diversity

MDPI

Review

How Might Climate Change Affect Adaptive Responses of Polar Arthropods?

Paige Matheson * and Angela McGaughran

Te Aka Mātuatua—School of Science, University of Waikato, Private Bag 3105, Hamilton 3240, New Zealand
* Correspondence: paige.matheson14@gmail.com

Abstract: Climate change is expected to impact the global distribution and diversity of arthropods, with warmer temperatures forcing species to relocate, acclimate, adapt, or go extinct. The Arctic and Antarctic regions are extremely sensitive to climate change and have displayed profound and variable changes over recent decades, including decreases in sea ice extent, greening of tundra, and changes to hydrological and biogeochemical cycles. It is unclear how polar-adapted arthropods will respond to such changes, though many are expected to be at great risk of extinction. Here, we review the adaptive mechanisms that allow polar arthropods to persist in extreme environments and discuss how the effects of climate change at the poles will likely favour non-native species or those with the ability to rapidly evolve and/or acclimate. We find that physiological, behavioural, plastic, and genetic data are limited in scope for polar arthropods and research on adaptive responses to change is scarce. This restricts our ability to predict how they may respond to a warming climate. We call for a greater investment in research that specifically targets the ecology and evolution of these taxa, including genomic and transcriptomic approaches that can evaluate the potential for plastic and evolved environmental responses.

Keywords: adaptation; Antarctic; Arctic; arthropods; biological invasions; climate change

check for updates

Citation: Matheson, P.; McGaughran, A. How Might Climate Change Affect Adaptive Responses of Polar Arthropods? *Diversity* **2023**, *15*, 47. https://doi.org/10.3390/d15010047

Academic Editor: Luc Legal

Received: 10 December 2022
Revised: 27 December 2022
Accepted: 28 December 2022
Published: 30 December 2022

1. Introduction

Climate change is having increasingly detrimental impacts on the natural environment. In particular, potential warming beyond 1.5 °C is predicted to increase extreme weather events (e.g., floods, droughts, cyclones), impact human livelihoods by limiting potable water/food availability and damaging infrastructure, and threaten many species with extinction due to physically intolerable conditions, changing the entire landscape of ecosystems [1].

Situated at opposite ends of the Earth, the polar regions (Arctic and Antarctic) are some of the most harsh, remote, and inhospitable habitats on the planet (Figure 1). Where the Arctic is an ocean covered by perennial sea ice and surrounded by land, Antarctica is a continent covered by thick ice and surrounded by the Southern Ocean. Both are considered 'barometers' of global health for the role they play in providing planetary-scale balance and circulation—regulating energy exchange between climatic and oceanic systems, driving atmospheric and weather processes, acting as sinks for carbon dioxide, and providing thermal density gradients that drive thermohaline circulation [2,3]. Observed and projected climatic changes in the Anthropocene are comparable to some of the largest environmental changes of the past 65 million years, though human activities such as fossil fuel combustion and land-use change have meant that this is occurring much more rapidly than previously observed in the geological record [4]. Despite their isolation from civilisation, the Arctic and Antarctic polar regions have responded rapidly to human-induced climate change, with small changes in temperature having large impacts on species diversity and distribution [5–7].

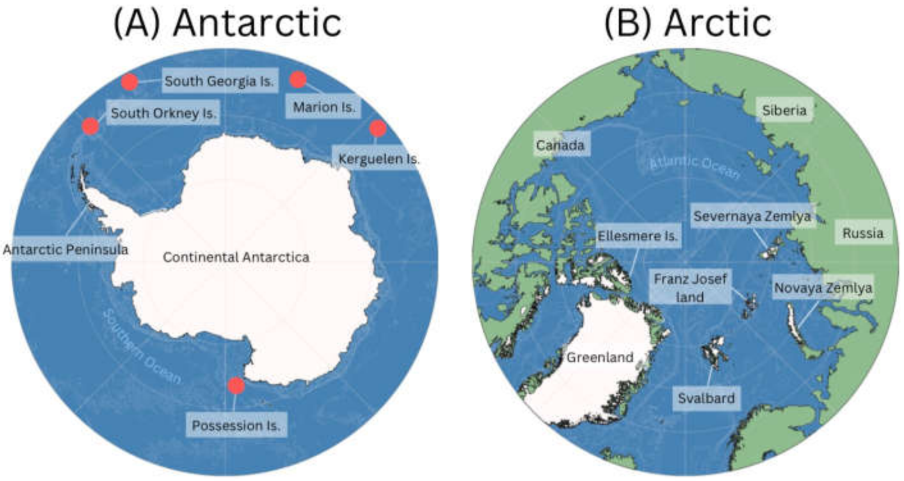

Figure 1. Map of (**A**) Antarctic and (**B**) Arctic regions identifying key locations. Red circles in (**A**) represent relative locations of the main sub-Antarctic Islands.

Arthropods—insects, arachnids, myriapods, and crustaceans—comprise the bulk diversity of species on Earth, with some taxa that have survived all five mass extinction events in evolutionary history (e.g., horseshoe crabs) [8]. As such, they are fundamental members of many ecosystems, playing crucial roles in food webs, pollination, decomposition, nutrient cycling, and pest control [9]. Polar regions are no exception, with some biota that have been present for millions of years throughout glacial cycles and since the breakup of Gondwana, and others that have arrived since the last glacial maximum (<30 kya) [10,11]. Resident polar arthropods must endure environmental stresses beyond the physiological limits of many other species, such as extremely low temperatures (routinely <−15 °C), intense heat stress due to solar radiation that exceeds air temperature (>20 °C) during summer months, dry and windy conditions, and 24 h of darkness during winter [12–14]. As a result, these taxa have evolved unique physiological adaptations to tolerate their local environment.

Nevertheless, arthropods are highly sensitive to environmental changes owing to their diverse life-histories, typically short generation times, large population sizes, and often high rates of adaptability [9]. Therefore, they are excellent research models for elucidating the extrinsic and intrinsic mechanisms that promote survival in a rapidly changing world. Here, we review the literature to ask how climate change might affect arthropods in polar regions. We first examine current Arctic and Antarctic arthropod diversity and some of the most important adaptations that have allowed these species to persist in extreme polar environments. Next, we evaluate how climate change might affect arthropod diversity and distribution in polar regions, with comments on biological invasions and ecological responses of native arthropods. Throughout, we examine both adaptive and acclimatory responses, which we delineate based on timescale—acclimation occurs over a shorter timescale and is more likely to be a temporary response compared to adaptation, which takes longer to express and tends to be more permanent. We consider examples from the high Arctic, low Arctic, and sub-Arctic in our definition of the Arctic region; and both continental Antarctica and nearby sub-Antarctic maritime islands in our definition of the Antarctic region (Figure 1).

2. Polar Arthropods Are Abundant and Diverse, and Exhibit a Range of Adaptations to the Cold

2.1. Abundance and Diversity

The biodiversity of polar arthropods was once thought to be scarce owing to an overly simplistic understanding of their ecology and roles in the ecosystem. For instance, past Arctic food web models collated individual species into related groups (e.g., considered all beetle species one entity), neglecting to account for the wide range of feeding specialisations and adaptations that exist at the species level [15]. In reality, arthropods are the most diverse and abundant phylum found near the poles, accounting for approximately 90% of all known species there, though many are small and have only basic body forms [15,16].

