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Response of an arctic predator guild to collapsing lemming cycles

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Alpine and arctic lemming populations appear to be highly sensitive to climate change, and when faced with warmer and shorter winters, their well-known high-amplitude population cycles may collapse. Being keystone species in tundra ecosystems, changed lemming dynamics may convey significant knock-on effects on trophically linked species. Here, we analyse long-term (1988–2010), community-wide monitoring data from two sites in high-arctic Greenland and document how a collapse in collared lemming cyclicity affects the population dynamics of the predator guild. Dramatic changes were observed in two highly specialized lemming predators: snowy owl and stoat. Following the lemming cycle collapse, snowy owl fledgling production declined by 98 per cent, and there was indication of a severe population decline of stoats at one site. The less specialized long-tailed skua and the generalist arctic fox were more loosely coupled to the lemming dynamics. Still, the lemming collapse had noticeable effects on their reproductive performance. Predator responses differed somewhat between sites in all species and could arise from site-specific differences in lemming dynamics, intra-guild interactions or subsidies from other resources. Nevertheless, population extinctions and community restructuring of this arctic endemic predator guild are likely if the lemming dynamics are maintained at the current non-cyclic, low-density state.

Keywords: Arctic; cyclic population dynamics; *Dicrostonyx groenlandicus*; predator–prey interaction; climate change

1. INTRODUCTION

The Arctic is warming faster than the global average, and this has already resulted in dramatic changes in species performance and distribution [1–3]. Much focus has been on the northwards movement of species ranges [4–6], rendering endemic arctic species particularly vulnerable to extinction [7]. In addition, Arctic warming is expected to impact *in situ* ecosystem functions, which ultimately may result in species extinctions. For instance, populations of lemmings, which play a key role in tundra ecosystem [8], have in some places recently ceased to exhibit their characteristic population cycles, probably as a result of altered climatic conditions [9–12]. A geographically widespread lemming cycle collapse can be expected to have substantial knock-on effects on a host of trophically related species in the tundra food web [3,13]. Predators specialized on lemming prey are expected to be particularly vulnerable, although predator responses may be moulded by factors

other than prey selection. In particular, life-history characteristics, composition of prey community and intra-guild interactions can make different predator species more or less resilient to the impacts of climate change. So far, however, the lack of analyses of long-term community-wide monitoring data has hindered assessments of ecosystem consequences of collapsed lemming cyclic dynamics that have been proposed in the recent literature [10,13] (but see [12] for model predictions).

In high-arctic Greenland, snow conditions are one of the prime factors shaping the population dynamics and performance of terrestrial vertebrates [14,15], including the collared lemming (*Dicrostonyx groenlandicus*), the only small rodent species present [16]. The previously regular approximately 4-year lemming cycle collapsed around the turn of the millennium, as documented from two sites with long-term monitoring, namely Traill Island [12] and Zackenberg [16] (figure 1a). Four species (stoat *Mustela erminea*, snowy owl *Bubo scandiacus*, long-tailed skua *Stercorarius longicaudus* and arctic fox *Vulpes lagopus*) constitute the predator guild preying on the lemming at both sites [16–18]. These species are known to respond functionally and numerically to the different phases of

