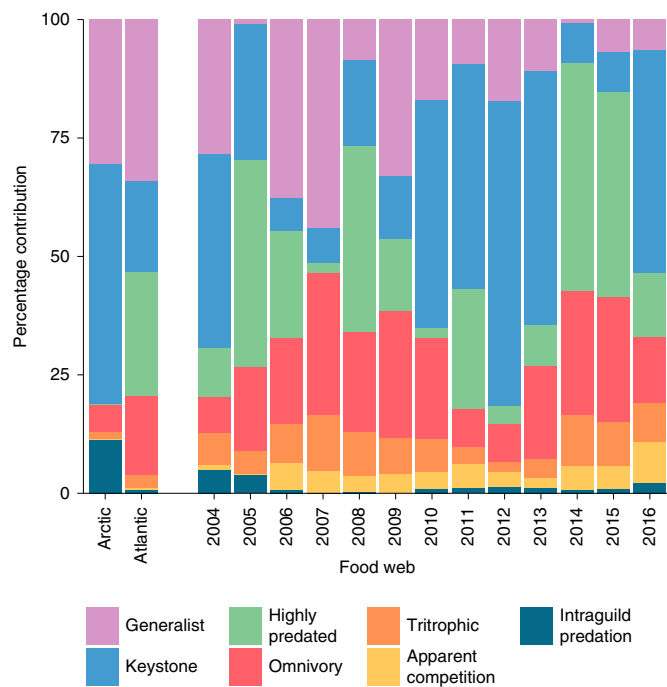
Fig. 2 | Core configurations of each observed food web. The percentage contribution of each of the core set of configurations (generalist, keystone, highly predated, omnivory, tritrophic, apparent competition and intraguild predation) of ecological processes that can explain the observed structures of the annual food webs.


Fig. 3 | System-wide ecological resilience. The changes in the ecological resilience of the observed Kongsfjorden annual food webs that emerge from the collective response of the core set of species interaction processes. The system-wide resilience of an Arctic and Atlantic food web are shown as a comparison. The error bars indicate the standard error for the most probable estimates. System-wide ecological resilience is the overall capacity of the food web to self-organize (and repair) (positive values) or not (negative values) to maintain core ecological processes in spite of changing conditions.

structural regime shift would be evidenced by one or more of the following. First, a smaller set of configurations that indicates a simpler food-web structure with biodiversity loss or loss of a core ecological process, such as a keystone Arctic species (for example, polar cod (*Boreogadus saida*)). Second, the inclusion or replacement with another configuration that represents a known ecological processes. For example, abundances of the Arctic seabirds, Brünnich's guillemot (*Uria lomvia*) and little auk (*Alle alle*) are declining[27]. This may alter the Arctic community structure for intraguild predation (combines aspects of both exploitive and apparent competition), which requires a configuration for exploitive competition. Third, the inclusion of a configuration to represent an emerging novel form of interaction. For example, additional feedback loops that may occur with increasing invasive large generalist fish species[28].

From a complex adaptive systems perspective, we did not interpret a system-wide structural regime shift. However, we found a significant decrease from positive to negative in the system-wide resilience of the Kongsfjorden food web between 2004 and 2011. The decline in the capacity of the ecosystem to self-organize and repair the core set of multiple and nested species interactions that comprise the food web corresponded to the influx of unusually large volumes of warmer Atlantic water in 2006–2008, which increased the mean winter temperature in Kongsfjorden by 2° C and decreased the winter sea-ice coverage in the region[29] (Supplementary Fig. 2). The change in system-wide resilience was driven by changes in the connectivity within the generalist, keystone and highly predated configurations (Fig. 4). We interpret this as a consequence of the observed sudden increased incidence of large Atlantic generalist and keystone fish species, such as Atlantic cod (*Gadus morhua*), which implies increased competition and predation pressure on Arctic species[3]. As the change has not been persistent, we do not interpret this as a system-wide regime shift. A system-wide regime shift requires a domino effect of a persistent and declining loss of local resilience that cascades to all the configurations[30]. Since 2011,

system-wide resilience has improved with an emerging pattern of repair of the species interactions within those configurations that previously showed a significant loss of local resilience. Although the 2° C increase in winter ocean temperature in 2006–2008 was not permanent and the degree of ice melting in the region varies interannually, 'Atlantification' of the fjord continues with a decadal trend (2004–2016) of declining ice cover, increasing influence of warm and saline Atlantic water and the appearance and persistence of species of Atlantic origin[31].