In Antarctica, most terrestrial arthropods are restricted to the less harsh sub-Antarctic islands. For example, at least 41 endemic species of insects and spiders occupy Possession and Kerguelen Islands alone [17]. However, some species inhabit mainland Antarctica in high densities—including soil microarthropods (e.g., springtails, mites), most of which are endemic to the continent [18], and two species of chironomid midges (endemic *Belgica antarctica* and native *Parochlus steineii*). The majority of Arctic arthropod diversity is similarly distributed in less harsh environments of the sub-Arctic and low-Arctic regions, and predominantly consists of springtails, lice, chironomid midges, crane flies, aphids, beetles, moths, and wasps. In the high-Arctic, the same orders exist, though with much fewer species [15,19].

2.2. *Adaptations to the Cold*

All polar-dwelling arthropods are exposed to cold temperatures, often below the freezing point of their body fluids. Resident species, at least to some degree, have a variety of adaptations that allow them to tolerate these local conditions, including physiological, plastic, behavioural, and genetic (Figure 2). For example, some microarthropods have developed parasitic relationships with warm-blooded hosts (e.g., ticks with seals or birds), while others buffer against immediate environmental temperatures by living in a microclimate (e.g., soil or water), or migrating seasonally [14]. By far the greatest focus of research to date has been on physiological adaptations of polar arthropods; we outline some of these below.

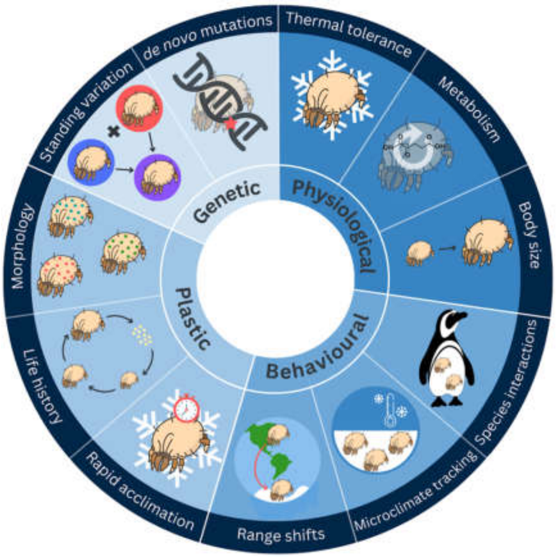

Figure 2. The potential physiological, behavioural, plastic, and genetic responses associated with surviving life at the poles. For simplicity, we depict discrete categories, though responses may fall into >1 category.

2.2.1. Thermal Tolerance

Thermal tolerance is the ability of an organism to survive short- or long-term exposure to temperature extremes. The ectothermic nature of arthropods means that temperature plays a major role in the effectiveness of their chemical and biological functions, therefore, thermal tolerance is a critically important trait for survival and success at the poles [20]. Polar arthropods can be classified as either freeze-avoidant or freeze-tolerant depending on their strategy to survive overwintering, although the factors that determine which species employ which strategy are largely unclear.

Freeze-Avoidance

Most polar arthropods are freeze-avoidant—they survive subzero temperatures in a supercooled state by lowering the point at which their body fluids freeze, referred to as the super-cooling point (SCP) [18,21]. This is achieved through the accumulation of antifreeze and/or heat shock proteins [22], or by the removal of ice-nucleating particles, such as food and microbes in the digestive tract. Bimodal SCP distributions are commonly described, with less cold-hardy species being more active and higher-foraging, while more cold-hardy species are thought to be non-feeding and therefore lacking in ice nucleators from food in the gut [18,23]. However, this is not the case for all species. For example, the Antarctic springtail *Gomphiocephalus hodgsoni* prevents inoculative freezing of body fluids to temperatures as low as −35.4 °C through the accumulation of thermal hysteresis proteins and increased haemolymph osmolality [18,24,25].

Freeze-Tolerance

Freeze-tolerant arthropods can withstand the formation of ice between their body tissues. They prevent intra-tissue damage by producing ice-nucleating and heat-shock proteins [26], and/or accumulating cryoprotectants (polyols and sugars) that control the rate of freezing and protect the membrane bilayer [27]. Freezing is often initiated slowly at relatively high subzero temperatures in order to promote the growth of small, site-specific ice crystals in the extracellular spaces, as opposed to the rapid formation of ice that can cause injury [22]. For example, an Arctic species of stonefly, *Nemoura arctica,* cools to around −1.5 °C before freezing and can then survive temperatures as low as −15 °C for over two weeks by increasing hemolymph glycerol concentrations and antifreeze proteins [28].

Cryoprotective Dehydration

Cryoprotective dehydration (CPD) is a form of freeze-tolerance that occurs when an organism loses extreme amounts of body fluids to reach a vapour pressure equilibrium with surrounding ice. It has only been observed in a handful of arthropod species, including several Arctic springtails (e.g., *Megaphorura arctica*, *Hypogastrura viatica*, and *Folsomia quadrioculata*) [29,30], the Alaskan beetle *Cucujus clavipes puniceus* [31], and larvae of the Antarctic midge *Belgica antarctica*. In *B. antarctica*, ~40% of the body fluid is lost and high concentrations of solutes, such as osmolytes, accumulate until vapour pressure equilibrium with the surrounding ice is reached. This prevents internal freezing, allowing survival over 7–8 months of continuous subzero temperatures in a matrix of soil and ice [32].

Rapid Cold Hardening

Polar environments provide increasingly variable microhabitat temperatures and unpredictable freeze–thaw periods in any season throughout the year. In response, some species have the ability to plastically enable cold tolerance via 'rapid cold hardening' (RCH)—a fast response to cold that can last a matter of minutes or hours [33]—providing an ecological advantage over species that must acclimate or adapt over much longer timescales. The mechanisms that underpin RCH are relatively unclear: it was thought that since RCH has similar ecological outcomes to seasonal freeze-tolerance or avoidance (i.e., higher survival rate, increased fitness at low temperatures), it is achieved through similar mechanisms albeit at shorter timescales. However, recent work suggests that RCH is rather mechanistically distinct to seasonal cold-hardening. For instance, cryoprotectant/antifreeze protein synthesis and up-regulated stress-related genes (i.e., heat shock proteins) are important factors associated with seasonal cold hardening, but either are not involved in, or act ambiguously during, RCH. Factors that are important to RCH include calcium signalling, inhibition of apoptotic cell death, membrane restructuring, and adjustments to ion transport mechanisms [34].

RCH has been identified in some native polar arthropods and microarthropods (e.g., Antarctic mites, *Alakaozetes antarcticus* and *Halozete belgicae*) [35] and is hypothesised to reduce the developmental cost of employing long-term overwintering strategies, such as freeze tolerance. However, others argue that RCH offers little advantage to some polar arthropods (such as the Arctic springtail, *Hypogastrura tullbergi*) that migrate through soil profiles during cold snaps, as this often offers sufficient protection from short-term low temperatures [36].

2.2.2. Metabolism

While metabolism is mainly driven by the availability of food and oxygen, environmental temperatures have profound effects on metabolic rate, with higher metabolic rates across all phyla generally occurring in warmer climates and vice versa [37,38]. However, some research proposes that ectotherms from cold habitats have elevated metabolisms compared to those from warm habitats, owing to short, cool growing seasons that select for an increase in growth rates and development times—referred to as 'metabolic cold adaptation' [39–42].