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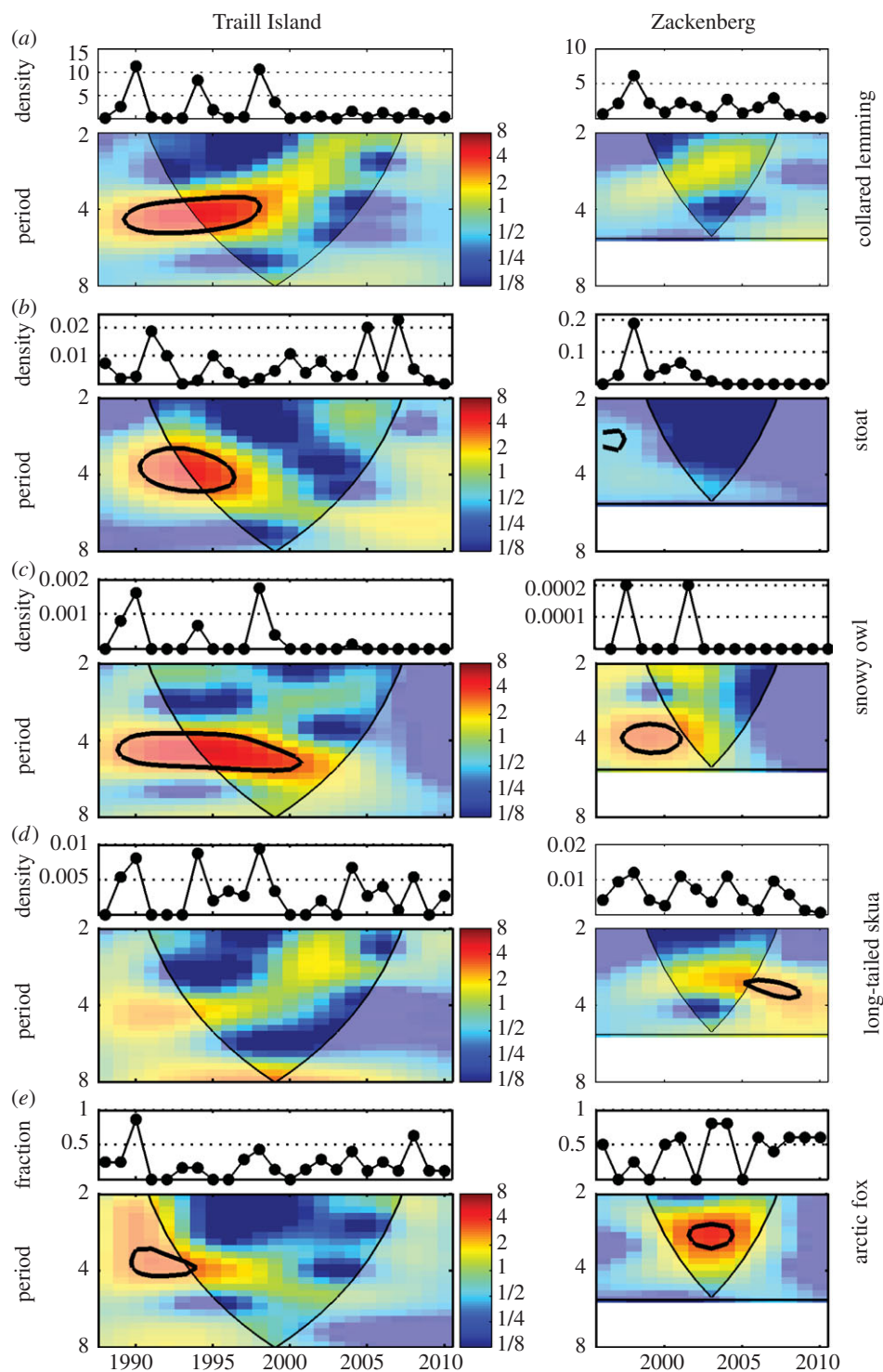


Figure 1. Predator–prey dynamics in northeast Greenland during the period 1988–2010: (a) collared lemmings, (b) stoat-depredated lemming nests, (c) snowy owl nests, (d) long-tailed skua nests and (e) the fraction of arctic fox dens used for breeding. Upper panels show numbers per hectare or fractions during the study period, whereas the lower panels show the continuous wavelet transform of the log- or arcsine-transformed time series. Heat colours denote the power of the spectra, and bold contour lines enclosing the red coloured spectrum denote significant periodicity. The cone marks the area of influence.

normal lemming cycles [17]. However, their resilience to lemming cycle collapses is likely to depend on factors such as their degree of specialization on lemming prey, site-tenacity, mobility and demographic parameters (i.e. longevity and reproductive rate), as well as their trophic and competitive ability within the predator guild. Here, we use community-wide monitoring time series (1988–2010) from the two sites on Greenland to assess the extent to which the populations of the four predator

species have become affected over the decade they have been subject to consistently low abundance of lemmings.

