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INTRODUCTION

The International Tundra Experiment (ITEX): 30 years of research on tundra ecosystems[1]

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Abstract: The International Tundra Experiment (ITEX) was founded in 1990 as a network of scientists studying responses of tundra ecosystems to ambient and experimental climate change at Arctic and alpine sites across the globe. Common measurement and experimental design protocols have facilitated synthesis of results across sites to gain biome-wide insights of climate change impacts on tundra. This special issue presents results from more than 30 years of ITEX research. The importance of snow regimes, bryophytes, and herbivory are highlighted, with new protocols and studies proposed. The increasing frequency and magnitude of extreme climate events is shown to have strong effects on plant reproduction. The most consistent plant trait response across sites is an increase in vegetation height, especially for shrubs. This will affect surface energy balance, carbon and nutrient dynamics and trophic level interactions. Common garden studies show adaptation responses in tundra species to climate change but they are species and regionally specific. Recommendations are made including establishing sites near northern communities to increase reciprocal engagement with local knowledge holders and establishing multi-factor experiments. The success of ITEX is based on collegial cooperation among researchers and

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the network remains focused on documenting and understanding impacts of environmental change on tundra ecosystems.

Key words: International Tundra Experiment (ITEX), tundra, ecosystems, climate change, coordinated distributed experiments.

Résumé : L'initiative ITEX (*International Tundra Experiment)* a été fondée en 1990 en tant que réseau de scientifiques étudiant les réponses des écosystèmes de la toundra aux changements climatiques ambiants et expérimentaux sur des sites arctiques et alpins à travers le monde. Des protocoles communs de mesure et de conception expérimentale ont facilité la synthèse des résultats entre les sites afin d'obtenir des informations sur les impacts des changements climatiques sur la toundra à l'échelle du biome. Ce numéro spécial présente les résultats de plus de 30 ans de recherche ITEX. L'importance des régimes des neiges, des bryophytes et de l'herbivorie est soulignée, et de nouveaux protocoles et études sont proposés. La fréquence et l'ampleur croissantes des événements climatiques extrêmes ont des effets importants sur la reproduction des plantes. La réponse la plus constante en termes de caractéristiques végétales sur l'ensemble des sites est une augmentation de la hauteur de la végétation, en particulier des arbustes. Cela affectera le bilan énergétique de surface, la dynamique du carbone et des nutriments et les interactions entre les niveaux trophiques. Les études de transplantation en jardin commun montrent des réponses d'adaptation des espèces de la toundra aux changements climatiques, mais elles sont spécifiques aux espèces et aux régions. Des recommandations sont faites, y compris l'établissement de sites près des communautés nordiques pour augmenter l'engagement réciproque avec les détenteurs de connaissances locales et l'établissement d'expériences multifactorielles. Le succès de l'ITEX repose sur la coopération collégiale entre les chercheurs et le réseau reste concentré sur la documentation et la compréhension des impacts des changements environnementaux sur les écosystèmes de la toundra. [Traduit par la Rédaction]

Mots-clés : expérience internationale sur la toundra (ITEX), toundra, écosystèmes, changement climatique, expériences distribuées coordonnées.

Introduction

Arctic and alpine tundra ecosystems form a distinctive biome, characterized by short, cool growing seasons, oligotrophic soils mostly underlain by permafrost, and strong influences of snow regimes and low stature plants (Bliss 1971; Chapin 1983; Billings 1987; Rixen et al. 2022). And as latitude and elevation increase there is an increase in the relative importance of bryophytes and lichens and a decrease in the diversity of vascular plants (Bliss and Matveyeva 1992; Walker et al. 2005; Lett et al. 2022). Along with northern Boreal ecosystems, especially bogs and fens, tundra ecosystems hold enormous stores of soil carbon—as much as 50% of the soil carbon on the planet (Tarnocai et al. 2009; Hugelius et al. 2014; Schuur et al. 2015). Tundra ecosystems provide important resources for the mostly Indigenous populations in northern high latitudes who have been part of these systems for thousands of years (Henry et al. 2012; Boulanger-Lapointe et al. 2019, 2020). However, these ecosystems are changing in response to the rapidly changing climate; the Arctic is warming at nearly four times the global rate (Rantenen et al. 2022). Furthermore, tundra ecosystems are experiencing increases in the frequency and magnitude of intense warm and cold growing seasons and extreme weather events such as warm spells in winter with rain on snow (Walsh et al. 2020), which can cause major effects on reproductive effort and success of tundra plants and wildlife (Bjerke et al. 2017; Post et al. 2019; Schmidt et al. 2019; Panchen et al. 2022).

Global climate models in the 1980s showed warming due to increased greenhouse gas concentrations in the atmosphere would be greatest at high latitudes (Maxwell 1992; Moritz et al. 2002; ACIA 2005). These early models captured the large-scale feedbacks in the polar regions that would lead to amplification of the warming (ACIA 2005;

Serreze and Barry 2011; IPCC 2018). The predictions of a rapidly warming Arctic spurred research in terrestrial, freshwater, and marine systems to understand and predict the responses and consequences of changes to the ecosystems, including feedbacks to the atmosphere (Serreze and Barry 2011). The decline in minimum sea ice extent has become a sentinel of global climate change, reported every September by the National Snow and Ice Data Center (http://nsidc.org/arcticseaicenews/). Similarly, the increased growth, cover, and height of shrubs is one of the major responses in terrestrial systems frequently observed across the Arctic in response to ongoing warming (Sturm et al. 2001; Myers-Smith et al. 2011; Elmendorf et al. 2012*a*; Bjorkman et al. 2018). These responses have important consequences for the structure and function of these ecosystems and feedbacks to the atmosphere, including a lower albedo and the net exchange of carbon (Chapin et al. 2005; Schuur et al. 2015; Wilcox et al. 2019; Mekonnen et al. 2021).

