Arctic ecosystem structure and functioning shaped by climate and herbivore body size

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Significant progress has been made in our understanding of species-level responses to climate change, but upscaling to entire ecosystems remains a challenge[1,2]. This task is particularly urgent in the Arctic, where global warming is most pronounced[3]. Here we report the results of an international collaboration on the direct and indirect effects of climate on the functioning of Arctic terrestrial ecosystems. Our data from seven terrestrial food webs spread along a wide range of latitudes (∼1,500 km) and climates (∆ mean July temperature = 8.5 °C) across the circumpolar world show the effects of climate on tundra primary production, food-web structure and species interaction strength. The intensity of predation on lower trophic levels increased significantly with temperature, at approximately 4.5% per °C. Temperature also affected trophic interactions through an indirect effect on food-web structure (that is, diversity and number of interactions). Herbivore body size was a major determinant of predator–prey interactions, as interaction strength was positively related to the predator–prey size ratio, with large herbivores mostly escaping predation. There is potential for climate warming to cause a switch from bottom-up to top-down regulation of herbivores. These results are critical to resolving the debate on the regulation of tundra and other terrestrial ecosystems exposed to global change[4–6].

The Anthropocene is characterized by exceptional environmental changes, leading to biodiversity loss and alterations in ecosystem functioning[7]. An estimated 37% of all terrestrial ecosystems may undergo biome-scale disruption of their structure and functioning during the twenty-first century[8]. Yet, forecasting the effects of climate change at the ecosystem level is challenging[1,2,9]. One approach is to search for general rules based on body size and temperature that could control food-web structure and dynamics[2,10,11]. Metabolic demand, which increases allometrically with body size, is known to influence a large array of biological processes[10]. For instance, biodiversity and interaction strength (the net effect of a species on another through both direct and indirect pathways[12]) generally increase with temperature and relatively smaller organisms are found at lower latitudes[2,10]. Scaling relationships between body size, temperature and metabolic rate are well known, but no studies have investigated whether these properties can be used to predict ecosystem processes[2,13]. Moreover, at present, empirical evidence for such scaling relationships is dominated by studies on ectotherms[14].

Nowhere else on Earth is the rate of global warming more pronounced than in the Arctic[3]. Climate warming is already affecting tundra ecosystems[15], but a comprehensive assessment of climate effects is hampered by our lack of understanding of fundamental mechanisms controlling food webs. Determining the relative importance of top-down versus bottom-up controls remains an epic debate in terrestrial ecology[4]. One view holds that the tundra is relatively uniform and dominated by plant–herbivore interactions due to low primary productivity[5]. An increasing number of studies, however, show that predator–prey interactions can also play an important role in controlling the tundra food web in a top-down manner[16]. A reconciliation of these contrasting perspectives is required for accurate predictions of the response of Arctic ecosystems to global warming. This could potentially lead to generalization of climate effects on species interactions across biomes[17].

We propose a conceptual framework linking climate and terrestrial ecosystem functioning to resolve the debate on the regulation of tundra ecosystems (Fig. 1). We hypothesize that a warmer climate can affect ecosystem functioning (or ecosystem properties[18]) through enhanced primary production[19]. Plant production is dependent on temperature, especially in cold environments, and recent increases in plant production with global warming have been documented in the Arctic[20]. We also hypothesize that temperature can affect ecosystem functioning through changes in food-web structure and species interactions[2]. These effects may be mediated by climate-induced changes in

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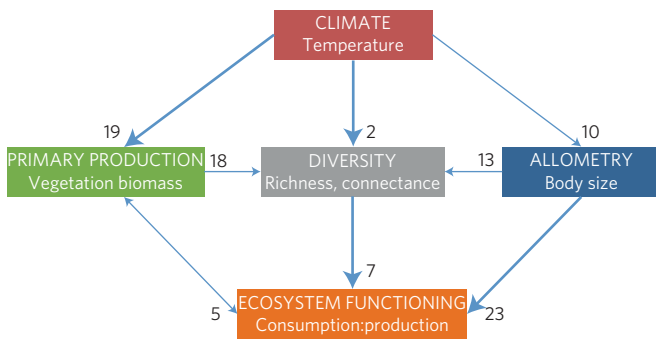
Figure 1 | Conceptual framework linking temperature and ecosystem functioning. Uppercase words indicate concepts and lowercase words indicate metrics used here (Methods). For each potential effect, numbers relate to references at the end. Ecosystem functioning was assessed by calculating C:P ratios, which represent the fraction of the production that is removed to satisfy the energetic demands of consumers. Thick lines show significant relationships found in this study.

community composition[2] and/or body size distribution[2,10] and interaction strength among species[9]. In particular, body size distribution is a fundamental property of ecological communities, which drives energy flows in ecosystems[21] and in turn can be influenced by climate through range shifts and metabolic constraints[13]. To study potential cascading effects of climate on trophic interactions, we combined standardized data from seven study sites monitored during the International Polar Year (IPY; 2007–2009, Fig. 2a). Our sites differ greatly with respect to temperature and species composition, allowing us to investigate the global effects of climate on plant–herbivore and predator–prey interactions.