We found evidence of a recent emergent pattern of improving system-wide resilience that suggested an improvement in the adaptive capacity of the system to self-organize or repair to changing conditions (Fig. 3). We speculate that the low number and consistent configurations of core species interaction processes may be a generic resilience feature of the structure of marine food webs to withstand perturbations. Our additional interpretation is that a persistent level of core species interactions to maintain ecosystem-wide structure and function is always present. Intriguingly, the observed architecture of the Kongsfjorden food webs has maintained functional redundancy despite significant environmental changes. We conjecture that this may be positive news on the adaptive response of marine food webs to continuing climate change effects. We acknowledge, however, that we are interpreting the changes within the perspective of complex adaptive systems and consider only climate change effects over a relatively short time period of 12 years.

The recent emerging pattern of improvement in the system-wide resilience was driven by improvements in the capacity of three of the configurations (generalist, keystone and highly predated) to repair lost connectivity. We conjecture that the recent improvement
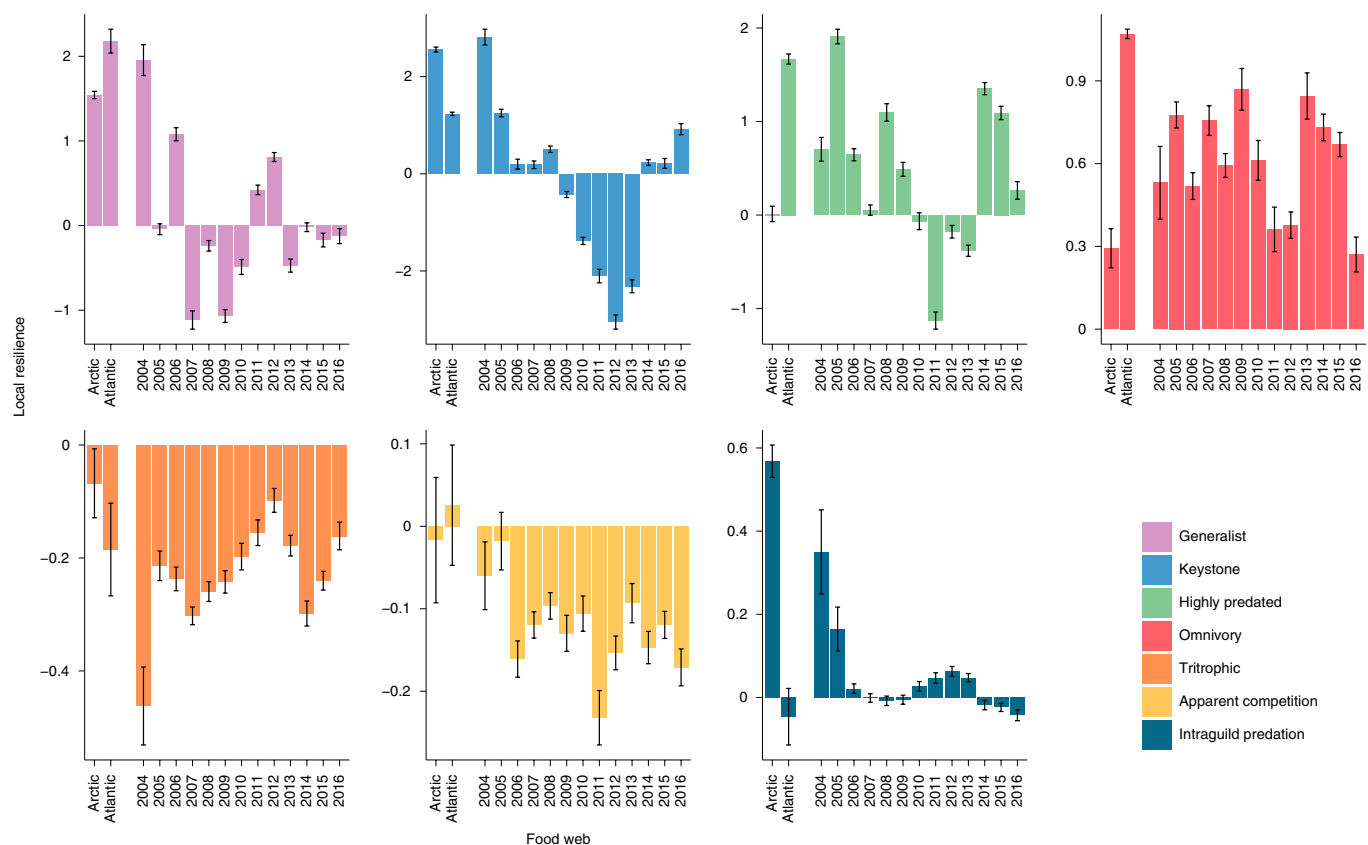
Fig. 4 | Local resilience. Changes in the local ecological resilience of core species interaction processes of the Kongsfjorden food web. Arctic and Atlantic are representative local resilience estimates for these food webs. The error bars indicate the standard error for the most probable estimates. Local resilience, is the capacity of individual ecological processes to self-organize (repair) to maintain their species interactions under changing conditions.

