REVIEW

Responses of terrestrial polar arthropods to high and increasing temperatures

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ABSTRACT

Terrestrial arthropods in the Arctic and Antarctic are exposed to extreme and variable temperatures, and climate change is predicted to be especially pronounced in these regions. Available ecophysiological studies on terrestrial ectotherms from the Arctic and Antarctic typically focus on the ability of species to tolerate the extreme low temperatures that can occur in these regions, whereas studies investigating species plasticity and the importance of evolutionary adaptation to periodically high and increasing temperatures are limited. Here, we provide an overview of current knowledge on thermal adaptation to high temperatures of terrestrial arthropods in Arctic and Antarctic regions. Firstly, we summarize the literature on heat tolerance for terrestrial arthropods in these regions, and discuss variation in heat tolerance across species, habitats and polar regions. Secondly, we discuss the potential for species to cope with increasing and more variable temperatures through thermal plasticity and evolutionary adaptation. Thirdly, we summarize our current knowledge of the underlying physiological adjustments to heat stress in arthropods from polar regions. It is clear that very little data are available on the heat tolerance of arthropods in polar regions, but that large variation in arthropod thermal tolerance exists across polar regions, habitats and species. Further, the species investigated show unique physiological adjustments to heat stress, such as their ability to respond quickly to increasing or extreme temperatures. To understand the consequences of climate change on terrestrial arthropods in polar regions, we suggest that more studies on the ability of species to cope with stressful high and variable temperatures are needed.

KEY WORDS: Climate change, Insects, Arctic, Antarctic, Heat stress, Adaptation

Introduction

Temperatures in polar regions are in many ways harsh and extreme, with long, cold winters, and short summers with periodically high temperatures (Convey, 1996; Danks, 2004). These conditions strongly influence the fitness of individual organisms, and the extreme and variable temperatures experienced in polar regions, together with the fast changes in climate currently taking place, are thus likely to be important drivers of evolutionary changes in polar species. Terrestrial arthropods living in Arctic and Antarctic regions are exposed to and have adapted to these extreme thermal conditions on different spatial and temporal scales (Danks, 2004; Denlinger

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and Lee, 2010). For example, development required to complete the life cycle of many arthropods is not possible within one season. Thus, different life stages can be exposed to very different thermal conditions at a temporal scale, suggesting selection for highly thermally plastic genotypes. Further, variation in microhabitat temperatures, as discussed below, suggests that different species may be exposed locally to very different thermal conditions.

Most studies on the thermal biology of terrestrial ectotherms from high latitudes, which we focus on here, have investigated how species cope with cold temperatures during winter (e.g. Block, 2003; Danks et al., 1994; Holmstrup, 2014; Sinclair et al., 2015). Currently, it is unclear how terrestrial arthropods from polar regions respond physiologically to stressful high temperatures, whether they are exposed to temperatures close to their upper thermal limit, and whether they show similar upper thermal limits to those of species from temperate and tropical regions. Because air temperatures in polar regions are typically low, it has been assumed that the temperatures that terrestrial polar species can tolerate are well above the temperatures experienced in their habitat (Addo-Bediako et al., 2000; Deutsch et al., 2008), and that episodes of extremely high temperatures will be countered behaviorally (Everatt et al., 2014; Hayward et al., 2003). Some polar species may even benefit from climate change; for example, warming of the polar regions may alleviate the stress of living in a low-temperature environment (Peck et al., 2006). However, as discussed below, microhabitat temperature recordings suggest that temperatures can easily reach 30–40°C in polar regions, and that development of polar species will take place under such conditions during the short polar summers. Such temperatures can be stressful for some species, but it is unclear whether the thermal tolerance limits of specific species are close to the microhabitat temperatures that they experience, and to what degree thermoregulatory behavior may help species to avoid stressful temperatures (Sunday et al., 2014).

In this Review, we provide an overview of current knowledge on thermal adaptation of terrestrial polar arthropods to high temperatures, and we discuss variation in heat tolerance across species, habitats and geographical regions. Furthermore, we discuss the potential for species to cope with increasing temperatures both within generations (thermal plasticity; see Glossary) and across them (evolutionary adaptation; see Glossary), and we investigate whether there is evidence that terrestrial arthropods in polar regions show unique physiological adjustments to heat stress. We argue that the ability to cope with high temperatures is increasingly important for the survival of terrestrial arthropods in polar regions, and that it is essential to generate additional data on this if we are to predict future species distributions and abundance of terrestrial invertebrates in Arctic and Antarctic regions.

Temperature regimes in polar regions and the impact of climate change

Although northern and southern polar regions share many features, they equally differ in many ways, and it is difficult to compare these

Glossary

Acclimation response ratio (ARR)
The change in the upper thermal tolerance relative to the change in mean temperature. Quantified in experiments as the slope of the relationship between the upper thermal tolerance and acclimation temperature.

Critical thermal maximum (CT$_{max}$)
Broadly defined as the high temperature at which individuals lose motor control or the ability to move body parts.

Critical thermal minimum (CT$_{min}$)
Broadly defined as the low temperature at which individuals lose motor control or the ability to move body parts.

Evolutionary adaptation
A process of genetic change of a population owing to natural selection.

Heat hardening
A process by which an organism's thermal sensitivity can be increased by a brief exposure to an intermediately high temperature which, in turn, provides protection from injury at a more severe high temperature.

Heat knockdown time (HKT)
The time at which an individual is unable to locomote effectively or remain upright in a static assay.

Rapid cold hardening
A process by which ectotherms rapidly enhance their cold tolerance in response to brief (minutes to hours) chilling or another acclimation cue.

Thermal acclimation
A physiological, morphological or behavioral phenotypic change of an individual in response to a change in temperature.

Thermal plasticity
Ability of an individual to produce more than one phenotype when exposed to different thermal environments.

Univoltine
Referring to organisms having one brood per year.

regions directly. For example, Antarctic latitudes are generally colder than their Arctic counterparts (Convey, 1996). Seasonally, temperatures may vary by as much as 80°C in the Antarctic (Peck et al., 2006). The continental or frigid Antarctic has mean monthly temperatures that rarely and only locally exceed 0°C in summer. However, temperatures in sub-Arctic continental Canada and Siberia are colder than in the equivalent sub-Antarctic zone (Convey, 1996; Pienitz et al., 2004). Further, surface temperatures vary as much as 35°C over the ice sheets, but only about 11°C over sea ice in the Southern Hemisphere, whereas in the Northern Hemisphere the temperatures over sea ice and the ice sheet vary by about 28°C (Comiso, 1994). Also, within Antarctic and Arctic regions, we see large differences in climate patterns. For example, the sub-Antarctic will experience positive mean monthly sea level air temperatures for at least 6 months of the year, whereas the maritime Antarctic will experience such temperatures for 2–4 months out of every 12, and the continental Antarctic will only rarely and locally experience temperatures above 0°C (Convey, 1996). Further, extreme temperature variation is reduced by the maritime climate in the cold Antarctic regions. Thus, in conclusion, large differences in thermal environments are observed between northern and southern polar regions and also within Arctic and Antarctic zones.