Metabolic cold adaptation does not appear to be a phenomenon characterising all polar arthropods and warrants further research at the species level [43]. Nevertheless, metabolism produces the energy required for movement, growth, healing, feeding, digestion, and reproduction; thus, the ability to metabolise efficiently in cold environments may represent an ecologically advantageous trait for polar arthropods [44]. For example, during chill coma, arthropods lose ionic and osmotic homeostasis as the cellular membrane structure is altered and metabolic processes are down-regulated. As temperature increases again, whole-organism recovery involves restoring neuromuscular movement, repairing damage, and re-establishing ionic and osmotic gradients to restore homeostasis, all of which is energetically expensive. Thus, faster metabolism (and therefore recovery time) may allow for additional opportunities for foraging, dispersal, and reproduction, while reducing susceptibility to predation [39,45]. Indeed, arthropods from high-latitude environments may have a quicker chill coma recovery time than those from temperate regions [46]. Meanwhile, metabolomic studies have revealed abundant variation in core metabolic enzymes between polar species in response to thermal stress [12,47]. For example, *B. antarctica* enhances thermotolerance by increasing concentrations of metabolites, such as α-ketoglutarate (a Krebs cycle intermediate), to aid the synthesis of cryoprotectants [12]. In contrast, the Arctic seed bug, *Nysius groenlandicus*, actively alters metabolite levels on a daily basis, with higher concentrations of sugars found in individuals that were caught at the lowest daily field temperatures [48].

2.2.3. Body Size

Body size is integral to an organisms' ecological success—larger individuals tend to produce more offspring and live longer, and may be better at competing and avoiding predators than smaller individuals [49]. Body size is influenced by many factors, including metabolic energy, resource availability, and selection (both sexual and predation-driven) [50,51].

The temperature size rule (TSR) describes how individuals maintained at low temperatures tend to grow slower, but attain a larger body size upon maturity [52,53]. Similarly, Bergmann's rule describes how larger individuals are found in higher latitudes and colder environments (i.e., higher altitudes) [52]. Body size distribution patterns have been found to be largely consistent with TSR and Bergmann's rule for many endothermic species, such as birds and mammals [54]. Some ectothermic species follow these trends to a degree, though much less consistently, while other species follow a contradictory trend where body size decreases in response to cold temperatures ('converse Bergmann's rule') [55]. For example, wing length in two high-Arctic butterfly species (*Boloria chariclea* and *Colias hecla*) decreased significantly between the years 1996 and 2013 in response to warmer Arctic temperatures, supporting TSR [52], whereas small insects characterised by rapid development (such as aphids and small flies) are dominant in both polar regions, in counter to Bergmann's rule [56]. Variability in body size is likely to be idiosyncratic, depending largely on a number of species-specific and abiotic (e.g., oxygen) variables [49].

3. Climate Change Will Bring New Challenges for Polar Arthropods: How Might They Cope?

3.1. Challenges of Climate Change

Anthropogenic activities, such as fossil fuel combustion, deforestation, land-use change, and pollution have variable and profound impacts on the global climate and are already driving changes in species' range extent [57]. The poles are no exception.

The Arctic warms at roughly twice the rate as the rest of the globe due to complex interactions between the cryosphere, atmosphere, and ocean, referred to as 'Arctic Amplification' [5,58]. Consequently, Arctic sea ice has rapidly declined in thickness and extent over the last four decades [59,60], particularly the Greenland Ice Sheet, which is melting faster than any climate models have projected [61]. Future climate projections suggest that this trend will continue well into the 21st century, with potential warming by an additional 1.5–4 °C predicted for scenarios that include completely ice-free summers [5,62,63].

Climate change in Antarctica has not been uniform. Despite the fact that the Antarctic Peninsula, Scotia Arc, and Magellanic sub-Antarctic were some of the most rapidly warming areas on Earth for the second half of the 20th century, Antarctic sea ice extent across the entire continent has increased slightly since the 1970s [64,65]. This paradox has been attributed to the ozone hole that occurs over Antarctica during the austral summer, which causes stratospheric radiative cooling from ozone depletion and strengthened wind speeds [64,66,67]. When the ozone layer repairs, as it is predicted to do within the next century under a 'business as usual' scenario (i.e., continued increase of greenhouse gas emissions) [68], Antarctic surface temperatures are expected to increase by ~4 °C by the year 2100 [6].

Even small changes in temperature can cause irreversible changes to polar landscapes. For example, tundra greening in the low Arctic due to warming creates opportunities for plants in nearby sub-Arctic regions to expand their range toward higher latitudes, as seen in *Hieracium aurantiacum* (orange hawkweed), *Elodea nuttallii* (western waterweed), and *Bromus tectorum* (cheatgrass)—all of which are capable of dramatically changing the local ecosystem through changes in biogeochemical cycles, fire regimes, and hydrological processes [69].

3.2. Potential Responses to a Changing Climate

The ability for a species to adapt to climate change depends on its life-history traits and genetic architecture, both of which will affect the speed at which responses may occur (i.e., rapid/plastic versus slower/genetic). Despite this, most methods for evaluating responses to climate change rely largely on correlative species distribution models and limited ecological community data, neglecting to consider evolutionary potential (i.e., adaptive response) or species-specific idiosyncrasies [70,71]. Yet, species in polar regions will almost certainly respond differentially to climate change, even those that occupy similar niches and/or are closely related. For example, larvae of the endemic Antarctic midge *B. antarctica* are freeze tolerant to −14 °C, but die within a week at 10 °C, and only survive a couple of hours at 30 °C [72]. By comparison, the native Antarctic midge *P. steinenii* has a wide thermal tolerance across all life stages, remaining active between temperatures ranging from −5 °C to 28.6 °C [73], while the crane fly *Trichocera maculipennis*—a recent Antarctic coloniser—has a lower thermal tolerance limit similar to *P. steineii* but a higher limit of 30.1 °C [73]. Though all three species will experience the same environmental changes, *P. steinenii* and *T. maculipennis* are better set to benefit from a warmer climate and may rapidly colonise new habitats as they become available.

Climate change may also impact the phenological patterns of polar arthropods, which are generally characterised by long periods of dormancy and development times [74,75]. For example, the Arctic woolybear caterpillar *Gynaphora groenlandica*, native to the high Arctic in the Canadian archipelago, is dormant for 11 months of the year. For just one month (June), *G. groenlandica* actively feeds, basks, and moves about the tundra, developing very slowly—for up to and sometimes over five years [74]. Elevated temperatures caused by climate change may stimulate the development of arthropods as well as increase the duration of the growing season, thereby increasing voltinism. In some cases, this may delay the induction of winter diapause, resulting in the production of an additional generation in autumn that cannot survive or enter diapause (i.e., the "lost generation hypothesis") [75–77]. Furthermore, if a chilling cue is not received, diapause expression may be delayed, reduced, or abandoned—causing individuals to emerge later or not at all [78]. Changes to phenology in polar arthropods may also result in other ecological consequences, such as seasonal mismatches between species and their key resources, as has been observed in honeybees [79,80], or lead to increased exposure to winter-active predators [81].

Studies on species life histories have found that, while warming may benefit Arctic herbivores [82], it will likely negatively impact detritivores, such as Collembola [83] as well as certain above-ground and soil-dwelling Arctic arthropods [15]. Thus, in polar regions as elsewhere, a major consequence of ongoing climate change will be the redistribution of arthropod diversity: (a) the reduction of native species diversity through extinction; (b) the movement of species as they track changes in temperature to meet optimal conditions determined by their physiology (including the poleward shift of endemic species and the arrival of species inadvertently introduced to polar regions with increased survival and the potential to become invasive); and/or (c) the response of native species to additional environmental and ecological pressures through changes in behaviour, physiology, plasticity, and/or genetics [15,16] (Figure 2). However, the intricacies of such responses are largely uncertain due to a lack of relevant knowledge at the species level. Additionally, as noted above, arthropods are likely to respond differentially to climate change: though many will respond negatively (e.g., heat stress, desiccation, phenological mismatches), some will benefit from warmer temperatures through alleviated cold thermal stress, lengthened active seasons that promote growth and reproduction, and increased habitat availability provided by new ice-free environments [84–86]. Overall, climate change may drive a variety of adaptive changes in species at the poles [7], as outlined in the following section.