To address the predictions that climate change would result in significant warming at high latitudes, a group of ecologists working in Arctic and alpine regions met in 1990 to consider ways to research and document the anticipated changes in tundra vegetation. The meeting resulted in the formation of the International Tundra Experiment (ITEX). The initial focus was on phenology, growth, and reproduction of common vascular plant species with circumarctic distributions that would facilitate comparisons across sites. The focus on plant responses was based in part on questions from northern residents across the Arctic about the effects of predicted climate change on species used by and of interest to them. It was also agreed that a simple passive warming experiment should be established to provide an ability to predict responses to warming across the tundra.

This special issue of *Arctic Science* is an acknowledgement of the scientific achievements and a celebration of more than 30 years of research and monitoring conducted by a group of researchers who established and maintain one of the earliest coordinated distributed experiments (Fraser et al. 2013). The results from the ITEX network, including those in this issue, have contributed to a better understanding of the responses of tundra systems to the rapidly changing climate and the consequences of the changes. In this introduction paper we provide a brief history of ITEX and the impact the network has had over the past three decades, summarize the research presented in the papers in this special issue, and provide an outlook for the future of research on tundra ecosystems.

History, structure, and evolution of ITEX

The meeting that resulted in the formation of the International Tundra Experiment (ITEX) was convened by Prof. Patrick Webber at the Kellogg Biological Station of Michigan State University, in December 1990. Participants agreed to establish the network and drafted the ITEX Resolution (Webber and Walker 1991; https://www.gvsu.edu/itex/). The ITEX Resolution laid out the context and general principles for protocols that would be developed for measurements, coordination, data sharing, and synthesis of the pooled datasets. The collaborative work at the founding meeting and the publication of the ITEX Resolution (Webber and Walker 1991) provided scientific and international context for proposals to national funding agencies. Many of the participants in the first ITEX meeting went on to establish sites and research based on the ideas, questions and protocols discussed at the initial meeting. In 1992, Alexandra Fiord on Ellesmere Island, Nunavut, in the Canadian High Arctic became the first site in the ITEX network and by 1995 there were sites in northern Sweden, Switzerland, Norway, Alaska, and Iceland. Most ITEX sites have remained active over the past three decades providing a rich understanding of the impacts and consequences of the warming climate on tundra ecosystems, and many are featured in this special issue (Fig. 1).

Fig. 1. Location of ITEX sites from papers in this special issue of *Arctic Science*. Sites with an asterisk are also in the ITEX special issue of *Global Change Biology* in 1997 (Henry and Molau 1997). Sites with experimental plots are shown with red symbols; sites with plots under ambient conditions only are shown in blue symbols. (Map created by C. Collins using the sf package (v 0.9.6) in R (Pebesma 2018)).

The governance structure of ITEX is outlined in the ITEX Resolution (Webber and Walker 1991) and in by-laws adopted at subsequent meetings. A Chair (or co-Chairs) is elected at the annual meeting and serves for a variable length of time (typically 5–7 years). A steering committee consisting of senior ITEX researchers, an early career researcher (usually at the postdoctoral level), a graduate student representative, and past chairs help to make network decisions with the Chair(s). Members of the steering committee generally consist of representatives from each of the countries in ITEX. The Chair(s) serve as the leaders and represent ITEX at international meetings or other initiatives, such as programs under the Circum-Arctic Flora and Fauna program of the Arctic Council (e.g., Circumpolar Biodiversity Monitoring Programme, CBMP). They work with hosts of the annual meeting to design the program, and help lead synthesis projects within the network, including this special issue; the author group of this introduction paper consists of the current members of the steering committee.

The success of ITEX stems from the collaborative and congenial relationships among the researchers, which are maintained by the annual meetings, communications through the ITEX email list and ongoing synthesis efforts. Each meeting is usually held in a different ITEX country and hosts volunteer to organize the meeting with help from the Chair(s). The relatively low number of participants (ca. 50–100) allows members to get to know each other on a personal and professional level. Meetings include working groups dedicated to protocols, data management, and synthesis. Local excursions, usually involving a hike in the region and local entertainment are a planned part of the workshop, all of which contributes to the congeniality among the ITEX group.

One of the most important of the founding principles in the ITEX Resolution was the agreement to develop protocols for the collation and exchange of data that allow for quantitative syntheses of responses across sites. Measurement protocols were established and tested in the early years, discussed and amended at annual meetings, and eventually published in the ITEX Manual (Molau and Mølgaard 1996; https://www.gvsu.edu/itex/). The ITEX Manual is a living document, and protocols can be added and modified. ITEX researchers have been at the forefront of sharing data and producing biome-wide syntheses of responses to experimental and observed climate change, and results are highlighted below.

Open-top chambers (OTCs)

At the initial meeting, it was agreed that a simple, passive warming experiment would be adopted and the focus would be on responses of major circumpolar vascular plant species. The warming experiment was to be simple, inexpensive and representative of predicted climate change. The open-top chamber (OTC), a passive warming device, was adopted as the experimental apparatus of choice for ITEX (Marion et al. 1997; Hollister et al. 2022). The average warming effect has been found to be 1–3 °C during the growing season, which is within the range of predictions from global climate models for Arctic summer temperatures (ACIA 2005), and generally less than the annual variability (Bokhorst et al. 2013; Elmendorf et al. 2015). Hence, the OTCs experimentally simulate a warm year at a site (Hollister and Webber 2000). As with any field experiment there are some confounding effects with the use of the OTCs, such as low wind speed, effects on snow depth (if left on through winter), slightly decreased soil moisture in some habitats, and potential interference with pollination and herbivory (Marion et al. 1997; Hollister et al. 2006; Post and Pedersen 2008; Bokhorst et al. 2013; Robinson and Henry 2018; Adamson and Iler 2021; Hollister et al. 2022). However, the effects of warmer years and ambient warming over the past 50 years on tundra plants and ecosystems have been consistent with predictions from experimental warming with OTCs (Arft et al. 1999; Hollister et al. 2005*a*, 2005*b*; Walker et al. 2006; Elmendorf et al. 2012*a*).

The establishment of each ITEX site as a platform for long-term monitoring and process studies has made the network increasingly more important over time, and the changes occurring in the control plots have become increasingly valuable to the scientific community. The importance of long-term observations is apparent in many of the studies in this special issue. The embedded warming experiment has been useful to understand the drivers of change occurring across the ITEX network (Hollister et al. 2015).