Even though polar regions are generally characterized by extremely low temperatures during winter, terrestrial microhabitats, such as south-facing slopes in the Arctic, can occasionally reach high and potentially stressful temperatures. Extreme temperature variation can thus be observed not only across seasons but also on a daily basis across microhabitats (Peck et al., 2006). Temperatures at the microhabitat scale may differ substantially from air temperatures, which are typically measured in the shade 2 m above the ground. For example, solar energy can result in short-term temperature maxima of 30–40°C at both High Arctic and Antarctic continental locations

(Hodkinson, 2005; Sinclair et al., 2006; Smith, 1988; Sørensen et al., 2019), and ground surface and soil temperatures can differ substantially from air temperature (Convey et al., 2018; Peck et al., 2006). Temperature recordings from 20 High Arctic and maritime Antarctic sites show that summer ground and sub-surface temperatures vary more than air temperatures, and that accumulated thermal sum (cumulative degree days – using 0°C as a baseline, the sum of mean daily temperature above zero multiplied by the number of days with that mean temperature) in the ground exceeds the sum in the air (Convey et al., 2018). Further, in the maritime Antarctic, maximum temperature recorded during spring/summer on Signy Island shows a high level of inter-day variation, whereas daily minimum temperatures are relatively constant and close to 0°C (Davey et al., 1992). This is similar to observations in southern Greenland (Sørensen et al., 2019). Together, this highlights the complex and highly heterogeneous terrestrial thermal environment in polar regions, where species are dependent both on maximizing development during a short summer, with variable and periodically high and stressful temperatures, and on survival over long, cold winters during which limited resources are available. Another important point is that we are currently lacking data that enable us to link air temperature warming trends with ground surface or microhabitat temperature trends (Convey et al., 2018). This may be further complicated by changes in plant communities caused by climate change. For example, researchers have found shifts in Arctic vegetation under climate change that will affect temperatures at both the macro- and micro-scale (Asmus et al., 2018; Pearson et al., 2013).

The Arctic and Antarctic regions are also vastly impacted by climate change, as demonstrated by some of the fastest temperature changes observed on Earth (Overland et al., 2017; Turner et al., 2014). For example, Arctic temperatures have exceeded previous records every year from 2014 to 2018, and – even more worrying – Arctic air temperature continues to increase at double the rate of the global mean air temperature increase (Overland et al., 2017), which will have major impacts on terrestrial ecosystems. Patterns of climate change in the Antarctic are more complex. Temperature records from the last 50 years collected at 19 stations show warming trends at 11 of these, whereas seven have cooling trends in their annual data, indicating the spatial complexity of change that has occurred across the Antarctic in recent decades (Turner et al., 2005, 2014). Thus, surface temperature trends show significant warming across the Antarctic Peninsula and to a lesser extent in the rest of West Antarctica since the early 1950s, with little change across the rest of the continent. Further, since the late 1990s, warming has paused on the Antarctic Peninsula, which reflects the extreme natural internal variability of the regional atmospheric circulation (Turner et al., 2016).

Current knowledge on heat tolerance in terrestrial arthropods from Arctic and Antarctic regions
Comparing upper thermal limits for polar arthropods
Here, we have compiled published data on upper thermal limits (measured as critical thermal maxima, CT$_{max}$; see Glossary) for terrestrial arthropods in polar regions (see Table 1). It can for many reasons be difficult to compare species' thermal responses across polar regions directly. For example, the terms Arctic, Antarctic, sub-Arctic and sub-Antarctic are commonly used to describe different regions, although they are not always used in the same way. For the purpose of this Review, we used a climatological aspect (the 10°C summer isotherms) to define polar regions, enabling us to compare the thermal tolerance of polar terrestrial arthropods in the most straightforward way. This criterion can be used for both polar regions and provides a solid basis for comparison of thermal

Table 1. Published studies on upper thermal limits of arthropods in polar regions

Species	Collection date	Time of day	Acclimation status	Ramping rate (°C min⁻¹)	Life stage	Collection latitude (°)	Collection longitude (°)	Ecotype	Habitat	CT_{max}	N	Reference
Eurois occulta	Aug. 2017	Night	Field collected	0.2	Adults	61	−45	Air	–	40.8±0.3	33	Unpublished*
Rhyacia quadrangula	Aug. 2017	Night	Field collected	0.2	Adults	61	−45	Air	–	41.5±0.3	27	Unpublished*
Spaelotis clandestina	Aug. 2017	Night	Field collected	0.2	Adults	61	−45	Air	Under stones	43.6±0.3	24	Unpublished*
Delia fabricii	Aug. 2017	Day	Field collected	0.2	Adults	61	−45	Air	Grassland	40.0±0.5	33	Unpublished*
Dolichopus groenlandicus	Aug. 2017	Day	Field collected	0.2	Adults	61	−45	Air	Banks of fresh waters	41.4±0.2	35	Unpublished*
Otiorhynchus arcticus	Aug. 2017	Day/ night	Field collected	0.2	Adults	61	−45	Surface	Grassland	43.4±0.1	44	Unpublished*
Nabis flavomarginatus	Aug. 2017	Day	Field collected	0.2	Adults	61	−45	Surface	Grassland	45.4±0.3	34	Unpublished*
Psammotettix lividellus	Aug. 2017	Day	Field collected	0.2	Adults	61	−45	Surface	Grassy south facing slopes	47.2±0.2	58	Unpublished*
Nysius groenlandicus	Aug. 2017	Day	Field collected	0.2	Adults	61	−45	Surface	Grassy south facing slopes	49.4±0.0	60	Unpublished*
Wyochernes asiaticus	–	Day	Field collected	0.25	Adults	66	−136	Soil	Stones	37.8±1.1	10	Anthony et al., 2016
Paradosa groenlandica	Jun.–Aug. 2016	Day	Field collected	0.25	Juvenile	61	−45	Surface	Rocky cobble	45.1±0.2	11	Anthony et al., 2019
Paradosa groenlandica	Jun.–Aug. 2016	Day	Field collected	0.25	Adult female	61	−45	Surface	Rocky cobble	45.3±0.1	10	Anthony et al., 2019
Paradosa furcifera	Jun.–Aug. 2016	Day	Field collected	0.25	Juvenile	61	−45	Surface	Moss- and lichen-dominated fen	43.4±0.4	10	Anthony et al., 2019
Paradosa furcifera	Jun.–Aug. 2016	Day	Field collected	0.25	Adult female	61	−45	Surface	Moss- and lichen-dominated fen	46.6±0.5	11	Anthony et al., 2019
Paradosa hyperborea	Jun.–Aug. 2016	Day	Field collected	0.25	Juvenile	61	−45	Surface	Moss- and lichen-dominated fen	46.0±0.2	11	Anthony et al., 2019
Paradosa hyperborea	Jun.–Aug. 2016	Day	Field collected	0.25	Adult female	61	−45	Surface	Moss- and lichen-dominated fen	43.6±0.2	16	Anthony et al., 2019
Paradosa glacialis	Jun.–Aug. 2016	Day	Field collected	0.25	Adult female	69	−53	Surface	Moss (hot springs)	43.2±0.3	14	Anthony et al., 2019
Paradosa glacialis	Jun.–Aug. 2016	Day	Field collected	0.25	Adult female	67	−136	Surface	Scree field	46.6±0.4	9	Anthony et al., 2019
Paradosa lapponica	Jul. 2015	Day	Field collected	0.25	Adult female	65	−137	Surface	Tundra	42.9±3.1	5	Anthony et al., 2019
Paradosa lapponica	Jul. 2015	Day	Field collected	0.25	Adult female	67	−136	Surface	Scree field	45.5±1.0	6	Anthony et al., 2019
Paradosa moesta	Jul. 2015	Day	Field collected	0.25	Adult female	67	−136	Surface	Scree field	44.7±0.5	7	Anthony et al., 2019
Paradosa sodalis	Jul. 2015	Day	Field collected	0.25	Adult female	65	−137	Surface	Tundra	46.4±0.5	4	Anthony et al., 2019
Paradosa sodalis	Jul. 2015	Day	Field collected	0.25	Adult female	67	−136	Surface	Scree field	46.8±0.3	3	Anthony et al., 2019
Megaphorura arctica	Aug. 2011	Day	Acclimation (4°C)	0.2	Adults	78	11	Soil	Moss covered slopes	31.7	30	Everatt et al., 2013a