2. MATERIAL AND METHODS

Data presented here were collected on two sites in high-arctic Greenland: Traill Island (72°30' N, 23°98' W) and Zackenberg (74°28' N; 20°34' W). Field methodologies were almost identical at the two sites, although sizes of census areas differed (see

the electronic supplementary material, table S1). Censuses were initiated in 1988 on Traill Island and in 1996 at Zackenberg, and have since then been conducted every year following the same protocols (see the electronic supplementary material). The census data supporting this study are available in the electronic supplementary material, tables S2 and S3.

(a) *Lemming abundance*

As an index of collared lemming abundance, we used the number of winter nests within designated census areas [16,19]. Each year after snowmelt, the entire census area was searched closely for fresh winter nests. Upon examination, nests were destroyed to avoid double counts. At both sites, the lemming census area was located on relatively flat tundra, and covered a variety of habitat types. The census area at Zackenberg may, however, be regarded as richer and more homogeneous than that on Traill Island [16]. For comparison between sites, we therefore applied the site-specific correction factor previously developed by Gilg *et al.* [12] to convert the lemming winter nest density into lemming density.

(b) *Predator abundance and reproduction*

We used the number of collared lemming winter nests taken over by stoats within the lemming census areas as a proxy of stoat abundance in winter [16,19], as direct measures are virtually impossible to obtain. In addition, each year, we located all nests of long-tailed skuas and snowy owls within the designated bird census areas. Avian productivity (i.e. number of fledged young produced per hectare) was estimated from multiple visits to the nests. Known arctic fox dens were surveyed multiple times early in the season to verify breeding, while the number of weaned cubs was estimated from visits to the dens in late July. The arctic fox productivity (i.e. number of weaned cubs produced per ha) was then estimated by multiplying the density of fox dens known at each site by the mean annual number of weaned young per den. As the survey of dens was not always exhaustive (see the electronic supplementary material, table S1), arctic fox productivity was in some years weighted by the fraction of dens surveyed [17].

(c) *Data analyses*

The periodicity of the lemming dynamics at the two sites was examined by subjecting the log-transformed lemming time series to wavelet analyses (continuous wavelet transform; Morlet wavelet; MATLAB package developed by Aslak Grinsted; <http://www.pol.ac.uk/home/research/waveletcoherence/>). Wavelet analyses were also used to examine the individual time series on predator abundance (log- or arcsine-transformed). Zero values were replaced by 0.0001 before transformation. To capture the likely nonlinearity in predator numerical responses to varying lemming abundance [17], we also related predator reproductive response to lemming density using generalized additive models (GAMs) with unpenalized regression splines with 2 degrees of freedom, using the *mgcv* package in R [20]. Remaining GAM parameters were set as default. Site-specific differences in predator responses were assessed by calculating 95 per cent confidence envelopes around the predicted site-specific responses curves. Finally, we compared the production of young (fledged young or weaned cubs) in the cyclic (prior to 2001) versus in the non-cyclic (2001 and onwards) period for arctic fox, long-tailed skua and snowy owl only

on Traill Island, as the shorter census period at Zackenberg did not allow for comparison of the two periods.