Contributions and impacts of ITEX research

Synthesis studies

The scientific success of ITEX as a coordinated distributed experiment is largely the result of the founding principle of sharing and synthesizing results. A set of papers comparing the early responses in common tundra plant species to experimental warming and environmental gradients was published in a special issue in *Global Change Biology* in 1997 (Henry and Molau 1997). Using the common protocols across the sites allowed comparisons and showed there were growth and phenological responses to the first 1–3 years of experimental warming in many species. In 1996, a group of ITEX researchers met at the new National Center for Ecological Analysis and Synthesis (NCEAS) at the University of California Santa Barbara, and used meta-analysis to compare responses of the common vascular plant species across ITEX sites to short-term experimental warming. The analysis was one of the first applications of meta-analysis to ecological observations. The synthesis of data from 13 sites using a single statistical method was scientifically exciting; however, much of the time was spent on data management—a lesson learned for subsequent syntheses. These early results indicated forbs and graminoids had relatively strong responses and there were important regional differences in responses among High Arctic, Low Arctic, and alpine sites (Arft et al. 1999). It also set the format for subsequent synthesis projects where a postdoctoral scientist would lead the effort with a principal investigator in ITEX, acquire data from participants, format and check the data, and conduct preliminary analyses before a meeting would be held to discuss the results, provide direction, and help with analysis and writing.

Phenological responses in a wide variety of species have been well-studied in climate change research (Parmesan and Yohe 2003; Parmesan 2006; Parmesan 2007; Wolkovich et al. 2012; Panchen and Gorelick 2017). Protocols for observing phenology in the common species were established in the first years of ITEX (Molau and Mølgaard 1996) and the phenology data form the most comprehensive ITEX data base (Prevéy et al. 2022). Besides the initial study by Arft et al. (1999), four syntheses have been based on the ITEX phenology data and they have been used in other studies. In a synthesis of the phenological responses to ambient climate in control plots at 12 ITEX sites, Oberbauer et al. (2013), using an early version of the data set, found no clear warming response likely because of the variability among years and sites. Subsequent studies verified the advance of flowering in response to experimental and ambient warming (Prevéy et al. 2017, 2019). Both Oberbauer et al. (2013) and Prevéy et al. (2017) found greater sensitivity to warming in leaf and flower phenology of species and populations in colder High Arctic sites, where a smaller heat sum was required for transitions to different phenophases. The extended growing season due to warmer conditions in the late summer has not had a strong effect on late season phenology, although there has been a slight delay in senescence in warmed plots (Collins et al. 2021). Late flowering plants have shown strong advances in phenology, resulting in convergence of flowering times between early and later flowering species (Prevéy et al. 2019). This could have effects on pollinators and other insects if their life cycles are coordinated with periods of maximum flower availability (Prevéy et al. 2019; Collins et al. 2021).

Walker et al. (2006) provided experimental verification of warming as a major cause of the increase in shrub cover that was being reported across the Arctic from remote sensing observations (Sturm et al. 2001; Myers-Smith et al. 2011). The biome-wide results also showed a decline in species diversity in plots due to the loss of bryophytes and lichens, most likely as a consequence of the increased cover and height of shrubs, especially deciduous shrubs. A second, more extensive, analysis of the data from experimental plots after up to 20 years of treatment showed the same general pattern of responses (Elmendorf et al. 2012*b*). However, the greatest increase in shrub cover was found in Low Arctic sites with warmer ambient temperatures, and evergreen shrubs were responding as strongly as deciduous shrubs, especially in wet tundra sites. Bryophytes and lichens showed declines, but there were differences among growth forms with pleurocarpous mosses and crustose lichens showing little change. These responses to long-term experimental warming were shown to be very similar to those found in plots at tundra sites with no warming treatment, including control plots at ITEX sites, that were resampled over time (Elmendorf et al. 2012*a*). With ambient warming there was an increase in vascular plant abundance and litter, with an increase in both evergreen and deciduous shrubs. There were also important regional and latitudinal differences, and responses were related to site temperature and soil moisture conditions: moist habitats in warmer sites had the greatest change in abundance.

One of the most common shifts in tundra plant communities in response to experimental and ambient warming has been an increase in canopy height, which has been found in all three synthesis studies using the ITEX vegetation data (Walker et al. 2006; Elmendorf et al. 2012*a*, 2012*b*). The increase in plant height was also found to be the most common change in an analysis of traits of tundra plants across the biome (Bjorkman et al. 2018). The greater canopy height has important implications for tundra systems, for feedbacks to the atmosphere and within the ecosystems. Taller shrubs usually translate into greater leaf area, which lowers albedo and increases regional warming (Chapin et al. 2005). The greater shrub height and volume of branches affects snow distribution and density, and can lead to increased melt rates as branches above the snow absorb solar radiation and contribute to warming the snow pack (Myers-Smith et al. 2011; Wilcox et al. 2019; Rixen et al. 2022). The greater shrub abundance can also affect other trophic levels, with greater forage availability, and will impact decomposition and nutrient cycling through changes in litter quantity and quality (Myers-Smith et al. 2011; McLaren et al. 2017). However, the effects will depend on the strength and relative responses of the shrub species and changes in the relative abundance of deciduous and evergreen species (e.g., Vowles and Björk 2019).

The effects of warming on net ecosystem exchange of CO_2 (NEE) in tundra systems was assessed in a study of results from four North American ITEX sites after 6–11 years of warming (Oberbauer et al. 2007). Fluxes of CO_2 were measured using chamber systems in different plant communities at each site over two field seasons and results showed variation in responses to warming depended on site and moisture conditions. Warming increased both ecosystem respiration (ER) and gross ecosystem photosynthesis (GEP), but the balance of the fluxes (NEE) depended on the tundra plant community. Warming increased NEE in wet tundra at three of the four sites, and was variable in dry and moist sites. Interestingly, the greatest response in both ER and GEP was in dry sites. These initial studies have yet to be replicated or linked to the changes in plant communities measured at all ITEX sites; however, a new synthesis is planned.