Table 1. (Continued)

Species	Collection date	Time of day	Acclimation status	Ramping rate (°C min⁻¹)	Life stage	Collection latitude (°)	Collection longitude (°)	Ecotype	Habitat	CT_{max}	N	Reference
Cryptopygus antarcticus	Jan.–Mar. 2012	Day	Acclimation (4°C)	0.2	Adults	−67	−68	Soil	Moss and algae	30.1	30	Everatt et al., 2013a
Alaskozetes antarcticus	Jan.–Mar. 2012	Day	Acclimation (4°C)	0.2	Adults	−67	−68	Soil	Moss and algae	34.1	30	Everatt et al., 2013a
Friesea grisea	Dec. 2002	Day	Field collected	0.25	Adults	−72	170	Soil	Moss banks	34.9±0.2	15	Sinclair et al., 2006
Cryptopygus cisantarcticus	Nov. 2002	Day	Field collected	0.25	Adults	−72	170	Soil	Algal flats	28.7±0.2	15	Sinclair et al., 2006
Isotoma klovstadi	Nov. 2002	Day	Field collected	0.25	Adults	−72	170	Soil	Scree field	33.2±0.3	13	Sinclair et al., 2006
Bothrometopus elongatus	Dec.–Feb. 1998/1999	Day	Field collected	0.25	Adults	−46	37	Surface	Supralittoral rock faces and fellfields	37.6±0.6	10	Klok and Chown, 2003
Bothrometopus parvulus	Dec.–Feb. 1998/1999	Day	Field collected	0.25	Adults	−46	37	Surface	Rock faces and fellfield	38.1±0.4	10	Klok and Chown, 2003
Bothrometopus randi	Dec.–Feb. 1998/1999	Day	Field collected	0.25	Adults	−46	37	Surface	Rock faces and fellfield	36.6±0.5	10	Klok and Chown, 2003
Ectemnorhinus marioni	Dec.–Feb. 1998/1999	Day	Field collected	0.25	Adults	−46	37	Surface	Rock faces and fellfield	38.0±0.2	10	Klok and Chown, 2003
Ectemnorhinus similis	Dec.–Feb. 1998/1999	Day	Field collected	0.25	Adults	−46	37	Surface	Moss field/lowland vegetation	38.7±0.2	10	Klok and Chown, 2003
Palirhoeus eatoni	Dec.–Feb. 1998/1999	Day	Field collected	0.25	Adults	−46	37	Surface	Moss field/lowland vegetation	39.2±0.2	10	Klok and Chown, 2003
Canonopsis sericeus	Dec.–Feb. 2000/2001	Day	Field collected	0.25	Adults	−53	73	Surface	Moss field/lowland vegetation	38.7±0.5	10	Klok and Chown, 2003
Bothrometopus brevis	Dec.–Feb. 2000/2001	Day	Field collected	0.25	Adults	−53	73	Surface	–	34.4±0.7	10	Klok and Chown, 2003
Ectemnorhinus viridis	Dec.–Feb. 2000/2001	Day	Field collected	0.25	Adults	−53	73	Surface	Rocky cobble/lowland vegetation	34.2±0.7	10	Klok and Chown, 2003
Bothrometopus graciliipes	Dec.–Feb. 2000/2001	Day	Field collected	0.25	Adults	−53	73	Surface	Moss field and fellfield	36.8±0.5	10	Klok and Chown, 2003
Embryonopsis halticella	May 1997	Day	Field collected	0.5	Larvae	−46	37	Surface	Tussock grassland	39.7±0.2	10	Klok and Chown, 1998
Halmaeusa atriceps	Apr. 2001/May 2002	Day	Field collected	0.5	Adults	−46	37	Surface	Coastal plain/decomposing plant material	33.2±0.3	10	Slabber and Chown, 2005
Halmaeusa atriceps	Apr. 2001/May 2002	Day	Field collected	0.5	Larvae	−46	37	Surface	Coastal plain/decomposing plant material	32.0±0.3	10	Slabber and Chown, 2005
Myro kerguelensis	2005	Day	Field collected	0.25	Adults	−46	37	Surface	Dry fellfield	35.4±0.2	10	Jumbam et al., 2008
Prinerigone vagans	2005	Day	Field collected	0.25	Adult female	−46	37	Surface	Mire vegetation	35.8±0.1	10	Jumbam et al., 2008
Mucrosomia caeca	–	Day	Acclimation (10°C)	0.05	Adults	−54	158	Soil	–	33.5	–	Kuyucu and Chown, 2021
Parochlus steinenii	Dec.–Feb. 2015–2019	Day	Field collected	0.1	Adults	−62	−58	Air	Herb–moss cover and fellfield	31.4±0.2	10	Contador et al., 2020

CT_{max}, upper thermal limit (means±s.e.m.); N, number of individuals. Dashes indicate that no data were available. If multiple populations or registrations were present, the highest value was chosen. *For more details, see Appendix (data are available from Dryad).

tolerance (Pienitz et al., 2004). The number of polar species that have been investigated is limited, and we have only been able to locate 10 published studies, as well as unpublished results from southern Greenland from our laboratory. This paucity is especially pronounced for studies on species obtained south of 60°S or north of 60°N (see Table 1). We found that the average values of CT_{max} across all investigated terrestrial arthropod species from the Antarctic and Arctic regions were 35.2 and 43.7°C, respectively. CT_{max} ranged from 28.7 to 49.4°C in species across polar regions. The variation in heat tolerance across species on a local scale was extensive. For example, CT_{max} values of species found in the same area of southern Greenland ranged from 40.0 to 49.4°C (Table 1; see Appendix).