in resilience is driven by the continuing input of highly predated Atlantic species (for example, capelin (*Mallotus villosus*), zooplankton (*Calanus finmarchicus*) and krill (*Meganyctiphanes norvegica*)) that have feeding interactions within and across the four configurations. Complex adaptive systems theory predicts that the effects of perturbation on the connectivity within a configuration can be reduced or eliminated by subsidiary inputs[30,32]. The ability of highly connected systems to be saved by subsidiary inputs is observed in many systems, ranging from ecosystems to financial systems[30,33]. Counterintuitively, the reduction in local resilience of the intraguild predation, omnivorous and tritrophic species interactions may have assisted the improvement in system-wide resilience. Intraguild predation imposes persistent predation and competition pressures on mid-trophic groups[12]. The reduction in the importance of intraguild predation since 2012 implies a reduction in the predation and competition pressure on mid-trophic species. In addition, we noted a reduction in the contribution of tritrophic food chains to the food-web structure. The bottom-up regulation of the food web becomes stronger with a decrease in the number of tritrophic food chains[25]. The pelagic communities in the Arctic region of the Barents Sea and within the fjords on the west coast of Spitsbergen have become increasingly dominated by Atlantic zooplankton and capelin[34]. This has been hypothesized to increase bottom-up regulation with an increase in Atlantic prey availability that favours the Atlantic top predator species. An emerging pattern of increasing bottom-up regulation would also explain the improvement in local resilience of the highly predated and keystone configurations. It is important to note that our approach does not explain why species are altering their feeding interactions; this requires the integration of our approach with mechanistic approaches.

Although the recent improvement in ecological resilience could hint at the adaptation of species interactions within configurations and possibly the appearance of novel types of interactions, we have an alternative viewpoint that the positive trend in resilience may be short-lived. Polar species may not be able to shift their geographical range northward in response to the warming. They must either adapt or go extinct. Within Arctic fjords they may also retreat to glacial refuges or colder inner basins, for which there is some empirical evidence[35]. Alternatively, Arctic species may persist, as they have persisted in some fjords along mainland Norway[36], increasing the resilience of marine food webs in Arctic fjords by co-existing with Atlantic species. The combination of changing outer fjords with the influx of new species and polar species being retained within the inner basins, however, may provide a false impression of improved resilience. Both empirical and theoretical studies show that the same prerequisites of the heterogeneity of the configurations and their connectivity that allow recovery from perturbations may give a false impression of resilience, and in fact the system may actually be approaching a tipping point to a permanent system-wide regime shift[30,32]. As conditions change, the polar refuges will shrink and may then set up the system for a large-scale persistent collapse. That is, the loss of glacial refuges may initiate a systemic persistent change to an Atlantic food web structure or a novel emergent structure that comprises new species interaction and different core ecological processes.

There is also increasing mechanistic evidence that the input of these species causes a negative effect on food-web energetics. Marine mammals, such as the harp seal (*Pagophilus groenlandicus*) appear to decline in body condition with the poorer nutritional quality of Atlantic prey fish[37]. The pelagic community has become increasingly dominated by

energy (lipid fatty acid)-poorer Atlantic zooplankton species, which potentially reduces the bottom-up energetics[38]. However, an increase of the total amount and faster turnover of Atlantic zooplankton might counteract the reduction of more lipid-rich Arctic species[39]. The paradox between improving resilience and potentially reduced food web energetics shows that, although our approach reveals changes in ecological resilience, the outcome of species interactions beyond considerations of who eats whom is hard to predict.