3.2.1. Invasive Species

Biological invasions occur when species are transported to regions beyond their native range by humans and there negatively impact native biodiversity, health, and economies. The invasion process can be viewed as a series of stages (transport, introduction, establishment, and spread), with the graduation of each stage dependent on overcoming specific barriers (e.g., founder effects, abiotic, and ecological pressures) [87].

The quantity and diversity of individuals being introduced to the Arctic and Antarctic every day is high. For example, 1376 individual alien invertebrates spanning 98 families were introduced to Antarctica during the summer field season in 2012–2013 [88]. However, very few individuals survive the journey and even less survive the extreme physical conditions they encounter when they arrive at the poles [89,90]. Increased patterns of human use in these areas (e.g., for research and tourism, shipping, fishing, etc.) will affect the rate of alien species introductions (Figure 3), while changes in climate can be expected to simultaneously select for, or otherwise promote, their survival upon arrival by creating conditions that are tolerable, if not favourable, to invasive species [11,69,89,91–95].

All 14 of the known non-native species established in Antarctica are found on the Antarctic Peninsula—the region where most warming has occurred since the 1950s—and almost exclusively in the direct vicinity of research centres and visitor sites [96]. Less data exists for invasive arthropods in the Arctic. However, a thorough inventory of species in the Svalbard region of the European high Arctic includes ten established alien arthropods (e.g., the springtail *Hypogastrura assimilis*), seven vagrants (e.g., the moth *Plutella xylostella*), and many other observed invasive species (e.g., the mite *Thanatus formicinus*), all of which were likely transported through imported soils [97].

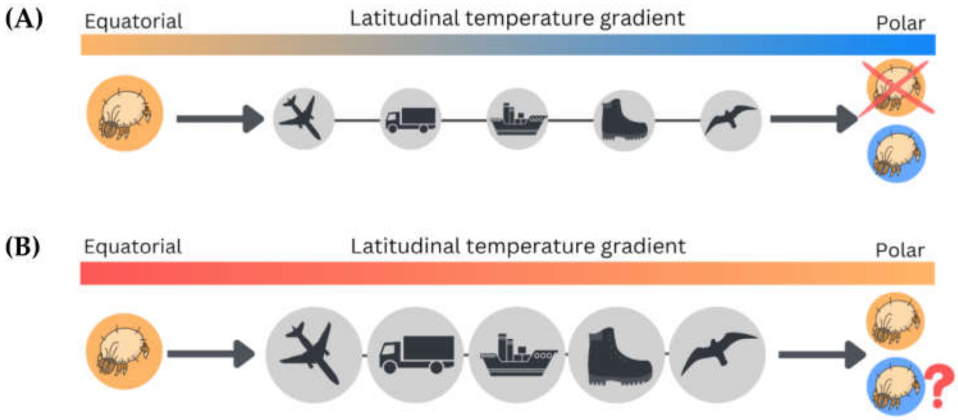

Figure 3. Depiction of possible arthropod distribution changes in response to warming temperatures associated with climate change. Blue circles represent native populations that prefer cold temperatures (i.e., polar regions) and orange circles represent non-native populations that prefer warm temperatures (i.e., non-polar regions). Grey circles represent different means of mediated dispersal, with size representing relative transport events to the poles (i.e., larger grey circles indicate higher propagule pressure). (**A**) Under a normal latitudinal temperature gradient with fewer introduction events, non-native species are unlikely to establish populations upon arrival to the poles due to mismatches between local environment (e.g., air temperature) and physiology; (**B**) Warmer temperatures and increased transport events may facilitate the establishment of non-native species at the poles by creating conditions within their optimal range, or facilitating rapid evolution in the new environment.

Of course, one of the greatest invasive risks at both poles is the local assisted dispersal of established or even native species to new areas, as such species are already tolerating polar conditions in their local habitats [98]. For example, the chironomid midge *Eretmoptera murphyi* was introduced to Signy Island (South Orkney Islands) from its native range on South Georgia Island and successfully established a population there due to pre-existing thermal adaptations [99]; it now significantly impacts local litter turnover and availability of nutrients [100,101]. With at least 25 distinct biogeographic regions within Antarctica and the surrounding maritime sub-Antarctic [102], and movement of personnel and cargo between these regions occuring at high frequency, the risk of human-assisted movement of species between local populations is high—especially for environments that are becoming increasingly fragmented [65].

3.2.2. Plastic and Genetic Responses to a Changing Climate

Phenotypic Plasticity

Phenotypic plasticity refers to the rapid expression of different phenotypes from the same genotype and is often initiated by an environmental change. For example, winter diapause in arthropods is triggered by shorter days and temperature responses from an earlier life stage or previous generation [103]. Plasticity may affect phenotypic outcomes—driving changes in the number of instars, or types and quantities of eggs or pupae produced—and also intrinsic processes, such as metabolism, gene expression, and protein/carbohydrate composition [104]. Though plasticity can be maladaptive (e.g., seasonal mismatches between species and their resources, as observed in pollinating insects [105]), the capacity and speed at which a species is able to adaptively respond by altering its behaviour, morphology, or physiology is an important component of its ability to cope with, and acclimate to, the effects of climate change [104–107].

Recent studies have suggested that invasive species may be more capable of responding plastically, suggesting that plasticity could be important for invasion success [108]. For example, the globally invasive European green crab (*Carcinus maenas*) demonstrates short-term acclimatory plasticity and high eurythermal tolerance compared to other crustaceans (18–31 days at either 5 or 25 °C), which has likely facilitated its ability to colonise a wide range of thermally unique environments [109]. RCH (see above) has been identified in many non-polar arthropods, particularly notoriously invasive species of Hemiptera (e.g., *Sitobion avenae*) [110], Diptera (e.g., *Culicoides variipenni*) [111], Lepidoptera (e.g., *P. xylostella*) [112], and Orthoptera (e.g., *Locusta migratoria*) [113], highlighting their risk of potentially establishing populations in polar environments. The ability to assume ideal phenotypes for environmental variance over short timescales will likely play an important role in determining species responses to rapid climate change [114], however, limited research is devoted to understanding phenotypic plasticity of arthropod taxa. This includes research that utilises next generation sequencing technologies, such as transcriptomics (the study of RNA transcripts that are expressed in the cell) to examine changes in gene expression under specific environmental conditions [115]. As a result, the ability of polar arthropods to respond plastically to increasing temperatures, or compete with invading species that may also be more plastic, is unclear.

Genetic Responses

Increasing temperature can create de novo genetic diversity by causing spontaneous replication errors and/or DNA damage [116], and can affect standing genetic variation by shifting allele frequencies in genes or linked genomic regions associated with climate response [117,118]. De novo variation tends to operate on a longer timescale, as new mutations have to occur and then sweep through a population [119]. Conversely, standing genetic variation can result in more rapid adaptation due to the co-option of existing variation towards new solutions [120].

Although the majority of mutations provide no additional fitness benefit (i.e., are most often deleterious or neutral), some give rise to variation within populations that provides an advantage to survival, with research identifying a clear link between temperature and mutation rate [121]. The tendency for species density to be greater in lower as opposed to higher latitudes—i.e., the latitudinal biodiversity gradient—may be partly underlain by differential rates of mutation among species. For example, temperate and tropical arthropods have shorter generation times and larger population sizes and are therefore predicted to have a greater supply and faster rate of mutations for evolution to act upon, thus driving adaptation [122]. In contrast, polar arthropods are expected to experience slower rates of mutation owing to the fact that many species must overwinter in a state of stupor and are only active for the few months of austral summer (thus have longer generation times overall) [116,122]. Therefore, de novo variation in polar arthropods may be insufficient to meet the demands of increased temperatures [123], including those driven by competition with invasives that have higher mutation rates.

