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Introduction

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Advancing the long view of ecological change in tundra systems

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Despite uncertainties related to sustained funding, ideological rivalries and the turnover of research personnel, long-term studies and studies espousing a long-term perspective in ecology have a history of contributing landmark insights into fundamental topics, such as population- and community dynamics, species interactions and ecosystem function. They also have the potential to reveal surprises related to unforeseen events and non-stationary dynamics that unfold over the course of ongoing observation and experimentation. The unprecedented rate and magnitude of current and expected abiotic changes in tundra environments calls for a synthetic overview of the scope of ecological responses these changes have elicited. In this special issue, we present a series of contributions that advance the long view of ecological change in tundra systems, either through sustained long-term research, or through retrospective or prospective modelling. Beyond highlighting the value of long-term research in tundra systems, the insights derived herein should also find application to the study of ecological responses to environmental change in other biomes as well.

1. Introduction

Both long-term studies and studies adopting a long-term perspective are instrumental, if not critical, to revealing the complex interactions that shape, characterize and drive ecological systems. Such studies are, furthermore, of prime value in understanding the ecological implications of global climate change. In many cases, however, long-term studies in ecology have been initiated for reasons other than those concerned with detecting and characterizing consequences of climate change. This is especially true in the case of studies that were initiated before the onset of the recent anthropogenic warming trend, and in the case of studies that have developed secondarily out of long-term records that have since been co-opted for use in climate change studies. We argue that the long view of ecological change is particularly important during periods of rapid change and where data sources are limited. In tundra systems, where abiotic conditions are undergoing rapid and pronounced change [1], a long-term perspective on ecological change may derive from continuous, multi-annual data, or, where such data are lacking, may depend on retrospective or prospective analyses. In this special issue, we present a series of papers representing both types of approach with the aim of advancing the long view on ecological change in tundra systems.

2. Landmark long-term studies in ecology

Whether initiated as ecological investigations or simply out of an interest in natural history, long-term studies and studies conducted with a long-term perspective have in general been instrumental in exposing the complexities of species interactions and the role of these in ecological responses to environmental change [1]. A classic example of the heuristic value of long-term studies in ecology is the ongoing investigation initiated in 1958 of wolf–moose dynamics in Isle Royale National Park, USA. One of the many epistemological highlights of this study is the evolution of insights into predator–prey dynamics it has generated, from the simple notion of wolf limitation of moose abundance, to the more

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nuanced understanding of the selectivity of wolf predation on certain age classes of moose, to the role of winter weather in wolf kill rates of moose, to the role of wolf disease outbreaks in moose dynamics, and ultimately, to the secondary role of wolf predation relative to climatic fluctuation in moose dynamics and abundance on the island [2]. Such an evolution of our understanding of the nature of the complex interactions among climate, pathogens and predation in herbivore population dynamics would, quite obviously, have been impossible in the absence of continuous, long-term research. Perhaps more interestingly, however, the Isle Royale wolf–moose study highlights the value of long-term and continuous studies in capitalizing upon unexpected developments to the benefit of improving our understanding of and appreciation for ecological complexity.

In contrast to the Isle Royale wolf–moose study, the time series of observations comprising the Marsham phenological record [3] was not initiated as an ecological study, and yet it is perhaps one of the best-known long-term datasets on indicators of spring that has been adapted for the study of ecological responses to climate change. Comprising observations of up to 27 phenological events in 20 species, including the timing of flowering and leafing out in plants, and appearances or vocalizations of birds, amphibians and butterflies, the Marsham phenological record was initiated by Robert Marsham on his estate in Norfolk, England, in 1736, and continued through five generations of his descendants [4]. Although obviously not initiated with the intent to investigate ecological consequences of climate change, the Marsham phenological record has been used to illustrate long-term species-level responses to fluctuations and trends in weather and climate [4,5]. Notably, analyses of the Marsham record have demonstrated variation among species in the extent to which their springtime phenologies have changed over two centuries [4], as well as differences among species in the proximal drivers of variation in their springtime phenologies [6], thereby supporting the notion of individualistic species' responses to climate change. Similarly, analyses of phenological observations recorded by Henry David Thoreau in New England, USA, and contemporary repeat sampling of similar observations in the same area have provided important insights into changes in community composition [7] and species-specific variation in rates of phenological response to climate change [8,9] that would not have been possible in the absence of such a long-term perspective [10].