Primary productivity of vascular plants was positively related to summer temperature, although the relationship was marginally significant ($n = 21$: three groups of vascular plants per site; $r = 0.41$, $P = 0.06$), whereas mosses and lichens did not respond or tended to decline ($r = -0.27$; $P = 0.39$). Similar patterns were previously reported using a larger number of study sites[22]. Temperature was also strongly related to several structural food-web properties through physiological or biogeographical constraints. Specifically, the number of all functional groups (S; Supplementary Table 1) and connectance among these groups (number of links/S^2) were strongly related to July temperature ($n = 7$; $r = 0.89$, $P = 0.007$), with more complex and diverse food webs in warmer locations. Although our sites cover the range of typical Arctic wildlife species, species composition nonetheless differs among sites. For example, no large herbivores (reindeer *Rangifer tarandus* and muskox *Ovibos moschatus*) occur on Bylot Island and the Svalbard food web is the only one where lemmings are absent. Some species, such as the grizzly bear (*Ursus arctos horribilis*), wolverine (*Gulo gulo*) and red fox (*Vulpes vulpes*), are restricted to the most southerly locations. This explains the observed lack of relationship between body size and temperature ($n = 7$; $r = 0.59$, $P = 0.17$ and $r = 0.40$, $P = 0.37$ for skewness and median body size, respectively).

We investigated the relative importance of herbivory and predation along our climatic gradient by building mass-balanced food-web models. We estimated plant and herbivore consumption:production ($C:P$) ratios[16] and predator–prey interaction strengths[12]. For each species, the $C:P$ ratio represents the proportion of its net annual production that is consumed by higher trophic levels (Methods). A high $C:P$ ratio indicates elevated consumption (that is, high herbivory or predation) relative to production and hence a strong trophic interaction. We examined the relationship of plant–herbivore and predator–prey interactions with temperature. Theory predicts that the strength

of plant–herbivore interactions should decrease with temperature and that the reverse should be true for predator–prey interactions[5]. Indeed, owing to a higher primary productivity, food webs at warmer sites should have a higher density of predators, which may in turn depress herbivore abundance[5]. We found strong predator–prey interactions across a wide temperature gradient (Fig. 2b). Nonetheless, as predicted, we found that predation was stronger at warmer sites as $C:P$ ratios of herbivores, consumed by either mammalian or avian predators, increased significantly with July temperature (Supplementary Table 2; an increase of one degree resulted in a $C:P$ ratio increase of 4.5% $\pm$ 2.0 s.e.m. on average). $C:P$ ratios of herbivores at the three northernmost sites (Alert, Svalbard and Zackenberg) were only about half those of the three southernmost ones (Fig. 2b). Similarly, herbivory ($C:P$ ratios of vascular plants consumed by herbivores) tended to decrease at warmer sites, where productivity was highest (Fig. 2b; $\beta = -0.013 \pm 0.006$ s.e.m.). $C:P$ ratios of Bylot Island, a relatively high-latitude site, tended to be more similar to those of more southern sites, possibly owing to the lack of large herbivores at this site (see below).

As body size distribution is expected to vary with temperature (Fig. 1), we also investigated the relationship between body size, predator–prey interaction strength and temperature. Studies in African savannahs suggest that large herbivores can escape predation and be more resource-limited than small herbivores[23]. We found that body size was an important feature driving trophic interactions across the different sites (Supplementary Table 2). $C:P$ ratios of herbivores were significantly related to their body size (Fig. 3) as small herbivores such as lemmings (*Lemmus* and *Dicrostonyx*), ptarmigan (*Lagopus*) and geese (*Anser* and *Branta*) were more impacted by predation than larger ones such as reindeer and muskox. The impact of predation started to decrease for herbivores > ~1 kg. Furthermore, the highest $C:P$ ratios were found at intermediate body sizes (ptarmigan, hares or geese), which suggests the presence of some predator refuges for small rodents. In addition to our sensitivity analyses based on resampling (to account for parameter uncertainties; see Supplementary Information), we also ran models by increasing ermine abundance by a factor of 40 to account for uncertainty about ermine density in response to high fluctuations in lemming abundance. The hump-shaped predation pattern was maintained regardless of the density of ermine used, suggesting that our pattern was robust to those uncertainties (Supplementary Table 2).