Adaptive responses that build from standing variation have not been identified for polar arthropods to date, however temperate species show that existing genetic variation across the genome in response to human impacts can drive changes in diapause timing [124], contribute to insecticide resistance [125], and/or lead to phenotypic changes such as melanism or wing-loss [126,127].

Genetic responses to climate warming (whether building from de novo or standing variation) for polar taxa have yet to gain great research traction more generally. This is an area that would clearly benefit from more focus—particularly because, even if such responses are unable to occur rapidly for endemic taxa, they may well promote rapid adaptation of newly invading species [127].

4. Future Steps

Published physiological studies on terrestrial Arctic and Antarctic arthropods are limited to a small number of species—undoubtedly driven by the various challenges associated with working at the poles, including financial, time, and resource burdens. For those taxa that have been studied, physiology is the target of the majority of research (e.g., freeze-tolerance, metabolism), with a view towards understanding how these unique adaptations promote survival in the cold.

However, physiology is dynamic across populations in time and space, as are other factors that shape evolutionary potential, such as genetic diversity, gene expression, population size, population structure, and mutation rates [106]. Recent population genomic technologies have shown great potential for elucidating demographic and adaptive processes and, when combined with ecological niche modelling, can be used to reconstruct evolutionary and ecological histories and predict future trajectories [128], aiding evaluation of the risk of localised biological invasions. Moreover, transcriptomic studies can shed light on the capacity of species to respond plastically to climate change [129]. However, little research in these fields targets arthropods, and even less employs a polar lens. Thus, evolutionary potential, the fitness implications and influence of plasticity, and their interacting effects on the other potential responses of polar species to climate change are key areas in which future research would provide exceptionally valuable insights.

Author Contributions: A.M. and P.M. conceptualised the manuscript, P.M. wrote the first draft and created the figures, and A.M. and P.M. together finalised the text. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Institutional Review Board Statement: Not applicable.

Data Availability Statement: Not applicable.

Acknowledgments: We wish to thank the University of Waikato and members of the Invasomics Lab for support during writing.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Pörtner, H.O.; Roberts, D.C.; Adams, H.; Adler, C.; Aldunce, P.; Ali, E.; Begum, R.A.; Betts, R.; Kerr, R.B.; Biesbroek, R.; et al. Climate change 2022: Impacts, adaptation and vulnerability. In *IPCC Sixth Assessment Report*; IPCC: Geneva, The Netherlands, 2022; pp. 37–118.
2. Shadwick, E.H.; De Meo, O.A.; Schroeter, S.; Arroyo, M.C.; Martinson, D.G.; Ducklow, H. Sea ice suppression of CO2 outgassing in the West Antarctic Peninsula: Implications for the evolving southern ocean carbon sink. *Geophys. Res. Lett.* **2021**, *48*, e2020GL091835. [CrossRef]
3. Monteiro, M.R.; Marshall, A.J.; Hawes, I.; Lee, C.K.; McDonald, I.R.; Cary, S.C. Geochemically defined space-for-time transects successfully capture microbial dynamics along lacustrine chronosequences in a polar desert. *Front. Microbiol.* **2022**, *12*, 4201. [CrossRef] [PubMed]
4. Diffenbaugh, N.S.; Field, C.B. Changes in ecologically critical terrestrial climate conditions. *Science* **2013**, *341*, 486–492. [CrossRef]
5. Koenigk, T.; Key, J.; Vihma, T. Climate change in the Arctic. In *Physics and Chemistry of the Arctic Atmosphere*; Kokhanovsky, A., Tomasi, C., Eds.; Springer International Publishing: Cham, Switzerland, 2020; pp. 673–705.
6. Hughes, K.A.; Convey, P.; Turner, J. Developing resilience to climate change impacts in Antarctica: An evaluation of Antarctic Treaty System protected area policy. *Environ. Sci. Policy* **2021**, *124*, 12–22. [CrossRef]
7. Høye, T.T. Arthropods and climate change–Arctic challenges and opportunities. *Curr. Opin. Insect Sci.* **2020**, *41*, 40–45. [CrossRef]
8. Rudkin, D.M.; Young, G.A. Horseshoe crabs–an ancient ancestry revealed. In *Biology and Conservation of Horseshoe Crabs*; Tanacredi, J.T., Botton, M.L., Smith, D., Eds.; Springer: Boston, MA, USA, 2009; pp. 25–44.
9. Høye, T.T.; Culler, L.E. Tundra arthropods provide key insights into ecological responses to environmental change. *Polar Biol.* **2018**, *41*, 1523–1529. [CrossRef]
10. Convey, P.; Gibson, J.A.; Hillenbrand, C.D.; Hodgson, D.A.; Pugh, P.J.; Smellie, J.L.; Stevens, M.I. Antarctic terrestrial life–challenging the history of the frozen continent? *Biol. Rev.* **2008**, *83*, 103–117. [CrossRef]
11. Hughes, K.A.; Worland, M.R. Spatial distribution, habitat preference and colonization status of two alien terrestrial invertebrate species in Antarctica. *Antarct. Sci.* **2010**, *22*, 221–231. [CrossRef]
12. Michaud, M.R.; Benoit, J.B.; Lopez-Martinez, G.; Elnitsky, M.A.; Lee, R.E., Jr.; Denlinger, D.L. Metabolomics reveals unique and shared metabolic changes in response to heat shock, freezing and desiccation in the Antarctic midge, *Belgica Antarctica*. *J. Insect Physiol.* **2008**, *54*, 645–655. [CrossRef]
13. Turner, J.; Lu, H.; King, J.; Marshall, G.J.; Phillips, T.; Bannister, D.; Colwell, S. Extreme temperatures in the Antarctic. *J. Clim.* **2021**, *34*, 2653–2668. [CrossRef]
14. Vanstreels, R.E.T.; Palma, R.L.; Mironov, S.V. Arthropod parasites of Antarctic and sub-Antarctic birds and pinnipeds: A review of host-parasite associations. *Int. J. Parasitol. Parasites Wildl.* **2020**, *12*, 275–290. [CrossRef] [PubMed]