Generally, CT_{max} seems to be lower for soil-dwelling species, whereas some surface-dwelling species, such as spiders and seed bugs, show high upper thermal limits (Table 1, Fig. 1). As discussed above, microhabitat temperatures can vary substantially across spatial scales, and this may partly explain the differences in thermal tolerance observed across habitats. For example, more variable and extreme surface and air temperatures may have led to selection for genotypes with higher thermal tolerance, whereas species in the soil are inhabiting a more buffered thermal environment (Bahrndorff et al., 2009a).

Assessing thermal tolerance – methods and limitations

Different ways of assessing heat tolerance in insects are extensively discussed in the literature (Kristensen et al., 2008; Rezende et al., 2011; Santos et al., 2011; Sinclair et al., 2015; Terblanche et al., 2011) and will not be elaborated on here. Studies addressing thermal tolerance typically use static or dynamic ramping assays with predetermined endpoints, where the temperature at which individuals succumb to heat (or cold) stress is registered, e.g. CT_{max} (Box 1). In this analysis, we chose to focus on results from dynamic temperature-ramping assays, where individuals are exposed to gradually increasing temperatures, and the temperature where activity ceases is registered as the CT_{max}. Results from this assay provide measures of heat tolerance that enable comparison
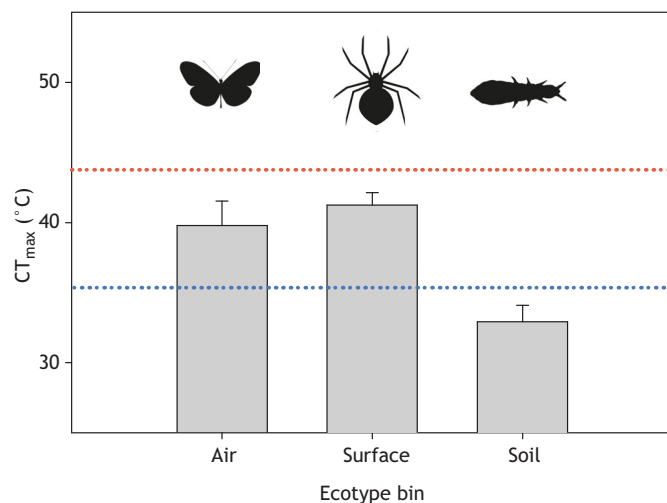

Fig. 1. Upper critical thermal limits (CT_{max}) of terrestrial invertebrates across habitats (air, surface and soil) found in polar regions. Data (means±s.e.m.) are based on published studies and unpublished results (Table 1). The dotted red line indicates mean CT_{max} of data from terrestrial invertebrates from Arctic regions, and the dotted blue line indicates mean CT_{max} of data from terrestrial invertebrates from Antarctic regions. Illustrations above columns indicate species representatives of each habitat.

across studies (but see the potential pitfalls discussed in Box 1). Other studies have examined heat tolerance using other assays on a range of species from polar regions, including midges (Rinehart et al., 2006), collembolans (Aunaas et al., 1983; Block et al., 1994; Everatt et al., 2013b; Hodkinson et al., 1996; Slabber et al., 2007), mites (Deere et al., 2006; Everatt et al., 2013b; Hodkinson et al., 1996), bumblebees (Martinet et al., 2015), spiders and beetles (Aunaas et al., 1983; Bale et al., 2000; van der Merwe et al., 1997), and other arthropods (Slabber and Chown, 2004). However, experimental protocols, cross-tolerance examination and life stages differ between studies, which makes comparisons difficult. Some studies suggest that heat tolerance of polar species is lower than that observed for their temperate counterparts or compared with that of invasive species (Martinet et al., 2015; Slabber et al., 2007).

Studies on ectotherms have shown that adult tolerance to thermal extremes correlates well with their current distribution (Kellermann et al., 2012; Overgaard et al., 2014), but polar arthropods are not included in such studies. Of course, the ecological relevance of the results obtained from both static and dynamic ramping assays can be questioned. Individuals in nature might avoid extreme temperatures by migrating to more benign microhabitats. Thus, they might never be exposed to extreme high or low temperatures in their natural environments. Further, sub-lethal impacts of temperature on many fitness components – such as predation capability, behavior or reproduction traits – might be affected negatively by temperatures much lower (or higher) than those established for critical thermal thresholds in laboratory tests (Walsh et al., 2019; Yao et al., 2019). Less is known about the impacts of sub-lethal stress on surviving individuals, although it has been argued that these traits may be of greater ecological importance than the ability to survive temperature extremes per se (Everatt et al., 2013a). Many polar arthropods need more than a year to complete their life cycle, which can make it difficult to include reproduction output as an endpoint. Thus, some sub-lethal endpoints may be more suited than others addressing the effects of thermal extremes on polar arthropods. For example, locomotion may be a suitable sub-lethal endpoint to consider. Everatt et al. (2013a) showed that locomotion in a species of Antarctic mite, *Alaskozetes antarcticus*, was affected by thermal exposure, increasing with increasing temperature until reaching 25°C. Thus, at temperatures above 25°C, locomotion will decrease; this is well below the CT_{max} of this species (approximately 31°C for summer-acclimated individuals). We argue that future studies examining the ecological and evolutionary impacts of climate change in polar regions should investigate field-relevant measures of thermal robustness, which is vital for the assessment of biodiversity impacts of climate change in these vastly understudied parts of the world. In the context of new assays allowing more ecologically relevant traits to be assessed, it is important that frameworks that allow for comparison of trait values across species and studies are developed, as suggested for thermal fertility limits by Walsh et al. (2019).
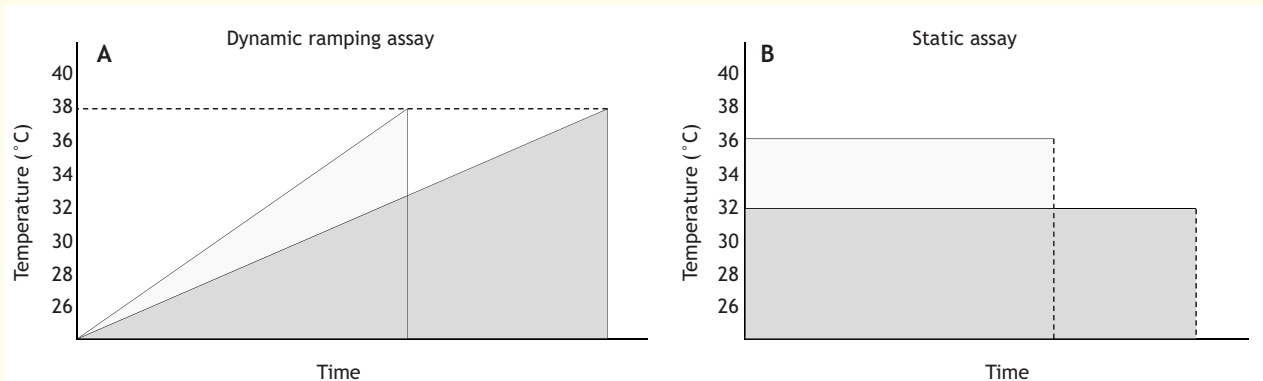
The effect of humidity