3. RESULTS

It is evident from the Traill Island data (figure 1*a*) that at the turn of the millennium the lemming population collapsed there, both in terms of actual densities and periodicity. Although the statistical evidence (cf. power from the wavelet spectra) for changed dynamics was weak for Zackenberg (owing to the limited length of the time series), the populations at the two sites followed the same general trajectory (i.e. with the last density peak towards the end of the last century followed by low amplitude dynamics; figure 1*a*). The dynamics of the breeding populations (i.e. nests) of long-tailed skua and snowy owls, as well as the index of stoat abundance (depredated lemming nests), mostly reflected the changed lemming dynamics, albeit most clearly for snowy owl. The responses of stoat and in particular arctic fox were more ambiguous and showed some interesting site-specific differences (figures 1*b,e* and 2). There was an almost complete cessation of snowy owl breeding following the lemming collapse on Traill Island (figure 1*c*), and a complete disappearance of stoat-depredated lemming nests from 2004 and onwards at Zackenberg (figure 1*b*). On the other hand, while on Traill Island the cyclic predation pattern of stoats disappeared after the collapse of the lemming cycle, there were still a few large spikes in the abundance of depredated nests towards the end of the series (figure 1*b*). On Traill Island, only indications of approximately 4-year cycles in the breeding dynamics of arctic fox and long-tailed skua were found prior to the lemming collapse (figure 1*d,e*). At Zackenberg, long-tailed skua breeding did not exhibit any indications of cyclic pattern (figure 1*d*), whereas arctic fox breeding actually exhibited weak, approximately 3-year cycles (figure 1*e*). After the shift in the lemming dynamics, the linkage between lemming abundance and long-tailed skua and arctic fox reproduction became even less apparent on Traill Island (figure 1*d,e*). However, no clear declines in the frequencies of breeding attempts were observed following the lemming collapse in these two predator species (figure 1*d,e*). At Zackenberg, the fraction of active arctic fox breeding dens actually seemed to have stabilized at a relative high level in recent years compared with the early years. Examinations of the reproductive response as analysed by the GAMs revealed a generally tight linkage to lemming abundance on Traill Island in all three predator species for which such data were available (figure 2). At Zackenberg, the reproductive response of the long-tailed skua was also closely coupled to the abundance of lemmings, whereas the reproduction of the arctic fox was not (figure 2).

Contrasting the mean annual reproductive output on Traill Island before and after the lemming cycle collapse demonstrates that the three predator species were differentially negatively impacted in the order snowy owl (most), long-tailed skua (intermediate) and arctic fox (least; table 1).

4. DISCUSSION

Long-term community-wide data from the Arctic tundra region are rare [21], and the dataset presented here is