15. Hodkinson, I.D.; Coulson, S.J.; Webb, N.R. Community assembly along proglacial chronosequences in the high Arctic: Vegetation and soil development in north-west Svalbard. *J. Ecol.* **2003**, *91*, 651–663. [CrossRef]
16. Giribet, G.; Edgecombe, G.D. The phylogeny and evolutionary history of arthropods. *Curr. Biol.* **2019**, *29*, R592–R602. [CrossRef] [PubMed]
17. Maurice, H.; Philippe, V. Terrestrial macro-arthropods of the sub-Antarctic islands of Possession (Crozet Archipelago) and Kerguelen: Inventory of native and non-native species. *Zoosystema* **2021**, *43*, 549–561. [CrossRef]
18. Sinclair, B.J.; Terblanche, J.S.; Scott, M.B.; Blatch, G.L.; Jaco Klok, C.; Chown, S.L. Environmental physiology of three species of Collembola at Cape Hallett, North Victoria Land, Antarctica. *J. Insect Physiol.* **2006**, *52*, 29–50. [CrossRef]
19. Høye, T.T.; Forchhammer, M.C. Phenology of high-Arctic arthropods: Effects of climate on spatial, seasonal, and inter-annual variation. In *Advances in Ecological Research*; Academic Press: Cambridge, MA, USA, 2008; Volume 40, pp. 299–324.
20. Sinclair, B.J.; Coello Alvarado, L.E.; Ferguson, L.V. An invitation to measure insect cold tolerance: Methods, approaches, and workflow. *J. Therm. Biol.* **2015**, *53*, 180–197. [CrossRef]
21. Rozsypal, J.; Košťál, V. Supercooling and freezing as eco-physiological alternatives rather than mutually exclusive strategies: A case study in *Pyrrhocoris apterus*. *J. Insect Physiol.* **2018**, *111*, 53–62. [CrossRef]
22. Duman, J.G.; Bennett, V.; Sformo, T.; Hochstrasser, R.; Barnes, B.M. Antifreeze proteins in Alaskan insects and spiders. *J. Insect Physiol.* **2004**, *50*, 259–266. [CrossRef]
23. Worland, M.R. Factors that influence freezing in the sub-Antarctic springtail *Tullbergia antarctica*. *J. Insect Physiol.* **2005**, *51*, 881–894. [CrossRef]
24. Zettel, J. The significance of temperature and barometric pressure changes for the snow surface activity of *Isotoma hiemalis* (Collembola). *Experientia* **1984**, *40*, 1369–1372. [CrossRef]
25. Sinclair, B.J.; Sjursen, H. Cold tolerance of the Antarctic springtail *Gomphiocephalus hodgsoni* (Collembola, Hypogastruridae). *Antarct. Sci.* **2001**, *13*, 271–279. [CrossRef]
26. Rinehart, J.P.; Li, A.; Yocum, G.D.; Robich, R.M.; Hayward, S.A.L.; Denlinger, D.L. Up-regulation of heat shock proteins is essential for cold survival during insect diapause. *Proc. Natl. Acad. Sci. USA* **2007**, *104*, 11130–11137. [CrossRef] [PubMed]
27. Storey, K.B.; Storey, J.M. Insect cold hardiness: Metabolic, gene, and protein adaptation. *Can. J. Zool.* **2012**, *90*, 456–475. [CrossRef]
28. Walters, K.R., Jr.; Sformo, T.; Barnes, B.M.; Duman, J.G. Freeze tolerance in an arctic Alaska stonefly. *J. Exp. Biol.* **2009**, *212*, 305–312. [CrossRef]
29. Clark, M.S.; Thorne, M.A.S.; Purać, J.; Burns, G.; Hillyard, G.; Popović, Ž.D.; Grubor-Lajšić, G.; Worland, M.R. Surviving the cold: Molecular analyses of insect cryoprotective dehydration in the Arctic springtail *Megaphorura arctica* (Tullberg). *BMC Genom.* **2009**, *10*, 328. [CrossRef]
30. Sørensen, J.G.; Holmstrup, M. Cryoprotective dehydration is widespread in Arctic springtails. *J. Insect Physiol.* **2011**, *57*, 1147–1153. [CrossRef]
31. Sformo, T.; Walters, K.; Jeannet, K.; Wowk, B.; Fahy, G.M.; Barnes, B.M.; Duman, J.G. Deep supercooling, vitrification and limited survival to −100°C in the Alaskan beetle *Cucujus clavipes puniceus* (Coleoptera: Cucujidae) larvae. *J. Exp. Biol.* **2010**, *213*, 502–509. [CrossRef]
32. Elnitsky, M.A.; Hayward, S.A.; Rinehart, J.P.; Denlinger, D.L.; Lee, R.E., Jr. Cryoprotective dehydration and the resistance to inoculative freezing in the Antarctic midge, *Belgica antarctica*. *J. Exp. Biol.* **2008**, *211*, 524–530. [CrossRef]
33. Teets, N.M.; Gantz, J.D.; Kawarasaki, Y. Rapid cold hardening: Ecological relevance, physiological mechanisms and new perspectives. *J. Exp. Biol.* **2020**, *223*, jeb203448. [CrossRef]
34. Teets, N.M.; Denlinger, D.L. Physiological mechanisms of seasonal and rapid cold-hardening in insects. *Physiol. Entomol.* **2013**, *38*, 105–116. [CrossRef]
35. Worland, M.R.; Convey, P. Rapid cold hardening in Antarctic microarthropods. *Funct. Ecol.* **2001**, *15*, 515–524. [CrossRef]
36. Hawes, T.C.; Couldridge, C.E.; Bale, J.S.; Worland, M.R.; Convey, P. Habitat temperature and the temporal scaling of cold hardening in the high Arctic collembolan, *Hypogastrura tullbergi* (Schäffer). *Ecol. Entomol.* **2006**, *31*, 450–459. [CrossRef]
37. Clarke, A.; Fraser, K.P.P. Why does metabolism scale with temperature? *Funct. Ecol.* **2004**, *18*, 243–251. [CrossRef]
38. Schulte, P.M. The effects of temperature on aerobic metabolism: Towards a mechanistic understanding of the responses of ectotherms to a changing environment. *J. Exp. Biol.* **2015**, *218*, 1856–1866. [CrossRef] [PubMed]
39. Williams, C.M.; Szejner-Sigal, A.; Morgan, T.J.; Edison, A.S.; Allison, D.B.; Hahn, D.A. Adaptation to low temperature exposure increases metabolic rates independently of growth rates. *Integr. Comp. Biol.* **2016**, *56*, 62–72. [CrossRef]
40. Terblanche, J.S.; Clusella-Trullas, S.; Deere, J.A.; Van Vuuren, B.J.; Chown, S.L. Directional evolution of the slope of the metabolic rate–temperature relationship is correlated with climate. *Physiol. Biochem. Zool.* **2009**, *82*, 495–503. [CrossRef]
41. Addo-Bediako, A.; Chown, S.L.; Gaston, K.J. Metabolic cold adaptation in insects: A large-scale perspective. *Funct. Ecol.* **2002**, *16*, 332–338. [CrossRef]
42. Ayres, M.P.; Scriber, J.M. Local adaptation to regional climates in *Papilio canadensis* (Lepidoptera: Papilionidae). *Ecol. Monogr.* **1994**, *64*, 465–482. [CrossRef]
43. Lardies, M.A.; Bacigalupe, L.D.; Bozinovic, F. Testing the metabolic cold adaptation hypothesis: An intraspecific latitudinal comparison in the common woodlouse. *Evol. Ecol. Res.* **2004**, *6*, 567–578.
44. Nespolo, R.F.; Lardies, M.A.; Bozinovic, F. Intrapopulational variation in the standard metabolic rate of insects: Repeatability, thermal dependence and sensitivity (Q10) of oxygen consumption in a cricket. *J. Exp. Biol.* **2003**, *206*, 4309–4315. [CrossRef]