Species responses of polar terrestrial arthropods to high temperatures are also dependent on humidity, although the nature of the relationship between heat stress and humidity varies. For example, for some polar species, survival following heat stress increases with increasing humidity or shows no dependence (Block et al., 1994; Hodkinson et al., 1996), whereas other species tolerate heat stress better at low humidity levels (Benoit et al., 2009). Increasing temperatures in polar regions will also increase the likelihood of summer drought. It will therefore be relevant in the future to look at

Box 1. Quantifying heat tolerance and plasticity

Two different approaches are typically used to quantify arthropod heat tolerance. The first is a dynamic ramping assay (left panel), where the organism is exposed to gradually increasing temperatures and the temperature at which a predetermined endpoint (e.g. heat coma, death, loss of motor function) is reached is recorded. The second (right panel) is a static assay, where an organism is exposed to a constant, stressful temperature, and the time it takes to reach the predetermined endpoint is recorded (Hoffmann et al., 2003; Lutterschmidt and Hutchison, 1997; Overgaard et al., 2012). Which assay is the most ecologically relevant has been widely discussed. The dynamic ramping assay reflects the temperature changes that species might encounter in nature, and thus provides a relevant measure of the accumulation of deleterious effects of heat stress (Somero, 2005; Terblanche et al., 2007). However, the dynamic assay is long lasting (typically >3 h), creating an unnatural environment with interacting stressors such as starvation and desiccation that may confound results. The static assay is shorter (typically lasting <1 h); however, species are rarely exposed to such acute temperature changes in nature (Rezende et al., 2011). Several studies have thus also focused on the intensity of heat stress and the exposure duration (Jørgensen et al., 2019; Rezende et al., 2014, 2020). For example, static and dynamic assays give comparable information on heat tolerance across *Drosophila* species (Jørgensen et al., 2019), but static assays may prove superior to measure small differences in thermal tolerance (Bak et al., 2020).

The static assay may better reflect plasticity in heat tolerance for species with a very fast hardening response because such species will undergo hardening during temperature ramping, thus concealing the effects of pre-hardening treatments (Sørensen et al., 2019). However, this effect will depend on the thermal sensitivity of the species and the assay conditions applied, which affect time–temperature interactions on heat tolerance. For the dynamic assay, high starting temperature and fast ramping rates (left panel; steeper line) will probably result in higher critical thermal maximum (CT_{max}) estimates for most species compared with low starting temperatures and slow ramping rates, and thus are also more likely to estimate thermal plasticity. Likewise, the time it will take to reach an endpoint using the static assay depends on the chosen knockdown temperature (right panel; indicated by the two lines; Sørensen et al., 2013). These time–temperature interactions can be problematic, as comparison of CT_{max} and knockdown times across species and treatments is dependent on assay conditions as well as the species' thermal tolerance and level of plasticity (Bak et al., 2020; Overgaard et al., 2011; Sørensen et al., 2019).

not only the effect of high temperatures alone but also heat tolerance at different humidity levels. As pointed out by Everatt et al. (2015), studies addressing the effect of cross-tolerance between desiccation and high temperatures in polar organisms are few, and the outcome may be dependent on the species' strategy to cope with water stress.

More data are needed

Given the limited number of published studies on thermal biology of terrestrial arthropods in response to high temperatures in polar regions, there is a need for additional data on the ability of such species to thrive under increasing future temperatures if we are to expand our understanding of thermal adaptation across species, habitats and polar regions. It is also important that we include species from different classes, orders, etc., as this will allow for an evaluation of the importance of phylogenetic relatedness in determining thermal tolerance. For example, results suggest a strong phylogenetic signal in heat resistance for some species groups – reflecting phylogenetic inertia rather than common selection pressures (Kellermann et al., 2012) – but not in other groups (García-Robledo et al., 2016). Such information may help us better understand thermal responses across species and the extent to which changes in upper thermal limits, through physiological changes within the lifetime of an individual or through evolutionary responses, might be constrained (Hoffmann et al., 2013). In general, such data will be instrumental in forecasting the impact of climate change on arthropods in polar regions and for

our basic understanding of possible differences across regions. It is clear that there will be some limitations in comparing the thermal tolerance of polar organisms directly with that of temperate species; for example, as biodiversity is generally lower in polar regions. Similarly, differences in species richness exist across the Arctic and Antarctic regions. Considering the Antarctic region, the sub-Antarctic has the most species-rich animal community, but still shows a low biodiversity when compared with habitats at corresponding Arctic latitudes (Peck et al., 2006). These differences reflect the evolutionary history of the polar regions, e.g. results suggest post-glacial colonization and the presence of glacial refugia for the Arctic region (Coulson et al., 2014), whereas the Antarctic is extremely isolated (Convey, 2007). The bio-geographical biodiversity patterns may thus partly explain the dearth of ecophysiological information available within and across polar regions (Convey, 1996).

Evolutionary adaptation to high and increasing temperatures

Adaptation to high temperatures through evolutionary changes is typically slow, and in some species heat tolerance has been shown to be constrained by genetic trade-offs and a lack of adaptive genetic variation (Araújo et al., 2013; Hoffmann et al., 2013). In polar regions, where climate change is most extreme, the developmental rate of arthropods is typically slow – as discussed above, many species require several years to complete their life cycle (Convey,

1996; Denlinger and Lee, 2010). Thus, it is likely that evolutionary adaptation of polar arthropods will proceed at an even slower pace compared with that of tropical or temperate species that are exposed to higher average temperatures and typically have faster life cycles (Bleiweiss, 1998; Dillon, 2006; but see Berteaux et al., 2004). Thus, the relative contribution of evolutionary adaptation to increasing temperatures in insects from polar regions might be limited; evolution may not proceed with sufficient speed to enable adaptation to rapidly changing temperatures (Chown and Nicholson, 2004; Sørensen et al., 2016). Studies suggest that some polar species display genetic variation in thermal tolerance across populations (e.g. Bahrndorff et al., 2007), though there is a lack of studies addressing variation in upper thermal limits across populations. It is clear from the literature that large differences in upper thermal limits exist across polar arthropod species (Table 1). This demonstrates the importance of past evolutionary processes on current ecological dynamics. However, as emphasized, we have little information on the levels of genetic variation present within and across populations for different species of arthropods and thus also their evolutionary potential to respond to future environmental changes. Thus, evidence for past natural selection on heat tolerance in polar arthropods needs to be investigated. Further, we need to pinpoint whether adaptation through evolutionary processes is likely to occur fast enough to keep up with climate change and whether genetic constraints exist, for example, as a result of a lack of genetic variation in upper thermal tolerance limits or genetic trade-offs limiting the potential for evolutionary changes. Together, this will increase our fundamental understanding of the ability of polar arthropods to cope with warmer and more variable temperatures.