Whereas long-term studies, such as that on Isle Royale, produce powerful datasets that can reveal non-stationary dynamics (i.e. those attributable to differing drivers as the time series and investigators' understanding of the system-level nuances expand) [11,12], studies with a long-term perspective may not necessarily produce long-term datasets, but may expand upon historic datasets or use retrospective analyses to produce insights into long-term dynamics and processes [13,14]. Studies of the nesting ecology of tits in the UK initiated decades ago [15] have since, for example, provided compelling case studies of the role of resource availability and timing in consumer responses to climate change [16–18]. Persistent, ongoing monitoring of body condition and birth rates in polar bears in Western Hudson Bay, Canada, begun in 1981, eventually resulted in the first evidence of population ecological consequences in this species of recent warming [19]. Long-term observations of the annual timing of clutch initiation among Mexican jays breeding in the Chiricahua Mountains in Arizona, USA, produced seminal insights into the role of rising minimum monthly temperatures in egg-laying trends in avian species [20]. Long-term experimentation involving multi-annual exclusion of granivorous rodents in the Chihuahuan Desert revealed lagged responses to the El Niño Southern Oscillation and the relaxation of competition among members of this guild, neither of which would have been elucidated through shorter nor discontinuous experiments [21,22].

The demonstration of lagged responses to species removals and legacy effects of environmental disturbance are two key features of studies with long-term perspective. The local extinction of grizzly bears and wolves from the southern Greater Yellowstone Ecosystem, for instance, promoted, over one and a half centuries, the irruption of moose, decline of riparian willows browsed by moose, and subsequent decline of neotropical migratory birds specialized upon nesting among riparian zone willows [23]. Long-term surveys of heavily logged areas of forest in Kibale National Park, Uganda, conducted over nearly three decades, were necessary to reveal the legacy effects of this disturbance on the recovery of primates, populations of some species of which continued to decline decades after logging [24], illustrating the importance of the extinction debt deriving from habitat destruction [25] that may also apply to species' responses to climate change [26,27].

In contrast to the extremely long-term datasets applied to the study of ecological responses to climate change that characterize some mid- and lower latitude systems, such as the aforementioned Marsham record [4,6,28] and more recently published records from continental European [29] and Mediterranean systems [30–32], in tundra systems long-term datasets and multi-decadal studies are, with the occasional exception [33], comparatively rare. There are multiple explanations for this, among which logistical challenges inherent to conducting ongoing research in remote locations is clearly important. Perhaps for this reason, retrospective, prospective and comparative studies are often employed in tundra systems to derive long-term perspective on ecological dynamics and trends in response to past and expected climate change [1,34]. In our judgement, the examples given above from lower latitudes demonstrate that unique insights can be gained from adopting a long view on ecological change either through long-term observations at the same site, by detailed studies of novel phenomena, or through modelling temporal dynamics. We argue that such an approach is imperative to understanding and adapting to the dramatic abiotic changes projected for the Arctic. The papers in this special issue employ multiple approaches to the study of long-term changes in tundra ecosystems along four major thematic lines, and will, we hope, stimulate new initiatives necessary for current and future understanding of this rapidly changing biome.

3. Plant phenology

A previous analysis of long-term phenological monitoring data from the high Arctic demonstrated that mean phenological advancements averaged across observations of the timing of flowering in plants, emergence in arthropods and egg-laying in birds were much stronger than similar reports from temperate latitudes [35,36]. The magnitude and apparently linear nature of these phenological advances raise the question of whether they will be sustained in the context of ongoing warming. The degree of potential phenological advance within the lifespan of the individual is, after all, controlled by limits to phenotypic plasticity. The alleviation of current environmental constraints on the timing of life-history events by climate change may result in thresholds in plant phenological responses to warming [1]. With long-term observations of the timing of flowering from an Arctic and a subalpine site, Iler *et al*. [37] in this issue assess whether phenological variation in recent decades provides evidence of such nonlinear responses. As Iler *et al*. report, their results provide surprisingly little evidence of nonlinear patterns of flowering phenology in response to environmental variation, although some species appear to be approaching their limit in responding to earlier snowmelt. In contrast, a separate analysis in this issue by Oberbauer *et al*. [38] using long-term control (observational) data from the circum-Arctic distributed International Tundra Experiment initiated in 1990 reveals minimal phenological advancement across the compiled dataset. Instead, the observed phenological dynamics were highly species- and site specific, and the lack of any observable overall trend is, the authors contend, likely due to strong interannual variability in annual temperatures and variability among sites in long-term climatic trends [38].