The ITEX data have also been used to test the similarities between the three major approaches to derive inferences about the impacts of climate change and the future states of ecosystems: field experiments, historical comparisons (e.g., repeated measurements) and space-for-time substitution (sampling along gradients). Using the plant cover data set, Elmendorf et al. (2015) showed that all three methods had the same direction of change in tundra communities but the space-for-time substitution overestimated the magnitude of change, whereas monitoring and experimental approaches had similar magnitudes. This study provided strong verification of using all three approaches, and emphasized the usefulness of the experiment and monitoring approaches used in ITEX and other coordinated distributed experiments.

One indication of the impact of ITEX research over the past 30 years is the number of citations of the synthesis papers that have been published since 1997 (Table 1). The two most cited papers from the first special issue in *Global Change Biology* are shown as part of the list of synthesis papers – there were 16 papers in the special issue (Henry and Molau 1997). Using data from journal web sites the citations range between 10 and 60 per year, showing these studies are read and cited frequently. The highest citation rate is for a synthesis of tundra plant traits (Bjorkman et al. 2018), that involved many ITEX sites and researchers, but also other studies and sites. The ITEX Google Scholar page (https://scholar.google.com/citations?hl=en&user=fTF80xoAAAAJ) gives an estimate of citations for all papers linked to the site (25280) and an h-index of 85 (as of 2022-06-09).

The ITEX design for the OTCs has been adopted for use in warming experiments in other ecosystems, including grasslands (e.g., Cowles et al. 2017; Welshofer et al. 2018;

Table 1. Number of citations documented for papers presenting results from an ITEX synthesis effort (as of 2022-05-05).

Publication	Journal	Citations (GS)*	Citations (J)**	Citations/y (GS)	Citations/y (J)
Henry and Molau (1997)[a]	Global Change Biol.	550	266	22.4	14.4
Marion et al. (1997)[a]	Global Change Biol.	750	485	30.6	26.2
Arft et al. (1999)	Ecol. Monog.	1089	252	48.4	11.2
Walker et al. (2006)	PNAS	1401	854	90.4	55.1
Oberbauer et al. (2007)	Ecol. Monog.	329	207	22.7	14.3
Elmendorf et al. (2012*a*)	Nat. Clim. Change	779	627	74.2	59.7
Elmendorf et al. (2012*b*)	Ecol. Lett.	923	568	87.9	54.1
Oberbauer et al. (2013)	Phil. Trans. R. Soc. B	143	82	16.8	9.6
Elmendorf et al. (2015)	PNAS	231	145	35.5	22.3
Prevéy et al. (2017)	Global Change Biol.	134	104	29.8	23.1
Bjorkman et al. (2018)[b]	Nature	388	269	110.9	76.9
Prevéy et al. (2019)	Nat. Ecol. Evol.	65	45	26.0	18.0
Collins et al. (2021)	Nat. Comm.	11	11	11	11
Total citations	—	6793	3915	—	—

*Google Scholar.
**Journal web site.
[a]Journal citations since 2003.
[b]ITEX-inspired synthesis.

Carlyle et al. 2014), temperate deserts (e.g., Yue et al. 2018), and forests (e.g., De Frenne et al. 2010). More than 700 published studies cite the initial study evaluating OTC performance in tundra systems (Marion et al. 1997), indicating the researchers had adopted the design from ITEX studies.

Participation in international scientific programs

Other impacts of ITEX research and researchers include participation in international scientific programs or projects. During the International Polar Year (2007–2008), ITEX was chosen as a full project (Henry et al. 2012), which allowed researchers to access funds for IPY research in their country. In Canada, a large project linked to ITEX involved researchers, students and communities across the Canadian Arctic (Henry et al. 2012). Successful proposals for IPY research in Canada and the U.S.A. led to the first complete data bases for phenology and species composition and abundance from ITEX sites (Elmendorf et al. 2012*a*, 2012*b*; Oberbauer et al. 2013; Prevéy et al. 2017, 2019; Collins et al. 2021).

As ITEX became known as a pan-Arctic network, participants have been asked to contribute to assessments and programs in the Arctic Council, including the Arctic Climate Impact Assessment (ACIA 2005), the Arctic Biodiversity Assessment (CAFF 2013), and the Circumpolar Biodiversity Monitoring Program. Members of the ITEX steering committee have been leaders and members of the Terrestrial Ecosystem Working Group of the International Arctic Science Committee (IASC) since its inception in 1996. ITEX researchers are often asked to contribute as participants in Arctic research coordination activities including the International Conference(s) on Arctic Research Planning (ICARP) and the Arctic Science Summit Week (ASSW). ITEX is also part of the Arctic Observing Summit (AOS), which attempts to coordinate monitoring of environmental variables across the Arctic (Henry et al. 2013). Members of the ITEX Steering Committee also contribute to the IPCC (IPCC 2018). In addition, ITEX researchers are often authors of the terrestrial ecosystems report for the annual Arctic Report Card, which covers the responses of Arctic systems to ongoing climate change (http://www.arctic.noaa.gov/Report-Card)

ITEX—the first 30 years: Introduction to the special issue

This special issue is dedicated to 30 years of ITEX research as a coordinated distributed experiment. The papers in this special issue show the breadth, depth, and maturity of ITEX research, covering responses of plant phenology, growth, and reproduction to experimental and ambient warming, but also studies that were inspired by and facilitated by the ITEX network. The first special issue on ITEX research (e.g., Henry and Molau 1997) focused on studies of the impacts of first three years of experimental warming on common vascular plant species; 25 years later, the topics covered in this current special issue shows the evolution of ITEX into a comprehensive ecological network examining the structure and function of tundra ecosystems and their responses to environmental change at a variety of scales. In this section, we summarize the topics covered by the papers in the special issue at the time of publication. Additional papers on ITEX research will be linked to the special issue as they are published in *Arctic Science*.