There is a large uncertainty on how the interplay of changing species interactions with climate change effects is altering the structure and functioning of Arctic marine food webs. Our whole-system approach suggests the emergence of some positive changes in the ecological resilience of Arctic marine food webs. As the highly observed Kongsfjorden is recognized as a 'natural laboratory' of climate change in the Arctic[6], the results from our study may also be an indication of whole-system structural changes elsewhere in the Arctic. Key to predicting the effects of climate change on marine food webs is to incorporate the complex adaptive systems approach with existing mechanistic functional approaches, such as accounting for changes in whole-system energy pathways.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, statements of code and data availability and associated accession codes are available at https://doi.org/10.1038/s41558-019-0601-y.

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Author contributions

G.P.G. conceived the idea, methods and wrote the paper. All the co-authors contributed to the final version. G.P.G., H.H., G.W.G. and M.V. interpreted the results. M.V., K.K. and A.W. prepared the data.

Competing interests

The authors declare no competing interests.

Additional information

Methods

Food web data. We constructed two sets of food webs. First, a representative Arctic (159 species (Supplementary Table 1)) and Atlantic food web (180 species (Supplementary Table 2)) using the dataset were constructed from the Norwegian BarEcoRe project (http://www.esapubs.org/archive/ecol/E095/124/)[17]. The spatial coverage is the Barents Sea (68.5–82.58° N, 8.0–68.4° E) and the temporal coverage of the dataset was 1927–2015. We defined Arctic data as northeast and Atlantic data as southwest of the average position of the polar front (2004–2012), the main oceanographic demarcation that separates the Atlantic and Arctic biogeographical regions of the Barents Sea. Second, annual food webs 2004–2016, with up to 160 species in Kongsfjorden (79° N, 12° E), were constructed using observational data from the Norwegian Government Environmental Monitoring of Svalbard and Jan Mayen (http://www.mosj.no/en/)[18] annual surveys and specific Norwegian and international research projects conducted in the fjord. All food-web data were composed into species by species matrices with species as prey in rows and the same list of species as consumers in columns, and a '1' indicated that the species in the column consumes the species in the row.

Potential bias and limitations. Our food webs are biased by the uncertainties associated with the observational data available and food-web construction. To address this bias, we constructed our food webs based on the rigorous protocol and general methodology developed to construct the Barents Sea food webs for the BarEcoRe project[17]. The food-web topology includes components of the ecosystem from detritus to polar bears (Supplementary Tables 1 and 2). A trophospecies is defined as one or more species that share predators and prey. The relationship is directional from the prey to the predator. Each annual food web was constructed based on three primary sources: (1) observational survey data of Kongsfjorden (2004–2016) from the Norwegian Government Environmental Monitoring of Svalbard and Jan Mayen)[18], (2) peer-reviewed publications and institution reports and (3) discussions with institutional experts. Species were included if they had been observed that year within the fjord irrespective of sampling stations. Our data are seasonally biased to summer only, the main observational period for Arctic fjord monitoring.

Empirical random graph models. Our approach assumes that food webs are networks that consist of a set of species and relationships between them. The relationships are the directional feeding links between prey and predators. The food web structure is defined by a random adjacency matrix Y of a graph on n nodes (species) and a set of edges (relationships) $\{Y_{ij}: i = 1, \ldots n; j = 1, \ldots n\}$ where $Y_{ij} = 1$ if the pair (i,j) is connected, otherwise $Y_{ij} = 0$. Edges that connect a species to itself are not permitted, and hence $Y_{ii} = 0$. We analysed each food-web structure using ERGMs, a recently developed stochastic statistical network modelling approach founded on complexity theory[4]. The underlying hypothesis of these models is that edges (relationships) self-organize into small structures, termed configurations. An ERGM models the probability distribution function of the range of possible configurations within the network. The model then estimates the core set of configurations that can together give rise to the observed network structure. ERGMs represent the probability distribution of Y as:

$$\pi(y|\theta) = \frac{q\theta(y)}{z(\theta)} = \frac{\exp[\theta^t s(y)]}{z(\theta)}, \; z(\theta) = \sum_{y \in y} \exp[\theta^t s(y)]$$