4. Dynamics among and within species

The notion that Arctic ecosystems are inherently simple and form ideal test beds for understanding ecosystem properties such as stability and resilience prevails, despite numerous examples of complexity in food web structure [39], species diversity [40] and trophic interactions [41] from high-latitude systems. Olofsson *et al*. [42] provide a compelling example in this issue of a shift in long-term vegetation dynamics from ostensible regulation by rather predictable dynamics towards more complex dynamics once a new component of the ecosystem becomes more important. In this case, field-layer vegetation accumulated over 15 years was eliminated by the combination of a major caterpillar outbreak and an increase in disease severity of a pathogenic fungus infecting the dwarf-shrub *Empetrum hermaphroditum*. Such an example supports the need for long-term observational and experimental studies because, similar to the Isle Royale study, it questions the generality of the results of shorter term studies. In another installment to this issue, Gauthier *et al*. [43] present unique information on long-term dynamics of multiple trophic levels from the Canadian high Arctic, demonstrating that directional trends in phenology, demography and life-history changes at their site are rare, despite its warming trend. These results are at odds with the strong trends documented at Zackenberg in high Arctic Greenland [44], but confirm apparent regional variation documented by Oberbauer *et al*. [38]. The results presented by Gauthier *et al*. [43] also suggest that, for at least one aspect of their monitoring programme, changes in graminoid biomass, sampling less frequently (every other year) would have revealed similar results, while shorter yet continuous time series would have yielded potentially contrasting results.

While few clear cases of trophic mismatch imposing demographic consequences at the population level have been published [45,46], the datasets required to assess their importance are rare in most systems, particularly the Arctic. In this issue, Kerby and Post [47] expand upon observations initiated in 1993 [48] at a long-term study site near Kangerlussuaq, Greenland, of the timing of plant phenology and reproduction by two herbivores with contrasting life-history strategies, caribou and muskoxen [1]. Characterizing caribou and muskoxen as species representative of income and capital breeding strategies, respectively, Kerby & Post [47] illustrate that mismatch with the timing of resource availability exerts negative demographic consequences in an income breeder but not in a capital breeder, and urge the application of this conceptual framework in other studies of match/mismatch.

Mismatches are not confined to trophic interactions among species. In fact, there is a growing awareness that mismatches can also happen within species [46,49]. Sex-specific phenology is often associated with territoriality and the competition for mates [50,51]. For instance, in birds, males typically arrive on breeding grounds before females, and early arrival is associated with higher reproductive success [52]. In arctic ground squirrels, winter hibernation imposes a challenge to time spring arousal so that it coincides with the optimal time for breeding. In this species, males emerge before females, and Sheriff *et al*. [53] in this issue demonstrate that males at an Alaskan site with late snowmelt accelerate the time between end of hibernation and emergence relative to males at another Alaskan site with earlier snowmelt. Males at the early site emerge despite incomplete sexual maturation, presumably because early emergence is critical for access to females. The authors base their findings on long-term data on interannual variation in male emergence phenology acquired by implanting temperature loggers in the abdominal cavity of individual male arctic ground squirrels. Using this approach, Sheriff *et al*. [53] were able to assess correlations among different phenological events in the life cycle of this species, illustrating how males adapt their reproductive phenology to interannual variation in prevailing environmental conditions at the time of arousal in spring. Only through such detailed physiological studies can we begin to understand the extent to which organisms may exhibit phenotypic plasticity in response to climate change.

5. Long-term vegetation dynamics and ecosystem function

One of the oldest ongoing tundra studies is that at the Abisko Scientific Research Station in subarctic Sweden. In this issue, Callaghan *et al*. [54] present a comprehensive overview of the multitude of ecological changes that have been observed through ongoing observations and experiments conducted at and around the Abisko site since 1913. Among the insights deriving from this remarkably sustained and inter-disciplinary history of research is that ecological dynamics at and around Abisko have been characterized by the full suite of complexity characteristic of ecological dynamics across the Arctic as a whole, including increased vegetation growth and range expansion, as well as decline and, in some cases, stasis in vegetation growth.