Snow regimes

Seasonal snow dynamics have strong impacts on tundra ecosystems as the depth, duration, and distribution of snow affects the winter microenvironment of plants (insulation and protection from dehydration), the start of the growing season and moisture supply. These factors affect phenology and species composition of vascular species (Moriana-Armendariz et al. 2022*b*). Rixen et al. (2022) provide a comprehensive review of the role of snow regimes in tundra systems and snow studies at ITEX sites. They found the variation in snow melt dates in snow manipulation experiments (e.g., snow addition and removal, and snow fences) is much less than in natural snow melt gradients across most sites. This has important implications for interpreting the effects of manipulations. Combining manipulations along a natural gradient could be a more integrative approach and provide a better understanding of the effects of changes in the snow regime.

Many ITEX sites have snow manipulations either separately or in combination with OTCs to test effects of warming and snow addition and removal to delay or accelerate the start of the growing season. Extending a warmed growing season by removing snow from OTCs at a High Arctic site had the greatest effect on growth of two shrub species relative to warming or snow removal alone (Frei and Henry 2022). Some of the longest running snow fence studies in ITEX were established in 2006 at Adventdalen Valley, Svalbard (Björkman et al. 2010). Results from these experiments show that there was a similar effect on timing of autumn senescence in an evergreen shrub (*Dryas octopetala*) between snow fence experiments and natural snow gradients (Gehrmann et al. 2022). Establishing OTCs at the end of the growing season in these snow fence plots, delayed senescence of *D. octopetala* and resulted in a 10% increase in the length of the growing season. Hence, late season warming may extend the growing season for some species. In the snow fences, deepened snow changed the vegetation over a decade, with an increase in bryophytes and a decrease in shrub cover (Mörsdorf and Cooper 2022) and these changes were further enhanced by warming in OTCs. These findings are in contrast to general predictions in ITEX synthesis studies of a decrease in bryophytes due to strong responses in shrubs (Walker et al. 2006; Elmendorf 2012*a*, 2012*b*); however, in High Arctic sites the dwarf shrubs generally do not shade the bryophytes, and the warmer and wetter environment in the OTCs promotes bryophyte growth, an effect also found at another High Arctic site (Hudson and Henry 2010). The deepened snow also promoted the occurrence of parasitic fungi: one that infects the evergreen shrub *Cassiope tetragona* and another that infects the moss species *Sanionia uncinata,* indicating that climate change with increased snow fall could result in greater incidence of fungal–plant disease (Moriana-Armendariz et al. 2022*a*). In addition, the snow fences were used to study plant–insect visitation rates in an effort to understand the effect of snow melt timing on flower phenology and availability for (potential) pollinators. However, the delayed timing of flowering in the snow fences and along natural gradients did not affect visitation rate (Gillespie and Cooper 2022). There is usually a mosaic of snow melt timing across a tundra landscape, so insects should find flowers available over much of the growing season.

Bryophytes—a growing component in ITEX studies

The importance of bryophytes is often not fully included in ITEX studies, largely because of the difficulty of identification of species in the field and the lack of taxonomic experts. As a result, this very diverse group of organisms in tundra ecosystems, both taxonomically and functionally, often gets grouped into a single "bryophyte" or "moss" category. The relative diversity and importance of bryophytes increases with latitude (Vitt and Pakarinen 1977; Wielgolaski et al. 1981; Geffert et al. 2013), and their role in ecosystem functions is still poorly understood. Bryophytes are known to be important for moisture holding capacity in soil, hosting N-fixing organisms and mycorrhizae and can have strong effects on carbon and energy fluxes, especially in forming carbon rich organic matter in wet tundra soils (Turetsky et al. 2012.). In an effort to increase the resolution of bryophytes in ecological studies of tundra systems, Lett et al. (2022) propose 12 bryophyte functional groups that are relatively easy to distinguish in the field based on shoot morphology and colony structure and are shown to vary in moisture holding capacity—an important bryophyte trait. Testing these groups and determining the diversity of species within each of them is a priority for ITEX researchers and will be a subject for an upcoming synthesis study.

Related to this effort to better understand bryophytes in tundra systems, van Zuijlen et al. (2022*a*) found that bryophyte abundance, diversity, and evenness increased in ambient plots over 20 years, but were suppressed in experimentally warmed plots at Finse, Norway. In a related study, they found that bryophyte and lichen traits did not respond to experimental warming as predicted (van Zuijlen et al. 2022*b*). This indicates differences in how bryophyte taxa respond to environmental change, and perhaps that the OTCs have more confounding effects for bryophyte responses to experimental warming than for vascular plants. There is a need to conduct more studies on the responses and roles of bryophytes in tundra (and other) ecosystems.

Trophic interactions: pollination and herbivory

Biological interactions may impact the responses of individuals in the plots at ITEX sites (e.g., Post and Pedersen 2008); however, ITEX protocols have not yet been developed specifically to deal with intraspecies or interspecies interactions (e.g., competition, and facilitation), or trophic level interactions (e.g., pollination, and herbivory). As mentioned there were concerns that the OTCs may interfere with access to the plants by insects, which would affect pollination and herbivory. There are contrasting reports of the effect of the OTCs on pollination by insects. A study by Robinson and Henry (2018) found no effect on pollination rates at a High Arctic site, whereas another study found reduced seed production in OTCs by two obligate outcrossing alpine plant species (Adamson and Iler 2021). It is likely that the impact of OTCs on pollinators is site and species specific.

Similarly, discussions at early ITEX meetings involved how the experiments would affect herbivory, and specifically insect herbivory. A group of ITEX researchers began to work on protocols to determine the effects of warming on herbivory and to include herbivory in measurements at ITEX and other tundra sites. This group eventually established a sister network (the Herbivory Network: https://herbivory.lbhi.is) and they have developed and tested a set of protocols to assess insect herbivory at ITEX sites and vertebrate herbivory across sites (Barrio et al. 2022). Their assessment of insect herbivory at ITEX sites showed warming had site-specific responses on herbivory rates and there may not be common responses due to complexities involved in these interactions.