45. MacMillan, H.A.; Sinclair, B.J. Mechanisms underlying insect chill-coma. *J. Insect Physiol.* **2011**, *57*, 12–20. [CrossRef]
46. David, J.R.; Gibert, P.; Moreteau, B.; Gilchrist, G.W.; Huey, R.B. The fly that came in from the cold: Geographic variation of recovery time from low-temperature exposure in *Drosophila subobscura*. *Funct. Ecol.* **2003**, *17*, 425–430. [CrossRef]
47. Marden, J.H. Nature's inordinate fondness for metabolic enzymes: Why metabolic enzyme loci are so frequently targets of selection. *Mol. Ecol.* **2013**, *22*, 5743–5764. [CrossRef] [PubMed]
48. Noer, N.K.; Sørensen, M.H.; Colinet, H.; Renault, D.; Bahrndorff, S.; Kristensen, T.N. Adjustments in thermal tolerance and the metabolome to daily environmental changes-a field study of the arctic seed bug *Nysius groenlandicus*. *Front. Physiol.* **2022**, *13*, 818485. [CrossRef] [PubMed]
49. Horne, C.R.; Hirst, A.G.; Atkinson, D. Seasonal body size reductions with warming covary with major body size gradients in arthropod species. *Proc. R. Soc. B Biol. Sci.* **2017**, *284*, 20170238. [CrossRef]
50. Verberk, W.C.E.P.; Atkinson, D.; Hoefnagel, K.N.; Hirst, A.G.; Horne, C.R.; Siepel, H. Shrinking body sizes in response to warming: Explanations for the temperature–size rule with special emphasis on the role of oxygen. *Biol. Rev.* **2021**, *96*, 247–268. [CrossRef]
51. Klok, C.J.; Harrison, J.F. The temperature size rule in arthropods: Independent of macro-environmental variables but size dependent. *Integr. Comp. Biol.* **2013**, *53*, 557–570. [CrossRef]
52. Bowden, J.J.; Eskildsen, A.; Hansen, R.R.; Olsen, K.; Kurle, C.M.; Høye, T.T. High-Arctic butterflies become smaller with rising temperatures. *Biol. Lett.* **2015**, *11*, 20150574. [CrossRef]
53. Aguilar-Alberola, J.A.; Mesquita-Joanes, F. Breaking the temperature-size rule: Thermal effects on growth, development and fecundity of a crustacean from temporary waters. *J. Therm. Biol.* **2014**, *42*, 15–24. [CrossRef]
54. Scriven, J.J.; Whitehorn, P.R.; Goulson, D.; Tinsley, M.C. Bergmann's body size rule operates in facultatively endothermic insects: Evidence from a complex of cryptic bumblebee species. *PLoS One* **2016**, *11*, e0163307. [CrossRef]
55. Shelomi, M. Where are we now? Bergmann's rule *sensu lato* in insects. *Am. Nat.* **2012**, *180*, 511–519. [CrossRef] [PubMed]
56. Danks, H.V. Seasonal adaptations in Arctic insects. *Integr. Comp. Biol.* **2004**, *44*, 85–94. [CrossRef] [PubMed]
57. Thuiller, W.; Albert, C.; Araújo, M.B.; Berry, P.M.; Cabeza, M.; Guisan, A.; Hickler, T.; Midgley, G.F.; Paterson, J.; Schurr, F.M.; et al. Predicting global change impacts on plant species' distributions: Future challenges. *Perspect. Plant Ecol. Evol. Syst.* **2008**, *9*, 137–152. [CrossRef]
58. Cohen, J.; Zhang, X.; Francis, J.; Jung, T.; Kwok, R.; Overland, J.; Ballinger, T.J.; Bhatt, U.S.; Chen, H.W.; Coumou, D.; et al. Divergent consensuses on Arctic amplification influence on midlatitude severe winter weather. *Nat. Clim. Chang.* **2020**, *10*, 20–29. [CrossRef]
59. Meier, W.N.; Hovelsrud, G.K.; van Oort, B.E.H.; Key, J.R.; Kovacs, K.M.; Michel, C.; Haas, C.; Granskog, M.A.; Gerland, S.; Perovich, D.K.; et al. Arctic sea ice in transformation: A review of recent observed changes and impacts on biology and human activity. *Rev. Geophys.* **2014**, *52*, 185–217. [CrossRef]
60. Maksym, T. Arctic and Antarctic sea ice change: Contrasts, commonalities, and causes. *Annu. Rev. Mar. Sci.* **2019**, *11*, 187–213. [CrossRef]
61. Wunderling, N.; Willeit, M.; Donges, J.F.; Winkelmann, R. Global warming due to loss of large ice masses and Arctic summer sea ice. *Nat. Commun.* **2020**, *11*, 5177. [CrossRef]
62. Jahn, A. Reduced probability of ice-free summers for 1.5 °C compared to 2 °C warming. *Nat. Clim. Chang.* **2018**, *8*, 409–413. [CrossRef]
63. Overland, J.E.; Wang, M. When will the summer Arctic be nearly sea ice free? *Geophys. Res. Lett.* **2013**, *40*, 2097–2101. [CrossRef]
64. Convey, P.; Peck, L.S. Antarctic environmental change and biological responses. *Sci. Adv.* **2019**, *5*, eaaz0888. [CrossRef]
65. Contador, T.; Gañan, M.; Bizama, G.; Fuentes-Jaque, G.; Morales, L.; Rendoll, J.; Simoes, F.; Kennedy, J.; Rozzi, R.; Convey, P. Assessing distribution shifts and ecophysiological characteristics of the only Antarctic winged midge under climate change scenarios. *Sci. Rep.* **2020**, *10*, 9087. [CrossRef] [PubMed]
66. Turner, J.; Comiso, J.C.; Marshall, G.J.; Lachlan-Cope, T.A.; Bracegirdle, T.; Maksym, T.; Meredith, M.P.; Wang, Z.; Orr, A. Non-annular atmospheric circulation change induced by stratospheric ozone depletion and its role in the recent increase of Antarctic sea ice extent. *Geophys. Res. Lett.* **2009**, *36*, L08502. [CrossRef]
67. Bandoro, J.; Solomon, S.; Donohoe, A.; Thompson, D.W.J.; Santer, B.D. Influences of the Antarctic ozone hole on southern hemispheric summer climate change. *J. Clim.* **2014**, *27*, 6245–6264. [CrossRef]
68. Solomon, S.; Ivy, D.J.; Kinnison, D.; Mills, M.J.; Neely, R.R.; Schmidt, A. Emergence of healing in the Antarctic ozone layer. *Science* **2016**, *353*, 269–274. [CrossRef]
69. Lassuy, D.R.; Lewis, P.N. Invasive species: Human-induced. In *Arcticbiodiversityassessment. Status and Trends in Arctic Biodiversity*; Meltofte, H.H., Josefson, A.B., Payer, D., Eds.; CAFF: Akureyri, Iceland, 2013; pp. 558–565.
70. Kellermann, V.; van Heerwaarden, B. Terrestrial insects and climate change: Adaptive responses in key traits. *Physiol. Entomol.* **2019**, *44*, 99–115. [CrossRef]
71. Bush, A.; Mokany, K.; Catullo, R.; Hoffmann, A.; Kellermann, V.; Sgrò, C.; McEvey, S.; Ferrier, S. Incorporating evolutionary adaptation in species distribution modelling reduces projected vulnerability to climate change. *Ecol. Lett.* **2016**, *19*, 1468–1478. [CrossRef]
72. Lee, R.E., Jr.; Elnitsky, M.A.; Rinehart, J.P.; Hayward, S.A.; Sandro, L.H.; Denlinger, D.L. Rapid cold-hardening increases the freezing tolerance of the Antarctic midge *Belgica antarctica*. *J. Exp. Biol.* **2006**, *209*, 399–406. [CrossRef]