While the recent literature includes many examples of species ranges expanding northwards [55], it is also increasingly clear that multiple factors (e.g. dispersal limitation and biotic interactions) interact to determine how species distributions will respond to climate change [1,56–58]. Greenland is presently host to a more depauperate flora than most other parts of the Arctic at similar latitudes, ostensibly owing to its climatic and glacial history [59]. Greenland is therefore a suitable study system for quantifying the potential for colonization by non-native shrub and tree species as well as their migrational lags. Normand *et al*. [60] in this issue address this problem by applying both a physiologically based tree line model and species distribution models of an array of shrub and tree species currently found in Greenland or occurring elsewhere in high-latitude regions. Using both palaeoclimatic data from different periods back to the Last Glacial Maximum and data deriving from climate change projections, Normand *et al*. [60] conclude that the envelope of suitable climatic conditions for many of these species has existed in Greenland for several thousand years, despite their lack of establishment. Presumably, the distributions of these species, and their absence in climatically suitable areas of Greenland, are likely due to limitation by other factors than climate itself. In a future climate context, this study suggests that unintentional assisted migration by humans may be important in determining the rate and location of spread of new plants species in Greenland [60].

The so-called shrubification of the Arctic tundra biome that the contribution by Normand and colleagues addresses in Greenland is due to the presumably warming-driven spread of woody plants [61]. Such a transition towards an increasingly woody and leafy tundra biome may have important implications for ecosystem carbon exchange because of the increased photosynthetic capacity potentially deriving from such a transition. Shaver *et al*. [62] contribute the results of a pan-Arctic model of net ecosystem carbon exchange (NEE) parametrized using data collected over several field seasons at tundra sites in Alaska, Greenland, Norway (Svalbard) and Sweden [63,64]. The results of their model indicate an intriguing convergence across the Arctic tundra biome in drivers of NEE, despite the array of ecosystem diversity it represents: namely, nearly all (i.e. 75%) of the variance in NEE across the Arctic tundra biome is explained by a small suite of variables, including leaf area index [62]. This insight should improve the efficiency and accuracy of future efforts to model and analyse the consequences of increasing shrubification of the Arctic for ecosystem carbon dynamics at the biome level.

6. Extreme events

The final installment in this special issue is a thorough case study of a recent and extensive tundra wildfire that occurred in Alaska near the Anaktuvuk River in 2007. In their paper, Bret-Harte *et al*. [65] quantify the magnitude and rate of vegetation recovery following the massive displacement of long-term carbon accumulation that resulted from this fire. The Anaktuvuk River fire was one of the first major tundra fires and the largest ever on the North Slope of Alaska, releasing an estimated 2.1 Tg of carbon to the atmosphere, an amount similar to the total annual net primary production of the entire tundra biome [66]. An estimated 37 years of carbon accumulation, and nearly 400 years of nitrogen accumulation, was combusted in the fire [66]. Four years after the fire, Bret-Harte *et al*. revisited the site and quantified the vegetation recovery and nitrogen dynamics at sites of severe and moderate burn severity, as well as in nearby unburned tundra as a proxy for pre-fire vegetation and soils. The authors conclude that vegetation recovery has been rapid so far, re-growth from surviving underground parts was extensive, and that vascular plant communities were on track towards re-establishment of previous vegetation communities [65]. Importantly, however, the bryophyte species found were mainly disturbance-adapted species, and non-vascular biomass had recovered less than vascular plant biomass, suggesting that continued monitoring will be necessary to determine the full trajectory and compositional nature of the recovery [65].

There is yet more to learn about long-term changes in ecological systems by advancing the long view, either through promoting and maintaining long-term studies, or through conducting research with a long-term perspective, both forward and backward in time. In addition, there is much to be learned about the nature of long-term studies themselves in the literature about their value beyond the data and insights they generate. Others have emphasized the challenges inherent to long-term research in ecology, some of which may be circumvented by shorter term studies adopting a long-term perspective. Highlighting these here, as we conclude this introduction, serves to remind us, and, we hope, remind policy-makers and funding agencies, of the qualities that characterize such studies by virtue of surmounting them for the goal of securing precious data. To paraphrase others, the success of such research requires anticipating and adapting to variability in space and time not only of the study system itself, but also to the succession of investigators involved [67]. As well as sustained interest on the part of said investigators, continued financial resources, surviving the 'threat of rival ideologies', and the support of host institutions are also all vital components of successful long-term research in ecology [2]. To this we would add our own, final, requirement: that of the willingness of the individual scientist and those they leave behind each field season to make the personal sacrifices required by such sustained devotion to ongoing research. In each of the papers in this special issue, this last is the inconspicuous essential ingredient that led to its contribution to advancing the long view of ecological change in tundra systems.

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