Responses to extreme climate

Increases in the frequency and magnitude of extreme years (climatic conditions that are well above or below the normal conditions) had been predicted by climate models and analyses of annual climate data are confirming the predicted trend (Stott et al. 2016). Tundra regions are also experiencing these intense changes in climate, which have very strong effects because of the lower thresholds for change in high latitude ecosystems (Walsh et al. 2020). The growing season of 2018 was one of the coldest on record for some sites, including Zackenberg and Kangerlussuaq, Greenland, and the Canadian High Arctic. At a site near Kangerlussuaq, nesting for Lapland longspur (*Calcarius lapponicus*) may have been as much as 37 days later than normal, likely due to the cool spring and growing season (Post et al. 2019). And at Zackenberg, eastern Greenland, there was a collapse of bird and plant reproduction (Schmidt et al. 2019). The following season (2019) was abnormally warm, and the contrast between the two years provided a unique example of the responses of plants to these extreme years. Panchen et al. (2022) describe the effect of the weather of 2018 and 2019 on the reproductive effort and success of a set of tundra plant species in the Canadian High Arctic. Seeds of two of four species investigated in 2018 from ambient control plots had little or no germination, whereas plants in OTCs had low rates of germination, although they were also below normal. In 2019, the rates recovered but not to normal levels in either the experimental or control plots. These results show the important effect extreme years can have in tundra systems, and confirm that warming by OTCs simulates a warm year (Hollister and Webber 2000).

Long-term vegetation change

With 30 years of observations and measurements at ITEX sites, the network has some of the best plot-level data to assess changes over time in ecosystem components and to synthesize the responses to ambient and experimental warming (e.g., Walker et al. 2006; Elmendorf et al. 2012*a*, 2012*b*). Two studies in this special issue show the effects of long-term experimental and ambient warming on vegetation composition and abundance. After 26 years of experimental warming in five different tundra communities at one of the original ITEX sites in northern Sweden, Scharn et al. (2022) show there have been shifts in the diversity of growth forms but changes in relative abundance depended on the soil moisture status of the plant community. They found a general increase in shrub abundance, and soil moisture status was a major factor determining whether it was an increase in evergreen or deciduous species. However, they did not find a general decrease in diversity through the loss of bryophyte and lichen species, as noted in previous syntheses (Walker et al. 2006; Elmendorf et al. 2012*a*, 2012*b*).

In response to ambient warming, Harris et al. (2022) found increases in heights and cover of graminoids and shrubs at three sites in northern Alaska. Plant cover at one site increased 5-fold over the decade of annual measurements. Betway et al. (2022) also found increases in plant height, cover and N content of leaves over the same region and time period, but there were no changes in measured plant traits for major species at the three sites. Traits appeared to be conserved over time with no changes found in community weighted traits for any species. It appears the ecosystems are responding to warming evenly, with no species or growth form dominating the response. The results from these long-term vegetation studies are important regional expressions of the general trends reported in pan-Arctic studies (e.g., Elmendorf et al. 2012*a*, 2012*b*) and provide the details and context at the regional scale. Having these long-term records allows trajectories of change to emerge from early responses to experimental or ambient climate change.

Revegetation after disturbance

Recovery of tundra vegetation after disturbance can take decades, especially if the surface is depressed as in vehicle tracks across wet to mesic tundra (Forbes 1992; Forbes and Jefferies 1999). Industrial activity in some Arctic regions has increased over the past decades, and revegetation of disturbances is usually required (e.g., Mackenzie Valley Land and Water Board 2013). However, there are few studies of revegetation in the Arctic and hence few options for industrial entities to minimize and attempt to restore any surficial damage in tundra systems. Neby et al. (2022) conducted a revegetation study of a vehicle track after a single pass in a heath community on Svalbard. Although some vegetation recovered in the tracks after nine years, only the fertilizer treatment had a significant effect; however, the functional composition of the track was significantly different with increased bryophyte cover in the track relative to the undisturbed tundra. These major physical disturbances to tundra surfaces may result in permanent changes in the vegetation, through alteration of the ecohydrology.

Species-level responses

Potential for adaptation: Common garden studies

There is concern that extant populations and species in tundra communities will not be able to adapt to the pace of environmental change and may face local extinction at southern and northern ends of their range due to biological or physical constraints (e.g., competition or loss of optimum climatic regimes). Common garden studies along gradients, especially latitudinal gradients, provide an effective method to test the ability of populations or species to adapt to different climate, soil and biotic conditions and answer questions such as: (*a*) can southern populations grow well under the warming climate conditions at the northern end of their range (hinting at the role of migration and gene flow); and (*b*) do northern populations have the adaptive capacity to maintain growth and reproduction under expected warmer conditions? Despite the relatively simple design, the number of common species or congeners and the ability to answer important questions about adaptation and migration, the ITEX network has few common garden studies, especially including warming by OTCs. In one of the first of these studies, Bjorkman et al. (2017) found southern populations of two forb species did not survive or grow as well as local populations, even in experimentally warmed plots. This indicated factors other than temperature were limiting the establishment of southern populations, and likely included edaphic conditions, snow melt date and the light regime. In contrast, Parker et al. (2022) show that southern ecotypes of a foundational species (*Eriophorum vaginatum*) were able to adjust to the growing season snow melt dates, duration and temperatures and maintain their larger biomass relative to the local northern ecotypes at northern locations, and the effect was enhanced in OTCs. In addition, some of the northern ecotypes were able to adjust to the growing season length and temperatures at the southern common garden. The differences between the two common garden studies are likely due to the species and the latitudinal differences: southern populations of two forb species were moved north by ten degrees in Bjorkman et al. (2017) and a graminoid species (*E. vaginatum*) by two degrees in Parker et al. (2022). Establishing more common garden or reciprocal transplant studies in the ITEX network and elsewhere in tundra ecosystems would help to untangle some of the contrasting responses and provide better predictions of survivorship and adaptation in tundra plant species as their environment changes.