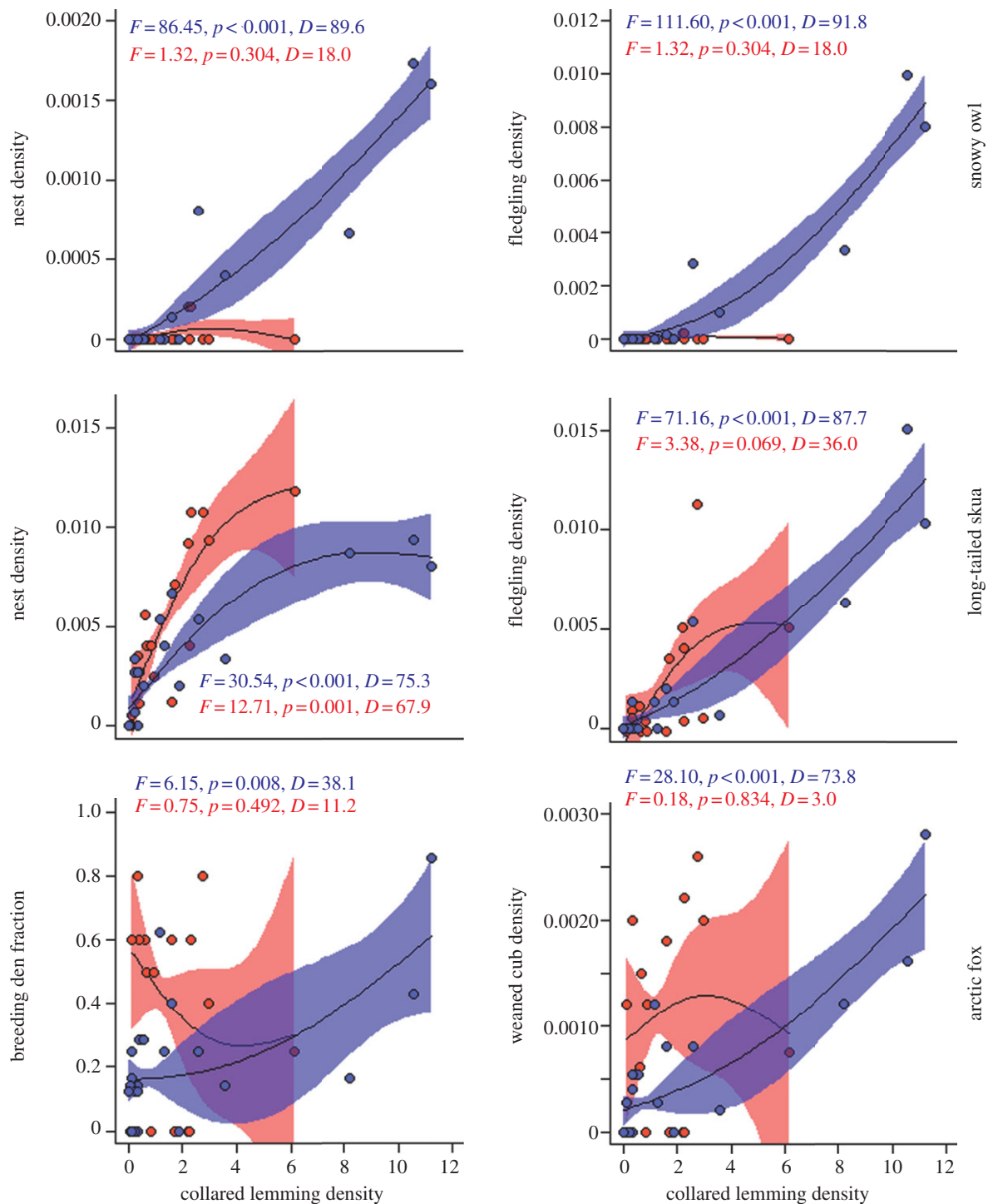


Figure 2. Generalized additive model (GAM) plots of predator reproductive response to high-arctic collared lemming densities on Traill Island (1988–2010) and Zackenberg (1996–2010). Densities are numbers per hectare. Blue colours indicate data from Traill Island, whereas red colours indicate data from Zackenberg. Shaded areas are the 95% confidence limits for the site-specific GAMs with 2 degrees of freedom. The F -statistics and p -values for the specific GAMs are given in each plot, while D shows the deviance explained.

Table 1. Mean annual reproductive output (number of young per km²) on Traill Island during the cyclic (1988–2000) and non-cyclic periods (2001–2010). Numbers in brackets are the standard errors. Also given is the percentage change in mean reproductive output from the cyclic to the non-cyclic period.

phase	arctic fox weaned cubs	long-tailed skua fledglings	snowy owl fledglings
cyclic	0.057 (0.024)	0.307 (0.138)	0.203 (0.099)
non-cyclic	0.040 (0.013)	0.047 (0.024)	0.002 (0.003)
change (%)	−29.7	−84.8	−98.7

the only one available for empirical testing of recent predictions about knock-on effects of collapsed lemming cycles on food web dynamics [9–11,13]. We demonstrate that at the turn of the millennium, the previously cyclic lemming populations on Traill Island in northeast Greenland collapsed completely, both in terms of periodicity and density. Owing to the shorter time series, a collapse at the other site, Zackenberg (also in northeast Greenland), could not be documented statistically, though the two populations follow the same general trajectory with only low-density dynamics in the current century.