The climate-related patterns in community composition also affected predator–prey interactions. Indeed, the strength of predator–prey interactions increased significantly with the predator–prey body size ratios (Supplementary Table 3 and Fig. 4) such that large predators had a greater impact on smaller than on larger prey. Interaction strength, however, was not related to temperature but was instead site-specific (Supplementary Table 3). Although studies on this topic in terrestrial ecosystems are scarce[14], the absence of a direct relationship between temperature and interaction strength suggests that terrestrial food webs dominated by endotherms may be physiologically less dependent on temperature than freshwater or marine food webs dominated by ectotherms[24].

Our results revealed a strong relationship between $C:P$ ratios and temperature in terrestrial ecosystems and shed some light on the long-standing debate of top-down versus bottom-up control of Arctic ecosystems[6]. The main differences among our study sites, besides latitude and temperature, were their predator–prey biomass ratios and body size distributions within and across trophic levels. Overall, we found that in the tundra biome, the strength of predation and herbivory was modulated by summer temperature and body size. Specifically, large herbivores seem to be mainly limited by primary production as the top-down control
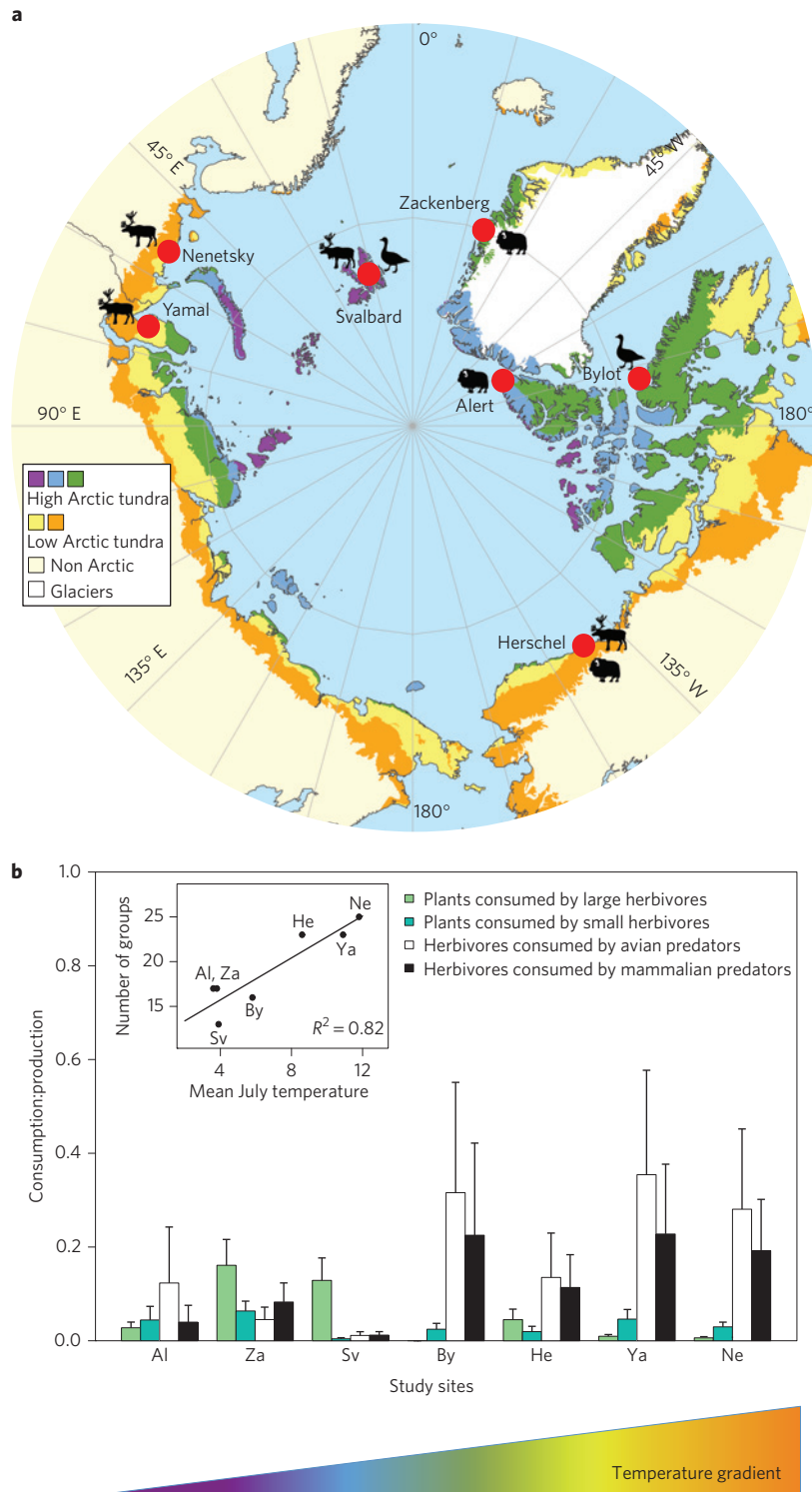
Figure 2 | Consumption rates across Arctic tundra study sites. a, Arctic tundra study sites (red dots on the map). Pictograms represent the most abundant herbivores for each site. Background map of bioclimatic zone is derived from maximum Normalized Difference Vegetation Index (NDVI) values[28]. **b**, Barplot (median + median absolute deviation from the sensitivity analysis; see Supplementary Information for details) of the *C:P* ratios according to sites. *C:P* ratios of plants were split according to the size of herbivores consuming them and *C:P* ratios of herbivores according to the predator types. Sites are ranked in increasing order of average July temperature. Relationship between richness (number of functional groups per site) and temperature is presented in the inner graph. Al, Alert; Za, Zackenberg; Sv, Svalbard; By, Bylot; He, Herschel; Ya, Yamal; Ne, Nenetsky.