Responses to shading

The increasing height of mainly deciduous shrubs across the Low Arctic is predicted to impact prostrate plants through increased shade (Billings 1987; Myers-Smith et al. 2011). The greater canopy height and density will lower light levels, temperatures, and evapotranspiration rates at the surface and these factors will affect the phenology, growth, and reproduction of prostrate species. May et al. (2022) tested these impacts using experimental shading in tundra communities near Toolik Lake, northern Alaska, over two years on two species of berry-producing evergreen shrubs. Shade did lower surface temperatures and caused an increase in soil moisture, likely due to decreased evapotranspiration. Both species showed delayed greening and lower flower production under the maximum shade treatment (80%). Hence, under dense cover of deciduous shrubs prostrate species may decline changing the diversity of the tundra. As many shrub species span the forest–tundra ecotone (Myers-Smith et al. 2011), and hence experience forest or tundra conditions, additional studies, including reciprocal transplant experiments, could provide further insights on the effects of shading.

Other studies of individual species and species traits

A unique study of warming, fertilization, and shading effects on the essential oil content of the evergreen shrub *Rhododendron tomentosum* showed that the highest oil concentrations were found in unmanipulated control plants and in those fertilized by a combination of N and P, whereas shading and addition of P resulted in the lowest concentrations. Warming also decreased the oil content by about 65% (Baldwin and Oberbauer 2022). The responses in essential oil content by *R. tomentosum* were also affected by the changes in the plant community after 14 years of treatments, especially the increase in shrub growth.

Leaf toughness is a trait related to defense against insect herbivory and lowered digestibility for larger herbivores, and is also related to litter quality. Fetcher et al. (2022) measured leaf toughness in 11 species in four functional groups along a gradient of sites in northern Alaska and in response to fertilization. Toughness was greatest in the graminoid species *Eriophorum vaginatum* and lowest in the dwarf berry-producing shrub *Rubus chamaemorus*, and evergreen shrubs had higher toughness values than deciduous shrubs. Toughness increased with summer temperature in *E. vaginatum* and a deciduous shrub and had little effect on other species, and fertilization decreased toughness but only in 40% of the species.

Ecosystem level responses

Although the original focus in ITEX was on responses of common vascular plant species, the research naturally involved questions at the ecosystem scale, especially regarding the supply of nutrients and how it could affect the responses measured aboveground. Nutrient addition studies alone and combined with warming consistently show tundra vegetation is generally more nutrient than temperature limited (e.g., Chapin and Shaver 1985; Chapin et al. 1995; Henry et al. 1986; Klanderud and Totland 2005). Changes in composition and abundance of tundra communities to greater cover of shrubs would lead to changes in litter abundance and quality (Wookey et al. 2009), and this will impact nutrient cycling in tundra soils and feedback to vegetation change (Pold et al. 2021). There is a growing number of studies of litter decomposition in tundra systems, and a common protocol across terrestrial ecosystems is the Tea Bag Index (TBI) (Keuskamp et al. 2013). Björnsdóttir et al. (2022) used the TBI to examine the influence of warming and plant community type on decomposition in two sub-Arctic tundra types in Iceland and three High Arctic types in Svalbard. Decomposition was only stimulated by OTCs in the warmer Icelandic site that was dominated by deciduous shrubs, but had little effect in a moss dominated site or the High

Arctic sites. This enhanced decomposition rate was most likely caused by the increased shrub and litter abundance and therefore an indirect effect of the OTCs.

Soil processes such as litter decomposition and mineralization depend on the microbial communities in these habitats. Vegetation composition and abundance has changed in response to experimental and ambient climate change across the tundra biome (Elmendorf et al. 2012*a*, 2012*b*), with an increase in shrub height and biomass, especially in Low Arctic sites. Greater plant growth and the shifts in vegetation have also increased litter accumulation (Elmendorf et al. 2012*a*, 2012*b*) which could affect the bacterial and fungal abundance and diversity in litter and soils. This hypothesis formed the basis of a study of the effect of OTC warming on bacterial and fungal abundance across 12 ITEX sites (16 sub-sites) by Jeanbille et al. (2022). In general, warming did not have an overall significant effect on microbial abundance and effects were specific to sites and community types. Increases in $\delta^{15}N$ in litter in warmed plots was linked to greater bacterial abundance, especially in sites dominated by deciduous shrubs. This could indicate changes in bacterial processes involved in nitrogen cycling under warmed conditions. However, other studies have found either no change in microbial abundance or process rates (e.g., Lamb et al. 2011) or significant positive or negative effects in response to experimental warming (e.g., Clemmensen et al. 2006; Christiansen et al. 2017). Resolving these differences and getting a clearer understanding of soil microbial dynamics and processes in tundra soils in a changing climate is the focus of researchers linked to ITEX.

What next for ITEX after 30 years?

The papers in this special issue show that ITEX is a vibrant network with an expanding horizon of studies into tundra ecosystems at nearly all scales: there are studies using plot scale remote sensing (NDVI; May et al. 2022) and molecular genetic methods (Jeanbille et al. 2022), and there are new studies of biological interactions and bryophytes (Barrio et al. 2022; Lett et al. 2022). The need to understand and predict the changes in tundra systems is growing more urgent (Overland et al. 2019), and the ITEX network of researchers and sites will be an important part of the research required. In the first special issue, the question "what next for ITEX?" was posed at the end of the summary paper (Henry and Molau 1997), and the list included studies of vegetation change, soil processes (mineralization and decomposition), and effects on and by herbivores. Papers in the current special issue deal with each of these research areas and more. However, there are areas of research and practice that should be pursued, and in some cases are being studied. Below we outline some of the research areas to which ITEX could contribute and expand over the coming years.

New locations—northern communities

ITEX sites have traditionally been located in remote research stations or sites familiar to the researchers. Locating research sites in proximity of northern communities allows possibilities of knowledge exchange and linking the studies with local schools. This approach has worked exceptionally well in Canada and northern Alaska (Henry et al. 2012; Boulanger-Lapointe et al., 2019, 2020). New research questions of interest to local people emerge with these interactions and can make the studies directly relevant to those living in the rapidly changing Arctic.