Physiological acclimation to high temperature

Individuals can show thermal acclimation (see Glossary) to changing and stressful environments by responding plastically, i.e. by altering their physiology, morphology or behavior in response to environmental changes (DeWitt and Langerhans, 2004; West-Eberhard, 2003). Plastic responses can be adaptive or maladaptive, but may be important for coping with diurnal and seasonal changes in temperature (Gunderson and Stillman, 2015; Jensen et al., 2019). There are several published examples of cold acclimation and rapid cold hardening (see Glossary) in polar arthropods (e.g. Bahrndorff et al., 2007; Everatt et al., 2013a; Lee et al., 2006; Teets and Denlinger, 2014; Worland and Convey, 2001), but few studies have investigated physiological acclimation of polar terrestrial arthropods to high temperatures. Further, thermal acclimation and heat hardening (see Glossary) typically increase heat tolerance by only a small fraction of the inducing temperature (e.g. a 10°C increase in temperature increases heat tolerance by 1°C; Chown and Nicholson, 2004). Morley et al. (2019) showed that polar terrestrial arthropods (>55° latitude) had a high acclimation response ratio (ARR; see Glossary) for CT_{max} (*Alaskozetes antarcticus*, ARR=0.3; *Cryptopygos antarcticus*, ARR=0.6); however, their study only included data for two species, both from the Southern Hemisphere. We have found that field-collected individuals of the seed bug *Nysius groenlandicus* from southern Greenland show a high basal heat tolerance (Box 2, Table 1), but a low acclimation response when using CT_{max} as the endpoint (Sørensen et al., 2019). Everatt et al. (2013a,b) found that rapid heat hardening had little effect on heat tolerance for two Antarctic species, and long-term acclimation (1 week at 10°C) did not enhance the heat tolerance of either species. Thus, there seems to be little or no acclimation ability allowing an increase in their upper thermal limits (CT_{max}), supporting the contention that thermal

tolerance shows less phenotypic plasticity at higher temperatures than at lower temperatures in invertebrates (Hoffmann et al., 2013). However, recent studies also suggest that the choice of assay may strongly affect conclusions drawn on the ecological role of thermal plasticity (Bak et al., 2020; MacLean et al., 2017; Sørensen et al., 2019). For example, for *N. groenlandicus*, thermal plasticity for heat tolerance was marked when using a static assay, but not when using a dynamic ramping assay (Box 2). Further, studies on temperate arthropods have shown that heat hardening can have both positive and negative effects, and it can affect other life-history traits, such as the ability to locate resources and reproductive traits (e.g. Alemu et al., 2017; Loeschcke and Hoffmann, 2007; Zizzari and Ellers, 2011). In addition, findings from lab studies on costs and benefits of heat and cold acclimation responses have led to different conclusions compared with findings under natural conditions (Kristensen et al., 2008). These studies highlight that, in order to fully understand the costs and benefits of heat hardening in polar arthropods, further studies are needed; such studies should look at sub-lethal endpoints and use different assays when scoring heat tolerance.

It is important that we increase our understanding of whether the basal thermal tolerance of polar arthropod species gives them sufficient capacity to cope with future climate scenarios or whether plasticity in heat tolerance will be necessary to allow them to cope with more variable and unpredictable temperatures in the future. We suggest that future studies should address the plasticity of the upper thermal limits of polar arthropods and should measure species-specific upper thermal limits using not only lethal but also sub-lethal endpoints. It is also crucial for future studies to obtain information on the microhabitat temperatures that reflect temperatures experienced by each species. We know from existing time series of Arctic and Antarctic microclimates that large temperature differences at soil surfaces and in the vegetation exist both within and across short temporal and spatial scales (e.g. Convey et al., 2018; Davey et al., 1992). For example, some Arctic species, such as seed bugs, may experience extremely high temperatures during daytime in the summer (Box 2). By contrast, nocturnal species, such as moths, may be more buffered from thermal fluctuations. In accordance with this, we found 9°C differences in CT_{max} when comparing day-active and night-active species from southern Greenland (Table 1). Further, we also lack information on thermal acclimation of single species under natural conditions and the importance of warming as a factor driving future extinction rates, particularly in polar regions (Seebacher et al., 2015).
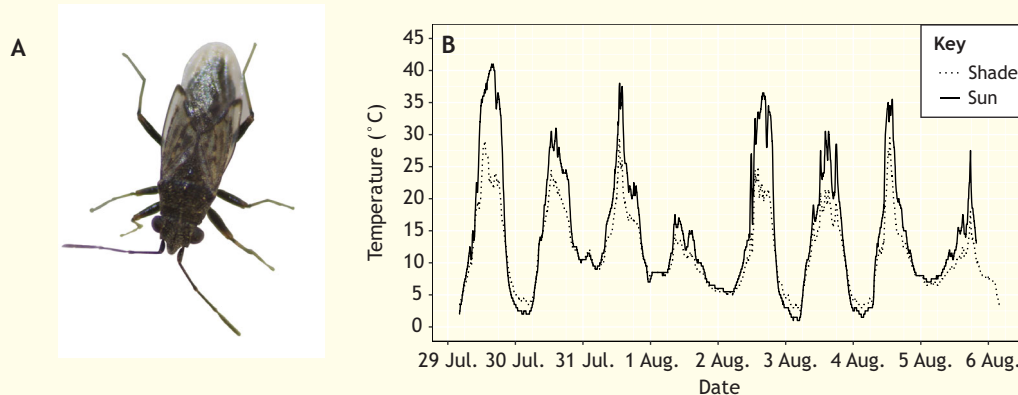
Underlying physiological mechanisms of heat response

Polar terrestrial arthropods can be exposed to high microhabitat temperatures and water stress during their lifetime as discussed above. Even though some polar species show upper thermal limits of up to ~50°C, many species show substantially lower thermal limits, and other life-history traits are likely to be affected at lower temperatures. Thus, polar organisms are highly dependent on physiological adjustments that allow them to cope with high temperatures. However, the physiological mechanisms underlying the plasticity and evolutionary adaptation of upper thermal limits in polar arthropods have not received as much attention as those underlying cold tolerance. Some reviews on the physiological mechanisms that allow insects to cope with high temperatures exist, and in recent years different -omics approaches have additionally increased our knowledge of the underlying physiological mechanisms (Denlinger and Yocum, 1998; González-Tokman

Box 2. An Arctic insect exposed to highly variable temperatures

One of the most widespread and abundant arthropod species inhabiting the Arctic is the seed bug *Nysius groenlandicus* (Zetterstedt), a true bug (Heteroptera) in the family Lygaeidae. The species is widely distributed across all of Greenland and often appears in dense communities in warm and dry sites dominated by herbs and grasses. It feeds on a wide variety of grass and flower seeds (Böcher, 1972). The species is univoltine and utilizes high local temperatures to complete its life cycle within the short summer season. In July–August, adults emerge, mate and lay eggs. The eggs overwinter in a diapause state, and the first of five nymphal stages appears after snowmelt (Böcher, 1975; Böcher and Nachman, 2001).