by predators weakened considerably with increasing herbivore body size, probably because large herbivores can escape predation to some extent. As the distribution of herbivore body size was independent of temperature in our data, an increase in predation

pressure on small herbivores was responsible for the strengthening of the predator–prey interaction with temperature. Although our study sites captured most of the structural complexity in Arctic terrestrial ecosystems, we recognize that our analysis is based on
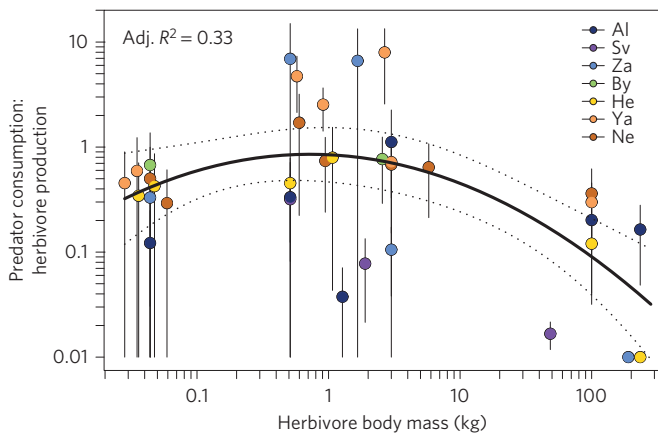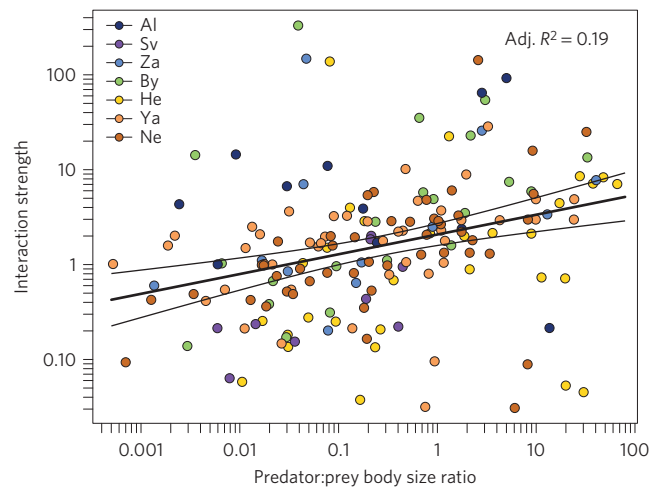
Figure 3 | Consumption rates and body size in the Arctic tundra.
Relationship between the predator–prey *C:P* ratio (median ± median absolute deviation from the sensitivity analysis; see Supplementary Information for details) and herbivore body size across study sites. Data points correspond to each herbivore taxon. The fitted curve (±95% confidence interval; dotted lines) represents the most parsimonious model (Supplementary Table 2). Abbreviations refer to study sites (Fig. 2). *x* and *y* axes are presented on a log scale.