where $s(y)$ is a known vector of statistics (for example, number of edges and so on) and $\theta \in \Theta$ are the model parameters $\theta_1, \ldots \theta_r$. The model parameters we applied are listed in Supplementary Fig. 1 and Supplementary Table 3. For instance, θ_1 (reciprocity A), θ_2 (in2star A), $\ldots$, $z(\theta)$ is a normalizing constant defined based on the graph space of networks of size n and the model parameters. Here, ERGM models are applied to find the core set of configurations of species interactions that can statistically explain each observed food-web structure. The analytical approach involves two steps. First, searching for the core combination of configurations out of all the possible configurations that will provide a well-fitting statistical model of the observed food web. In practice, ERGMs are difficult to handle statistically as y in the normalizing constant $z(\theta)$ consists of $2\binom{n}{2}$ possible undirected graphs[11,15]. The other issue is degeneracy that refers to a probability model defined by a certain value of θ that places most of its mass on a small number of graph topologies[15]. When the model is near degeneracy, classical inferential techniques using MCMC and MPLE are unlikely to generate networks close to the observed networks[15]. Our solution was to apply a Bayesian approximation using the exchange algorithm[19,20].

This circumvents the need to calculate the normalizing constant and significantly reduces degeneracy. Instead of obtaining the point estimates as in MCMC–MPLE, the Bayesian approximation generates the posterior distributions of the model parameters. Instead of the maximum likelihood estimation (MCMC–MPLE) and standard errors, point estimates and measures of uncertainty are calculated as averages and standard errors of each calculated posterior distribution. Second, we assessed how well the model captured the observed probability distribution functions of the various compartments. Classically, this is done by finding the best goodness of fit to the observed food-web structure. In contrast, for our Bayesian approach we used sample autocorrelation functions for different lags. All the ERGM analyses were performed with MPNET (V1.0) software (http://sna.unimelb.edu/PNet), Bergm (V4.1.0) (http://cran.r-project.org/web/packages/Bergm) and custom Matlab R2015a programs.

Analysis and model fit. Our empirical analysis aimed to find the most probable set of configurations that gave rise to the network structure of each observed food web of predator–prey (feeding) interactions. We examined a set of 39 configurations (Supplementary Fig. 1 and Supplementary Table 3). These represent all the possible combinations of pairwise feeding interactions from a simple one species feeding on another up to higher-order feeding interactions. All the analyses were performed with MPNET software (http://sna.unimelb.edu/PNet), Bergm (http://cran.r-project.org/web/packages/Bergm) and custom Matlab R2015a programs.

Steps to find core configurations. For each of the 16 observed food webs we employed the following steps to obtain the best fitting ERGM:

1. Using the observed presence/absence data for each food web, we composed a binary matrix of the feeding links between species,
2. We started to build the ERGMs by specifying the first model only with the simplest configuration (Arc in Supplementary Fig. 1). We then added additional configurations to the ERGM to see if this improved the posterior distribution of the model. In conventional ERGM, this is done by examining the changes in t ratios and Mahalanobis distance to obtain the combination of configurations with the best goodness of fit to the observed structure. We applied a Bayesian inferential framework that achieves fast convergence to yield parameter estimates consistent with all the observed food-web data using an exchange algorithm that overcomes the problem of sampling from a complicated posterior distribution with an intractable normalizing constant[15,19,20]. Although our approach overcomes the problems of the intractability of the normalizing constant and degeneracy, there is a computational bottleneck of the algorithm that has yet to be addressed. We carried out inference for up to 180 nodes in under 3 h on a Linux core processor of the STALLO supercomputer (https://www.sigma2.no/content/stallo).
3. During the analysis, we plotted the parameter draws of the posterior distribution using the exchange algorithm for each new iteration of the model and altered the proposal scaling to achieve better initial parameter values. That is, we aimed to reduce the autocorrelation between values. We also analysed autocorrelation and other potential indicators of critical transitions in the posterior distributions with the 'Early warnings signals toolbox' (https://cran.r-project.org/web/packages/earlywarnings).
4. We used sample autocorrelation functions, rather than goodness of fit for different lags up to a user-defined maximum. The maximum lag was set to the lag for which sample autocorrelation function was as close to zero as possible.
5. We tested for model stability by re-running the model. We also ran the model in reverse to examine the effect of removing configurations in the reverse order.

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The data used during the study are available at the Norwegian Polar Data Centre https://doi.org/10.21334/npolar.2019.4a851dd2 or are available from the corresponding author on reasonable request.