The Artic and sub-Arctic summer is characterized by cold average air temperatures, but extremely variable conditions close to the soil surface (Böcher and Nachman, 2011). We measured the temperature at ∼20 cm above ground in the sun (solid line) and shade (dotted line) in a grass-covered site in Narsarsuaq, southern Greenland from 29 July to 6 August, 2018. The highest measured temperatures were 29.5°C in the shade and 41°C in the sun, whereas the coldest temperatures were 2.5°C in the shade and 1.0°C in the sun. The largest daily temperature span reached 39 and 26.5°C in the sun and shade, respectively. The seed bug is well adapted to these changes in temperature; the adult life stage of the species has a critical thermal minimum (CT_{min}; see Glossary) of −3.2 to 3.4°C and a critical thermal maximum (CT_{max}) of 49.4 to 52°C (Bahrndorff et al., 2021a; Böcher and Nachman, 2001; Sørensen et al., 2019). Adult *N. groenlandicus* have a strong preference for high temperatures (above 30°C), which is thought to enable rapid growth, development and reproduction in the short and warm summers (Böcher and Nachman, 2001). Further, the heat tolerance is adjusted rapidly by means of phenotypic plasticity to cues in the microenvironment (Sørensen et al., 2019). For instance, the species shows a remarkable ability to quickly induce thermal tolerance to high temperatures [measured as the time spent at high temperatures (48°C) before going into heat coma (heat knockdown time, HKT; see Glossary)]. Individuals almost double their HKT within 45 min of exposure to a hardening temperature of 42°C. The gain in heat tolerance is quickly reversible: 2 h after the hardening treatment, HKT is back to pre-hardening level, indicating efficient regulatory mechanisms. The rapid reversal of the response may allow allocation of energy to processes that are important for completing a fast life cycle. Such rapid phenotypic adjustments seem to be an adaptation to the variable Arctic environment, and suggest that this species might even be able to cope with temperature rises and increased temperature fluctuations predicted in the near future.

et al., 2020; Neven, 2000). However, as pointed out by González-Tokman et al. (2020), the stress response mediated by heat shock proteins (Hsps) dominates investigations of the physiological mechanisms of heat tolerance in arthropods. Therefore, in this section, we begin by briefly discussing the role of Hsps and go on to consider what we know about other mechanisms by which polar arthropods may cope with high temperatures. There is a need for studies addressing not only the stress response mediated by Hsps but also neuronal mechanisms important for detecting and responding to heat, transcriptomic, proteomic and metabolic responses to heat, thermoregulation and the involvement of hormones that coordinate developmental and behavioral responses at warm temperatures (see review by González-Tokman et al., 2020). This is particularly true for polar organisms, as the nature of the thermal environment in which these species dwell is, in many ways, extreme (Box 2).

It is clear that Hsps play an important role in the heat shock response, but this group of proteins can also be induced by many different environmental stressors (e.g. low temperature, radiation and desiccation) (Sørensen et al., 2003). The heat shock response in invertebrates has received substantial attention, and results suggest that the underlying mechanisms differ across not only species but also habitats. Thus, soil-dwelling species inhabiting more temperature-buffered habitats show a distinct heat shock response compared with, for example, species inhabiting areas with more variable temperatures (Bahrndorff et al., 2009b; Dahlgaard et al., 1998). This suggests that unique physiological responses may also

be found for polar species exposed to extreme and highly variable temperatures. In accordance with this, results from our laboratory show that *N. groenlandicus* can quickly increase heat tolerance following heat hardening, but that the hardening response is reversible within hours of hardening, which is much faster than observed in other model arthropod species (Bahrndorff et al., 2009b; Dahlgaard et al., 1998; Sørensen et al., 2019). Several studies have investigated the underlying physiological mechanisms of the heat response in the Antarctic midge, *Belgica antarctica*. Rinehart et al. (2006) found unique thermal adaptations in the heat acclimation response of this insect: there is a dichotomy in survival strategies exploited at different stages of the life cycle. *Belgica antarctica* larvae constitutively up-regulate their Hsps (small hsp, hsp70 and hsp90): these proteins are not further up-regulated by high or low temperature exposure, and the larvae maintain a high inherent tolerance to temperature stress. In contrast, adults show no constitutive up-regulation of their Hsps, have a lower intrinsic tolerance to high temperatures, but are able to upregulate their Hsps when exposed to thermal stress, resulting in enhanced thermotolerance relative to that of adults not exposed to stress. The larval strategy of expressing Hsps continuously while still sustaining growth in *B. antarctica* is unusual and apparently costly. However, this strategy may facilitate proper protein folding in a continually cold habitat that is more thermally stable than that of the adults. Lopez-Martinez et al. (2008) looked at different stressors (all of which would normally be expected to increase the expression of

Hsps) and found that neither heat shock nor freezing and anoxia are able to induce Hsps in larvae of *B. antarctica*, whereas more recent studies have indicated that dehydration stress can induce Hsps (Lopez-Martinez et al., 2009; Teets et al., 2012).

It is not only Hsps that are constitutively up-regulated in the larvae of *B. antarctica*. Lopez-Martinez et al. (2008) also found that two enzymes, catalase and superoxide dismutase, are expressed continuously in larvae, but also in heat-exposed larvae. These enzymes prevent oxidative stress by inactivating reactive oxygen species, thereby limiting damage to lipids, proteins and DNA under stressful conditions. Additionally, Michaud et al. (2008) compared the abundance of metabolites in larvae of *B. antarctica* exposed to a short-term heat-hardening treatment and a control group. Alpha-ketoglutarate and putrescine levels were higher in the hardened group, and glycerol, glucose and serine levels were suppressed. By contrast, Benoit et al. (2009) found the sugar trehalose to be important for heat tolerance in larvae of *B. antarctica*. Larvae injected with trehalose show significantly increased survival following heat shock for 3 h at 30°C compared with control groups. Trehalose accumulates during slow dehydration of *B. antarctica* larvae at 98% and 75% relative humidity. Slow dehydration further increases heat tolerance 3.5-fold compared with that of fully hydrated controls. Together, these results suggest that trehalose is important for mitigating the effects of heat stress. The studies discussed above highlight unique physiological adjustments in polar arthropods to an extreme thermal environment that have not been found in temperate or tropical species.