Figure 4 | Interaction strength and body size in the Arctic tundra.
Relationship between per capita interaction strength (direct and indirect effect of consumption) and predator:prey body size ratio (using body mass as a metric), weighted by the prey proportion in the diet. Individual data points correspond to each pairwise predator–prey interaction at all sites. The fitted curve (±95% confidence interval; light black lines) is derived from the most parsimonious model (model selection is shown in Supplementary Table 3). Abbreviations refer to study sites (Fig. 2). *x* and *y* axes are presented on a log scale.

only seven sites, a relatively small sample. However, these sites were spaced out across most biogeographic regions of the circumpolar world and separated by >1,000 km in all cases but one, thereby ensuring independence among sites. Our multi-site approach is a first step towards a complete understanding of species interactions in response to climate changes[17].

Our results echo empirical studies conducted in other terrestrial ecosystems such as African savannahs, where the relative influence of predators or resources on herbivore abundance closely depends on herbivore body size[23]. Both ecosystems are also exposed to extreme seasonal bottlenecks (due to drought or temperature) that might impose similar constraints. However, given that Arctic tundra and African savannah ecosystems are so different in terms of structural complexity and productivity, finding a close match in the determinants of their functioning further emphasizes that body size may be a dominant factor explaining food-web structure and dynamics. Our results further reconcile classical studies on trophic regulation[5] with more recent ones that indicate a strong latitude-dependent predation risk[25] in tundra birds. Our circumpolar data set revealed that, although the impact of predation is lower at the highest latitudes, predation predominates over much of the tundra. This suggests a larger role for predation as a structuring force in the tundra biome than previously acknowledged.

Our objective was to understand the response of terrestrial Arctic ecosystems to climatic variations and test for possible relationships between climate and ecosystem functioning (Fig. 1). We found that climate may actually control food-web structure, species interactions and hence functioning of the tundra ecosystem. Strong direct relationships between ambient temperature and interaction strength had previously been reported but were largely based on studies in ectotherms[14], a group where metabolic rate and intake rate are closely related to ambient temperature[10]. Here, we did not find such direct relationships, possibly because our consumers were all endotherms whose metabolism may be affected differently by temperature than ectotherms. We propose an alternative mechanism (Fig. 1) by which temperature influences community structure (that is, species composition and connectance)[26], which in turn affects interaction strength (partly constrained by herbivore body size) and thereby ecosystem functioning. We suggest that the influence of temperature on ecosystem functioning is mediated by predation and that the most significant effects of the present

warming of the Arctic[3] on the tundra biome will be indirect. Our hypothesis is supported by empirical data and provides a broad-scale model[17] to better understand and predict the effects of rapid environmental changes on the strength of key ecological processes such as herbivory and predation.

Methods

Food-web models. Empirical data used to model food webs (see Supplementary Fig. 1 for the food web at each site) came mostly (79% of all data) from two IPY research programmes (ArcticWOLVES and Arctic Predators) conducted with similar standardized protocols across our circumpolar field sites from 2007 to 2009 (details are provided in Supplementary Table 4). We used average estimates of abundance over years to allow comparison among sites because herbivores and predators fluctuate both seasonally and annually. We built a mass-balanced food-web model similar to the one used in Ecopath[29], which had been successfully applied to one of our study sites in the past, Bylot Island[16]. In short, the model describes trophic flows within the food web with the following master equation:

$$\frac{dB_i}{dt} = \underbrace{\left(\frac{p}{m}\right)_i B_i}_{P} - \underbrace{\sum^i \left[DC_{ij}\left(\frac{q}{m}\right)_j B_j\right]}_{C} \qquad (1)$$