The observed change in the lemming dynamics has dramatically impacted the predator guild. The most pronounced response to the lemming collapse was found for the two lemming specialist predator species, snowy owl and stoat, though the response of the latter is more ambiguous. Following the lemming collapse, snowy owls almost ceased to breed on Traill Island, and the production of fledglings decreased by more than 98 per cent. The decline was dramatic, but not unexpected as snowy owls are known to breed in lemming peak years only [17,22]. Moreover, the immediate response in the snowy owl is probably accentuated by a nomadic lifestyle that enables it to move swiftly out of regions with low lemming abundance [23]. Also, the population of stoat, a year-round lemming specialist [17], apparently has declined severely at Zackenberg. This is in accordance with Gilg *et al.* [12], who suggested that the stoats may go locally extinct concurrent with global change. Surprisingly, the stoat population on Traill Island appeared to recover towards the end of the study period. While the causality behind this pattern is unknown, we speculate that the increased stoat activity on Traill Island in later years could reflect a competitive release and reduced intra-guild predation as a result of the disappearance of snowy owls. This hypothesis is partly supported by the observation of very high values of the density index of stoats in the early years at Zackenberg, where breeding snowy owls were virtually absent. Also noteworthy is that if stoat predation of lemming was substantial during winter [24], the apparent decline of the stoat population in the study area at Zackenberg should have released the lemming population from predation mortality. This does not appear to have been the case, suggesting that other factors (e.g. local and regional variation in snow conditions [11,12,25,26]) may now be a major driver of the lemming dynamics at both sites.

While the response of the long-tailed skua breeding population is weaker than that of the stoat and snowy owl, it is noteworthy that although the number of pairs arriving on the breeding grounds is relatively stable [27], the number of nests being initiated has declined in recent years. Fledgling success is low in most years, irrespective of lemming density, and is mainly due to intra-guild predation by arctic foxes [27], and at Zackenberg almost no young have been produced in recent years [28]. Hence, the combination of low lemming abundance and high nest depredation rates (which in itself may be a function of lemming abundance [13]) means that the long-tailed skua population at Zackenberg is already below the replacement threshold [27]. The dramatic decline in long-tailed skua reproductive output (i.e. by 85%) on Traill Island also questions whether this population is presently viable. The long-tailed skua is,

however, long-lived and site-tenacious [29], so the response of adult birds in the population can be expected to be slow.

Although lemming fluctuations have previously been reported to influence the opportunistic arctic fox reproduction elsewhere [22,30], Gilg *et al.* [12] expected arctic fox to be the least affected by reduced lemming abundance, which indeed was what we observed (i.e. reproductive decline by 30%). Nevertheless, on Traill Island, arctic fox reproduction was still coupled to lemming abundance, whereas at Zackenberg, arctic fox reproduction was not coupled to lemming abundance at all. Arctic fox may generally [31,32] (and at Zackenberg, in particular [16,33]) rely on alternative terrestrial and marine food sources, which may buffer arctic fox populations from the fluctuating lemming densities. The lack of coupling between arctic fox and its lemming prey at Zackenberg may also explain why no clear pattern of predation on alternative prey species, such as ground-nesting birds (including long-tailed skua), is found there [34], while it is observed elsewhere in the Arctic [35,36].

The collapse of the lemming cycles in northeast Greenland has already affected the tundra ecosystem, here demonstrated by reduced reproductive performance and declining populations of high-arctic predators. If the lemming populations remain at the same non-cyclic, low-density state as during the last decade, the result will probably be population extinctions and further impoverishment of this arctic endemic predator guild. Ultimately, this may cause cascading impacts on the entire tundra food web, with unknown consequences [1,3,13]. Our results also demonstrate that the nature of such trophic cascades is contingent on site-specific food web structure—characteristics of tundra ecosystems that are known to vary spatially [37]. Thus, improving our ability to predict the impacts of climate change on the vulnerable arctic ecosystems will require enhanced and coordinated spatial replication of long-term monitoring programmes.

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