Scientific directions and questions

Multiple climate drivers and extreme events

Although the original focus in ITEX was on effects of warming, there are multiple drivers of climate change that interact with different temporal and spatial thresholds and consequences. Some sites have experimental studies that combine drivers, such as warming

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and snow manipulations (e.g., Frei and Henry 2022; Mörsdorf and Cooper 2022; Rixen et al. 2022). However, these studies are limited and there are few studies with more than two drivers, mainly due to complexities in experimental design. Despite these issues, we need a better understanding of how drivers interact and the consequences for tundra ecosystems (Bjorkman et al. 2020). For instance, the winter season is warming more than the summer season and the frequency of extreme winter events, such as warm spells with rain on snow, are increasing (ACIA 2005; IPCC 2018; Walsh et al. 2020; Panchen et al. 2022). As an example, Le Moullec et al. (2019) describe a factorial experiment that combines summer warming with OTCs and winter icing events (rain on snow) at a site on Svalbard. Greater frequency and duration of icing events can damage and eliminate vegetation, and restrict access to forage for herbivores. In addition, parts of the Arctic are becoming wetter, with greater summer rainfall (Walsh et al. 2020). An increase in soil moisture will affect surface energy balance, species composition and abundance, and ecosystem function, with consequences for all trophic levels. Developing protocols for the combinations of warming and winter icing and increased summer rainfall could be developed for ITEX sites and would provide insights on the consequences of interactions of these drivers.

Biotic interactions

As described in Barrio et al. (2022), protocols for combined studies of warming and herbivory have been developed and tested at a few ITEX sites. Expanding these studies across the ITEX network would provide important insights on the reciprocal effects of warming-induced changes in vegetation on herbivory and the effects of changes in herbivory rates on vegetation responses.

Other biotic interactions, including pollination, competition, facilitation, and plant–soil microbial relationships will be affected directly and indirectly by climate change. Shifts in biotic interactions will affect the direction and magnitude of changes in tundra vegetation (e.g., Post and Pedersen 2008). New studies will be required at ITEX and other sites to better understand the influences of these interactions and how they may be altered by climate change.

Incorporating bryophytes

As Lett et al. (2022) discuss, bryophytes need to be better integrated into studies of tundra ecosystems to better incorporate the responses and influences of a major component. This will require early career researchers to become better trained in bryophyte taxonomy, but studies that test the proposed bryophyte functional groups will be an important step. Protocols can be developed for responses of bryophyte species and functional groups to experimental and ambient climate change, including better knowledge of their ability to adapt to the rapid environmental changes.

Vegetation change: verification of remote sensing

Myers-Smith et al. (2020) discuss some of the issues of relying on remote sensing to detect change over time without verification on the ground. ITEX sites have the actual measurements of these changes (e.g., Walker et al. 2006; Elmendorf et al. 2012*a*, 2012*b*). Combining the plot measurements with plot-level and landscape-level remote sensing will help to improve interpretations from satellite-based sensors. Use of spectral radiometers and cameras, either on platforms such as drones or kites or installed above plots at ITEX sites allows effective and efficient measurements of greening and flowering in plots and can be used to detect shifts in these variables in response to experimental and ambient climate change (e.g., Chen et al. 2010; Beamish et al. 2016; Depauw et al. 2022; May et al. 2022). A data base of plot photos at ITEX and other tundra sites linked to landscape images from plots and drone platforms has been established as part of the HiLDEN network

(Assmann et al. 2019), which will be useful for analyses of the continued changes in species composition and abundance.

Potential for adaptation and migration in tundra plant species

We need a concerted effort to better understand the potential for tundra plant species to adapt to the rapid environmental changes and whether migration of southern populations can help to maintain populations at the edges of their range. The common experimental designs across the ITEX network provide a unique opportunity to study the genomic responses in wild plants to abiotic change without the confounding effects of migration patterns that are found in studies along temperature or latitudinal gradients. Bjorkman et al. (2017) and Parker et al. (2022) used common garden and transplant studies with warming for three species to begin to test these questions without genomic data. In the future, as DNA sequencing becomes less expensive, common garden studies can be combined with genomic analyses (de Villemereuil et al. 2016) and the experimental manipulations to determine which traits and genetic pathways may be involved in promoting adaptation to warming, drought, changing precipitation regimes and extreme events.

Soil processes and belowground dynamics

There have been few studies at ITEX sites examining the effects of ambient or experimental warming on root dynamics and soil processes. For example, Sullivan and Welker (2005) show that OTCs can influence the timing of root growth, and Björk et al. (2007) showed that OTCs affect root traits, such as specific root length. Strong increases in soil carbon have been found after 10 years of OTC warming in wet tundra (Rolph 2003). The need to maintain the experimental plots over time has restricted the use of destructive sampling to minimize damage. Establishing plots for destructive sampling should be encouraged to allow for collection of soil cores or installation of root in-growth cores or mini-rhizotrons (Hollister and Flaherty 2010). The end of the life of an ITEX site would be an opportunity to obtain belowground biomass/phenology and soil information. A new synthesis is planned using root in-growth cores at some sites to link above and belowground phenology.

Concluding Remarks

The International Tundra Experiment has provided a platform for syntheses of plot-based studies to gain biome-wide insights on responses to the rapidly changing climate. Verification of increased shrub height and cover in response to experimental and ambient warming has been a major result from the network. Regional variation in responses indicates the potential and constraints for adaptation to rapid environmental change, whether in situ or from migrations. As shown in this special issue, ITEX researchers continue to broaden and deepen studies on tundra ecosystems leading to better predictions of changes and their consequences for tundra and at regional and global scales. The relatively small ITEX community has grown steadily over the past 30 years, including all of the authors on the papers in this special issue. Researchers wishing to join ITEX and to contribute to the next generation of studies in tundra ecosystems should visit the ITEX web site: https://www.gvsu.edu/itex/. We look forward to the next 30 years of ITEX research.

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Data availability

There were no primary data used in the manuscript.

Author contributions

Greg Henry: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Writing – original draft

Robert Hollister: Conceptualization, Funding acquisition, Investigation, Methodology, Writing – review & editing

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