Code availability

The software code for the ERGM models is available from https://www.melnet.org.au/pnet and http://cran.r-project.org/web/packages/Bergm.

nature research

Corresponding author(s):   Gary Griffith

Reporting Summary

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Statistical parameters

When statistical analyses are reported, confirm that the following items are present in the relevant location (e.g. figure legend, table legend, main text, or Methods section).

n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒	An indication of whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☒	☐	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistics including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☒	☐	For null hypothesis testing, the test statistic (e.g. F, t, r) with confidence intervals, effect sizes, degrees of freedom and P value noted *Give P values as exact values whenever suitable.*
☐	☒	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated
☐	☒	Clearly defined error bars *State explicitly what error bars represent (e.g. SD, SE, CI)*

Our web collection on statistics for biologists may be useful.

Software and code

Policy information about availability of computer code

Data collection	Observational data were collated using Microsoft Excel 2013 and/or Matlab R2015a.
Data analysis	All analyses were performed with MPNET software (V1.0) (http://sna.unimelb.edu/PNet)and Bergm (V4.1.0)(http://cran.r-project.org/web/packages/Bergm) and Matlab R2015a

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:
- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

Data, analysis and software are available from the Norwegian Polar Data Centre https://doi.org/10.21334/npolar.2019.4a851dd2

Field-specific reporting

Please select the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences   ☐ Behavioural & social sciences   ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/authors/policies/ReportingSummary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Our study employs a Bayesian analysis using Empirical Random Graph Models.
Research sample	We used publicly available data of the presence/absence of species based on field data collected from numerous scientific expeditions. The two data sources are: 1) observational data (2004-2006) from the MOSJ (Norwegian Government Environmental Monitoring of Svalbard and Jan Mayen- http://www.mosj.no/en/) and 2) observational data from the Norwegian BarEcoRe project (http://www.esapubs.org/archive/ecol/E095/124/).
Sampling strategy	We used all available presence/absence of up to 180 species.
Data collection	The data were collected using a range of sampling strategies. See http://www.mosj.no/en/ and http://www.esapubs.org/archive/ecol/E095/124/ for specific details.
Timing and spatial scale	The Arctic and Atlantic food webs were constructed from observation data over the period 1927-2015. The spatial scale is 68.5 N to 82.58 N, 8.0 E to 68.4 E. The Kongsfjorden data cover the period 2004 to 2016. The spatial scale covers annual sampling locations within Kongsfjorden (79 N, 12 E).
Data exclusions	For the Arctic and Atlantic food webs trophospecies selection was done using four criteria: (1) there is information on trophic interactions, i.e., prey and/or predator/s are known; (2) the spatial extent of the species exceeds 5% of the total Barents Sea area; (3) the temporal extent is sufficient, i.e., the species has been observed in several instances over several years or seasons.
Reproducibility	All analysis and results are based on field observation only. In most cases this was the presence of a species based on a single observation. For some trophic levels data such as phytoplankton and zooplankton ,the data is based on triplicate casts at each survey point.
Randomization	This is not applicable to our study as it is based on the presence and absence of species and not on the abundance.
Blinding	Blinding is not relevant to our study as it based on the presence and absence of species noted in field observations.

Did the study involve field work?   ☒ Yes   ☐ No

Field work, collection and transport

Field conditions	The observational data from Kongsfjorden were collected annually from 2004 to 2016. Field conditions were typically Arctic and variable.
Location	For the Arctic and Atlantic food webs, the location is the Barents Sea (68.5 N to 82.58 N, 8.0 E to 68.4 E). For the Kongsfjorden food webs (79 N, 12 E),
Access and import/export	All data collected in Kongsfjorden are subject to the strict Norwegian Government collection protocols for each of the species. These are covered through the Svalbard Environmental Protection Act (https://www.regjeringen.no/en/dokumenter/svalbard-environmental-protection-act/id173945/) and the Arctic Monitoring and Assesment Programme (www.enviroment.no). The data for the Arctic and Atlantic food web were based on: T(1) peer reviewed publications; (2) gray literature and institutional reports; (3) inference on the basis of knowledge on similar species or comparable regions. No surveys or field work were conducted.
Disturbance	For the Kongsforden field data, any disturbance etc was minimized as required under the Svalbard Environmental Protection Act (https://www.regjeringen.no/en/dokumenter/svalbard-environmental-protection-act/id173945/).