where B_i is abundance (kg km^{-2}) of species i, $(p/m)_i$ is the production rate (yr^{-1}) of species i per unit of biomass (m is the mass of a species), DC_{ji} is the proportion of species i in the diet of predator j and $(q/m)_j$ is the consumption rate (requirements in yr^{-1}) of predator j per unit of biomass. We used allometric relationships to determine production and consumption rates[9] to maintain consistency across the food webs. Using allometrical or empirical relationships to estimate p or q did not affect our estimates of predation and herbivory that came out from the detailed modelling of the Bylot Island food web[16]. We investigated the relative importance of consumption at each trophic level by calculating a *C:P* (equation (1)) ratio, representing the fraction of the production at a given trophic level (for example, plants) that is used to satisfy the energetic demands of consumers at the next trophic level (for example, herbivores). *C:P* ratios were calculated for each group of plants or species of herbivore or predator in the system. We adjusted the *C:P* ratio of plants to take into account annual senescence. In most Arctic plants, when senescence begins in autumn, some material is lost but most soluble nutrients are translocated to basal stems or belowground reserves as an adaptation to the harsh environment[16]. To account for plant senescence, we considered that vascular plant production was available only during frost-free days. Although this extreme situation may have artificially inflated the impact of herbivory for resident species,

this means that our results are robust with respect to the role of herbivory in our food webs.

Modelling interaction strength. The Ecopath model is a particular application of the general Lotka–Volterra model, a more conventional model in theoretical ecology[30]. We translated parameters of the Ecopath model into interaction coefficients of the Lotka–Volterra interaction equation following the approach of ref. 27. We obtained the following differential equation:

$$\frac{dB_i}{dt} = b_i \cdot B_i + \sum \left(\alpha_{ij} \cdot B_i \cdot B_j \right) \tag{2}$$

where b_i is the intrinsic growth rate (intrinsic rate of increase for autotrophs and natural mortality and losses for heterotrophs), B_i and B_j are the abundance (kg km^{-2}) of species i and j respectively and interaction strength coefficient α_{ij} corresponds to the per capita effect of species j on the growth rate of species i (b_i was calculated indirectly assuming equilibrium). We calculated the per capita effect of predator j on the growth rate of prey i as $\alpha_{ij} = -(q/m)_j \cdot DC_{ji}/B_i$. Effect of prey on their predator is defined as predator growth resulting from this predation. Consequently, the effect of prey i on the population of predator j was related to the effect of the predator on the prey according to: $\alpha_{ji} = -e_{ij} \cdot \alpha_{ij}$, where e_{ij} is the efficiency with which j converts food into biomass, from feeding on i, that is, $e_{ij} = (p/m)_j/(q/m)_j$.

Interaction coefficients for all pairwise interactions of a food web constitute the interaction matrix $A = (\alpha_{ij})$. Owing to the equilibrium assumption, a Jacobian matrix J can be constructed for each food web by multiplying the interaction matrix A with species biomasses[27]. Positive elements of J represent per capita interaction strength of the population of predator j on the population of prey i (refs 12,30).

Statistics. We used generalized linear mixed models to analyse the relationship between predator–prey $C:P$ ratios and herbivore body size (using body mass as a metric), study site, study site mean July temperature (JulyT), primary production and number of groups (diversity) as fixed effects and functional groups as a random factor to account for repetition among sites. Response variables were log-transformed to meet assumption of normality. By doing so, overdispersion was reduced (c-hat was 0.49 compared with 3.90 before transformation), allowing us to use a Gaussian error distribution. Some authors advocate that the sum of mean monthly temperatures $>0\,^\circ$C (Swi) could be a better proxy of bioclimatic Arctic condition[28]. JulyT, Swi and latitude were highly correlated (all $r > 0.85$) and similar results arose if Swi was used instead of JulyT. As JulyT is easier to understand, we used it as a proxy of climatic conditions in our models. To examine variations in predator–prey interaction strengths, we used linear models with predator:prey body size ratio, study site, JulyT per study site and primary production as explanatory covariates. All data were log-transformed to meet assumptions of normality. Maximum and restricted maximum likelihood fitted models were used for model comparison and parameter estimation, respectively. Model selection was based on the Akaike Information Criterion corrected for small sample size (Supplementary Tables 2 and 3). All the analyses were carried out using R 3.0.2.

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Author contributions

P.L. helped in designing the research, analysed the data, contributed to the interpretation of the results and writing of the paper. G.G., N.L., D.B., J.B., N.M.S., R.A.I., N.G.Y. and C.J.K. designed the research and contributed to data collection, interpretation of the results and writing of the paper; M-C.C., D.R. and R.I.G.M. contributed to data collection and interpretation of the results; S.L. and M.L. contributed to the interpretation the results and writing of the paper. D.G. analysed the data, contributed to the interpretation of the results and writing of the paper. P.L. and N.L. wrote the Supplementary Information with input from G.G., R.A.I. and N.G.Y.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to P.L. and N.L.

Competing financial interests

The authors declare no competing financial interests.