Altogether, we have a limited knowledge of the physiological responses to heat stress in polar arthropods, and more studies are needed across species in order to better understand the physiological adaptations (and maladaptations) to high and variable temperatures in polar regions. Such knowledge will provide basic information on physiological responses in an extreme environment and allow researchers to better understand what drives evolutionary responses to heat stress.

Responses to climate change in polar regions

As discussed above, we have limited knowledge of thermal tolerance, plasticity of upper thermal limits and the evolutionary adaptive potential for increased heat tolerance of polar terrestrial arthropods. The limited knowledge on species from polar regions means that we have little understanding of how species distribution and abundance in these regions, covering more than 20% of the Earth's area, will respond to climate change.

Several studies have linked shifts in species distribution, including polar arthropods, to changes in climate (e.g. Jepsen et al., 2011; Parmesan and Yohe, 2003; Pearson et al., 2013). There is currently an emphasis on understanding and modeling how future global warming scenarios will affect species abundance and distribution. This can be through the use of trait-based approaches for assessing the relative susceptibility of species to changing temperatures and/or through incorporation of acclimation and genetic adaptation into mechanistic species distribution models (Chown, 2012; Clusella-Trullas et al., 2011; Deutsch et al., 2008; Overgaard et al., 2014). Developments in modeling approaches now allow us to consider processes such as physiology, dispersal, demography and biotic interactions, which permits more robust predictions of future species distribution (Briscoe et al., 2019). However, for the most part, these models have not yet been applied to species in polar regions, partly because an understanding of the fundamental biology of most species is still not available. The modeling of species distribution under future climate scenarios for terrestrial ectotherms in polar regions is based on a very limited number of studies; we have a much better understanding for species living under temperate conditions. However, a recent study employed an ecological niche model using ecophysiological data to predict the future distribution of the Antarctic winged midge *Parochlus steinenii*; it was suggested that this species could be used as an indicator species of the impacts of climate change in the Antarctic (Contador et al., 2020). In addition, a combination of correlative and mechanistic niche models have been used to better understand, predict and manage biological invasions for an invasive insect in the sub-Antarctic; the mechanistic model indicated a slightly larger invasive potential based on larval performance at different temperatures (Bartlett et al., 2020; see also Pertierra et al., 2020). Thus, physiological data will help to provide input to species distribution models, enabling more accurate predictions of the effect of global climate change on terrestrial arthropods in Arctic and Antarctic regions.

The low biodiversity and simple trophic complexity of polar regions (Peck et al., 2006) can provide a unique opportunity to disentangle the effects of climate change on ecosystems, including both direct and indirect effects of factors such as changes in temperature (Høye, 2020). Currently, predictions on how terrestrial arthropods will respond to climate change in cold environments are conflicting. Increasing temperatures could alleviate cold stress and/or lengthen the growing season (Bale and Hayward, 2010), but may also lead to population declines as a result of heat stress (Block et al., 1994), desiccation (Hodkinson et al., 1998) and phenological mismatches (Høye et al., 2013). A number of approaches have been used to link environmental conditions with terrestrial invertebrate numbers (Coulson et al., 1996; Høye et al., 2018; Turney et al., 2018). For example, analysis of long-term datasets on terrestrial invertebrate numbers at a High Arctic site suggests that responses to warming differ for above-ground and soil-dwelling arthropods, and that herbivores, but not detritivores, may benefit from climate change (Koltz et al., 2018). However, most often, direct and indirect effects are not separated, and a deeper understanding of polar terrestrial arthropod responses to high temperatures is needed. We suggest that more species – inhabiting different microhabitats – should be studied, and that thermal tolerance should be more directly linked to habitat temperatures. Further, different thermal assays and a broader choice of traits should be included in future studies, and this should be done in a systematic way, allowing comparisons across studies. Some species may prove more suitable for this than others; for example, a species such as *N. groenlandicus* has a wide geographical distribution and a life cycle that is univoltine (see Glossary), it occurs at very high population sizes and may thus constitute an Arctic and sub-Arctic model species that can provide information on both evolutionary and plastic thermal responses. Likewise, the molecular work conducted on *B. antarctica* can provide a framework for a physiological understanding of thermal responses in polar arthropods in an extreme environment.

Conclusions

Terrestrial arthropods in polar regions have adapted to extreme and harsh environments, with low temperatures during winter, but where microhabitat temperatures can occasionally reach high and potentially stressful levels. Further, the Arctic and Antarctic regions are vastly impacted by climate change, as demonstrated by some of the fastest temperature changes observed on Earth. Generally, we see large variation in upper thermal limits across polar regions, habitats and species. Further, the polar species investigated thus far

show unique physiological adjustments to heat stress in, for example, being able to respond quickly to increasing temperatures. However, there is little information on the evolutionary potential of upper thermal limits and sub-lethal endpoints within and between species of arthropods in polar regions. Some studies have addressed thermal plasticity of terrestrial polar arthropods, but results seem to be dependent on the assay used. The polar regions could provide a unique opportunity to disentangle both the direct and indirect effects of climate change on ecosystems in general. By increasing our fundamental knowledge of key species, thermal tolerance of polar arthropods, how different life-history traits are affected by high temperatures, and the underlying physiological and molecular basis, we will better be able to predict the future abundance and distribution of arthropods in polar regions. This will be invaluable in the light of unprecedented anthropogenic changes affecting these habitats.

APPENDIX
Upper thermal tolerance limits (CT_{max}) data

Upper thermal tolerance limits (CT_{max}) were measured on nine species collected at two locations in Narsarsuaq, Greenland (Table S1). The individuals used for thermal assays were collected in the field using species-specific catch methods (Table S1). Adults of unknown age and sex were tested. To measure CT_{max}, a dynamic ramping assay was used. Field-caught individuals were placed in 15 ml plastic vials with screw caps with a droplet of 2% agar to prevent desiccation during exposure. The vials were mounted to a rack and lowered into a water bath with a temperature of 25°C. Subsequently, the temperature was increased by 0.2±0.01°C min^{-1} using an immersion circulator (Polyscience MX Immersion Circulator model: MX-CA12E). Individuals in each vial were continuously stimulated with a flashlight and tapping on the screw cap with a rod until reaching a temperature at which movement ceased (heat coma). The temperature of heat coma was recorded for each individual. Individuals were stored in 70% ethanol after the thermal assay for later identification. Species were identified based on morphological features using a species identification key (see Böcher et al., 2015).

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