Reporting for specific materials, systems and methods

Materials & experimental systems

n/a	Involved in the study
☐ ☐	Unique biological materials
☐ ☐	Antibodies
☐ ☐	Eukaryotic cell lines
☐ ☐	Palaeontology
☐ ☐	Animals and other organisms
☐ ☐	Human research participants

Methods

n/a	Involved in the study
☐ ☐	ChIP-seq
☐ ☐	Flow cytometry
☐ ☐	MRI-based neuroimaging

Unique biological materials

Policy information about availability of materials

Obtaining unique materials — *Describe any restrictions on the availability of unique materials OR confirm that all unique materials used are readily available from the authors or from standard commercial sources (and specify these sources).*

Antibodies

Antibodies used — *Describe all antibodies used in the study; as applicable, provide supplier name, catalog number, clone name, and lot number.*

Validation — *Describe the validation of each primary antibody for the species and application, noting any validation statements on the manufacturer's website, relevant citations, antibody profiles in online databases, or data provided in the manuscript.*

Eukaryotic cell lines

Policy information about cell lines

Cell line source(s) — *State the source of each cell line used.*

Authentication — *Describe the authentication procedures for each cell line used OR declare that none of the cell lines used were authenticated.*

Mycoplasma contamination — *Confirm that all cell lines tested negative for mycoplasma contamination OR describe the results of the testing for mycoplasma contamination OR declare that the cell lines were not tested for mycoplasma contamination.*

Commonly misidentified lines (See ICLAC register) — *Name any commonly misidentified cell lines used in the study and provide a rationale for their use.*

Palaeontology

Specimen provenance — *Provide provenance information for specimens and describe permits that were obtained for the work (including the name of the issuing authority, the date of issue, and any identifying information).*

Specimen deposition — *Indicate where the specimens have been deposited to permit free access by other researchers.*

Dating methods — *If new dates are provided, describe how they were obtained (e.g. collection, storage, sample pretreatment and measurement), where they were obtained (i.e. lab name), the calibration program and the protocol for quality assurance OR state that no new dates are provided.*

☐ Tick this box to confirm that the raw and calibrated dates are available in the paper or in Supplementary Information.

Animals and other organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research

Laboratory animals — *For laboratory animals, report species, strain, sex and age OR state that the study did not involve laboratory animals.*

Wild animals — *Provide details on animals observed in or captured in the field; report species, sex and age where possible. Describe how animals were caught and transported and what happened to captive animals after the study (if killed, explain why and describe method; if released, say where and when) OR state that the study did not involve wild animals.*

Field-collected samples — *For laboratory work with field-collected samples, describe all relevant parameters such as housing, maintenance, temperature, photoperiod and end-of-experiment protocol OR state that the study did not involve samples collected from the field.*

Human research participants

Population characteristics	*Describe the covariate-relevant population characteristics of the human research participants (e.g. age, gender, genotypic information, past and current diagnosis and treatment categories). If you filled out the behavioural & social sciences study design questions and have nothing to add here, write "See above."*
Recruitment	*Describe how participants were recruited. Outline any potential self-selection bias or other biases that may be present and how these are likely to impact results.*

ChIP-seq

Data deposition

☐ Confirm that both raw and final processed data have been deposited in a public database such as [GEO](#).

☐ Confirm that you have deposited or provided access to graph files (e.g. BED files) for the called peaks.

Data access links *May remain private before publication.*	*For "Initial submission" or "Revised version" documents, provide reviewer access links. For your "Final submission" document, provide a link to the deposited data.*
Files in database submission	*Provide a list of all files available in the database submission.*
Genome browser session (e.g. [UCSC](#))	*Provide a link to an anonymized genome browser session for "Initial submission" and "Revised version" documents only, to enable peer review. Write "no longer applicable" for "Final submission" documents.*

Methodology

Replicates	*Describe the experimental replicates, specifying number, type and replicate agreement.*
Sequencing depth	*Describe the sequencing depth for each experiment, providing the total number of reads, uniquely mapped reads, length of reads and whether they were paired- or single-end.*
Antibodies	*Describe the antibodies used for the ChIP-seq experiments; as applicable, provide supplier name, catalog number, clone name, and lot number.*
Peak calling parameters	*Specify the command line program and parameters used for read mapping and peak calling, including the ChIP, control and index files used.*
Data quality	*Describe the methods used to ensure data quality in full detail, including how many peaks are at FDR 5% and above 5-fold enrichment.*
Software	*Describe the software used to collect and analyze the ChIP-seq data. For custom code that has been deposited into a community repository, provide accession details.*

Flow Cytometry

Plots

Confirm that:

☐ The axis labels state the marker and fluorochrome used (e.g. CD4-FITC).

☐ The axis scales are clearly visible. Include numbers along axes only for bottom left plot of group (a 'group' is an analysis of identical markers).

☐ All plots are contour plots with outliers or pseudocolor plots.

☐ A numerical value for number of cells or percentage (with statistics) is provided.

Methodology

Sample preparation	*Describe the sample preparation, detailing the biological source of the cells and any tissue processing steps used.*
Instrument	*Identify the instrument used for data collection, specifying make and model number.*
Software	*Describe the software used to collect and analyze the flow cytometry data. For custom code that has been deposited into a community repository, provide accession details.*
Cell population abundance	*Describe the abundance of the relevant cell populations within post-sort fractions, providing details on the purity of the samples and how it was determined.*

| Gating strategy | *Describe the gating strategy used for all relevant experiments, specifying the preliminary FSC/SSC gates of the starting cell population, indicating where boundaries between "positive" and "negative" staining cell populations are defined.* |

☐ Tick this box to confirm that a figure exemplifying the gating strategy is provided in the Supplementary Information.

Magnetic resonance imaging

Experimental design

Design type	*Indicate task or resting state; event-related or block design.*
Design specifications	*Specify the number of blocks, trials or experimental units per session and/or subject, and specify the length of each trial or block (if trials are blocked) and interval between trials.*
Behavioral performance measures	*State number and/or type of variables recorded (e.g. correct button press, response time) and what statistics were used to establish that the subjects were performing the task as expected (e.g. mean, range, and/or standard deviation across subjects).*

Acquisition

Imaging type(s)	*Specify: functional, structural, diffusion, perfusion.*
Field strength	*Specify in Tesla*
Sequence & imaging parameters	*Specify the pulse sequence type (gradient echo, spin echo, etc.), imaging type (EPI, spiral, etc.), field of view, matrix size, slice thickness, orientation and TE/TR/flip angle.*
Area of acquisition	*State whether a whole brain scan was used OR define the area of acquisition, describing how the region was determined.*

Diffusion MRI   ☐ Used   ☐ Not used

Preprocessing

Preprocessing software	*Provide detail on software version and revision number and on specific parameters (model/functions, brain extraction, segmentation, smoothing kernel size, etc.).*
Normalization	*If data were normalized/standardized, describe the approach(es): specify linear or non-linear and define image types used for transformation OR indicate that data were not normalized and explain rationale for lack of normalization.*
Normalization template	*Describe the template used for normalization/transformation, specifying subject space or group standardized space (e.g. original Talairach, MNI305, ICBM152) OR indicate that the data were not normalized.*
Noise and artifact removal	*Describe your procedure(s) for artifact and structured noise removal, specifying motion parameters, tissue signals and physiological signals (heart rate, respiration).*
Volume censoring	*Define your software and/or method and criteria for volume censoring, and state the extent of such censoring.*

Statistical modeling & inference

| Model type and settings | *Specify type (mass univariate, multivariate, RSA, predictive, etc.) and describe essential details of the model at the first and second levels (e.g. fixed, random or mixed effects; drift or auto-correlation).* |
| Effect(s) tested | *Define precise effect in terms of the task or stimulus conditions instead of psychological concepts and indicate whether ANOVA or factorial designs were used.* |

Specify type of analysis: ☐ Whole brain   ☐ ROI-based   ☐ Both

| Statistic type for inference (See Eklund et al. 2016) | *Specify voxel-wise or cluster-wise and report all relevant parameters for cluster-wise methods.* |
| Correction | *Describe the type of correction and how it is obtained for multiple comparisons (e.g. FWE, FDR, permutation or Monte Carlo).* |

Models & analysis

n/a	Involved in the study
☐	Functional and/or effective connectivity
☐	Graph analysis
☐	Multivariate modeling or predictive analysis

Functional and/or effective connectivity

Report the measures of dependence used and the model details (e.g. Pearson correlation, partial correlation, mutual information).

Graph analysis

Report the dependent variable and connectivity measure, specifying weighted graph or binarized graph, subject- or group-level, and the global and/or node summaries used (e.g. clustering coefficient, efficiency, etc.).

Multivariate modeling and predictive analysis

Specify independent variables, features extraction and dimension reduction, model, training and evaluation metrics.