73. Pertierra, L.R.; Escribano-Álvarez, P.; Olalla-Tárraga, M.Á. Cold tolerance is similar but heat tolerance is higher in the alien insect *Trichocera maculipennis* than in the native *Parochlus steinenii* in Antarctica. *Polar Biol.* **2021**, *44*, 1203–1208. [CrossRef]
74. Bennett, V.A.; Lee, R.E., Jr.; Nauman, J.S.; Kukal, O. Selection of overwintering microhabitats used by the Arctic woollybear caterpillar, *Gynaephora groenlandica*. *Cryo Lett.* **2003**, *24*, 191–200.
75. Harvey, J.A.; Tougeron, K.; Gols, R.; Heinen, R.; Abarca, M.; Abram, P.K.; Basset, Y.; Berg, M.; Boggs, C.; Brodeur, J.; et al. Scientists' warning on climate change and insects. *Ecol. Monogr.* **2022**, *0*, e1553. [CrossRef]
76. Van Dyck, H.; Bonte, D.; Puls, R.; Gotthard, K.; Maes, D. The lost generation hypothesis: Could climate change drive ectotherms into a developmental trap? *Oikos* **2015**, *124*, 54–61. [CrossRef]
77. Kerr, N.Z.; Wepprich, T.; Grevstad, F.S.; Dopman, E.B.; Chew, F.S.; Crone, E.E. Developmental trap or demographic bonanza? Opposing consequences of earlier phenology in a changing climate for a multivoltine butterfly. *Glob. Chang. Biol.* **2020**, *26*, 2014–2027. [CrossRef] [PubMed]
78. Tougeron, K.; Brodeur, J.; Le Lann, C.; van Baaren, J. How climate change affects the seasonal ecology of insect parasitoids. *Ecol. Entomol.* **2020**, *45*, 167–181. [CrossRef]
79. Nürnberger, F.; Härtel, S.; Steffan-Dewenter, I. Seasonal timing in honeybee colonies: Phenology shifts affect honey stores and varroa infestation levels. *Oecologia* **2019**, *189*, 1121–1131. [CrossRef]
80. Renner, S.S.; Zohner, C.M. Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. *Annu. Rev. Ecol. Evol. Syst.* **2018**, *49*, 165–182. [CrossRef]
81. Cooper, E.J. Warmer shorter winters disrupt Arctic terrestrial ecosystems. *Annu. Rev. Ecol. Evol. Syst.* **2014**, *45*, 271–295. [CrossRef]
82. De Sassi, C.; Tylianakis, J.M. Climate change disproportionately increases herbivore over plant or parasitoid biomass. *PLoS One* **2012**, *7*, e40557. [CrossRef]
83. Hodkinson, I.D.; Webb, N.R.; Bale, J.S.; Block, W.; Coulson, S.J.; Strathdee, A.T. Global change and Arctic ecosystems: Conclusions and predictions from experiments with terrestrial invertebrates on Spitsbergen. *Arct. Alp. Res.* **1998**, *30*, 306–313. [CrossRef]
84. Wallingford, P.D.; Morelli, T.L.; Allen, J.M.; Beaury, E.M.; Blumenthal, D.M.; Bradley, B.A.; Dukes, J.S.; Early, R.; Fusco, E.J.; Goldberg, D.E.; et al. Adjusting the lens of invasion biology to focus on the impacts of climate-driven range shifts. *Nat. Clim. Chang.* **2020**, *10*, 398–405. [CrossRef]
85. Block, W.; Webb, N.R.; Coulson, S.; Hodkinson, I.D.; Worland, M.R. Thermal adaptation in the Arctic collembolan *Onychiurus arcticus* (Tullberg). *J. Insect Physiol.* **1994**, *40*, 715–722. [CrossRef]
86. Schmidt, N.M.; Mosbacher, J.B.; Nielsen, P.S.; Rasmussen, C.; Høye, T.T.; Roslin, T. An ecological function in crisis? The temporal overlap between plant flowering and pollinator function shrinks as the Arctic warms. *Ecography* **2016**, *39*, 1250–1252. [CrossRef]
87. Blackburn, T.M.; Pyšek, P.; Bacher, S.; Carlton, J.T.; Duncan, R.P.; Jarošík, V.; Wilson, J.R.U.; Richardson, D.M. A proposed unified framework for biological invasions. *Trends Ecol. Evol.* **2011**, *26*, 333–339. [CrossRef] [PubMed]
88. Houghton, M.; McQuillan, P.B.; Bergstrom, D.M.; Frost, L.; van den Hoff, J.; Shaw, J. Pathways of alien invertebrate transfer to the Antarctic region. *Polar Biol.* **2016**, *39*, 23–33. [CrossRef]
89. Williamson, M.; Fitter, A. The Varying Success of Invaders. *Ecology* **1996**, *77*, 1661–1666. [CrossRef]
90. Frenot, Y.; Chown, S.L.; Whinam, J.; Selkirk, P.M.; Convey, P.; Skotnicki, M.; Bergstrom, D.M. Biological invasions in the Antarctic: Extent, impacts and implications. *Biol. Rev.* **2005**, *80*, 45–72. [CrossRef]
91. Stachowicz, J.J.; Terwin, J.R.; Whitlatch, R.B.; Osman, R.W. Linking climate change and biological invasions: Ocean warming facilitates nonindigenous species invasions. *Proc. Natl. Acad. Sci. USA* **2002**, *99*, 15497–15500. [CrossRef]
92. Alsos, I.G.; Ware, C.; Elven, R. Past Arctic aliens have passed away, current ones may stay. *Biol. Invasions* **2015**, *17*, 3113–3123. [CrossRef]
93. Baird, H.P.; Moon, K.L.; Janion-Scheepers, C.; Chown, S.L. Springtail phylogeography highlights biosecurity risks of repeated invasions and intraregional transfers among remote islands. *Evol. Appl.* **2020**, *13*, 960–973. [CrossRef]
94. Duffy, G.A.; Coetzee, B.W.T.; Latombe, G.; Akerman, A.H.; McGeoch, M.A.; Chown, S.L. Barriers to globally invasive species are weakening across the Antarctic. *Divers. Distrib.* **2017**, *23*, 982–996. [CrossRef]
95. Hughes, K.A.; Pescott, O.L.; Peyton, J.; Adriaens, T.; Cottier-Cook, E.J.; Key, G.; Rabitsch, W.; Tricarico, E.; Barnes, D.K.A.; Baxter, N.; et al. Invasive non-native species likely to threaten biodiversity and ecosystems in the Antarctic Peninsula region. *Glob. Change Biol.* **2020**, *26*, 2702–2716. [CrossRef]
96. Coulson, S.J. The alien terrestrial invertebrate fauna of the high Arctic archipelago of Svalbard: Potential implications for the native flora and fauna. *Polar Res.* **2015**, *34*, 27364. [CrossRef]
97. Everatt, M.J.; Worland, M.R.; Bale, J.S.; Convey, P.; Hayward, S.A.L. Pre-adapted to the maritime Antarctic?–Rapid cold hardening of the midge, *Eretmoptera murphyi*. *J. Insect Physiol.* **2012**, *58*, 1104–1111. [CrossRef] [PubMed]
98. Worland, M.R. *Eretmoptera murphyi*: Pre-adapted to survive a colder climate. *Physiol. Entomol.* **2010**, *35*, 140–147. [CrossRef]
99. Hughes, K.A.; Worland, M.R.; Thorne, M.A.S.; Convey, P. The non-native chironomid *Eretmoptera murphyi* in Antarctica: Erosion of the barriers to invasion. *Biol. Invasions* **2013**, *15*, 269–281. [CrossRef]
100. Bartlett, J.C.; Convey, P.; Hughes, K.A.; Thorpe, S.E.; Hayward, S.A.L. Ocean currents as a potential dispersal pathway for Antarctica's most persistent non-native terrestrial insect. *Polar Biol.* **2021**, *44*, 209–216. [CrossRef]
101. Chown, S.L.; Convey, P. Antarctic entomology. *Annu. Rev. Entomol.* **2016**, *61*, 119–137. [CrossRef]
102. Hughes, K.A.; Convey, P.; Pertierra, L.R.; Vega, G.C.; Aragón, P.; Olalla-Tárraga, M.Á. Human mediated dispersal of terrestrial species between Antarctic biogrographic regions: A preliminary risk assessment. *J. Environ. Manag.* **2019**, *232*, 73–89. [CrossRef]

103. Zhao, C.; Guo, Y.; Liu, Z.; Xia, Y.; Li, Y.; Song, Z.; Zhang, B.; Li, D. Temperature and photoperiodic response of diapause induction in *Anastatus japonicus*, an egg parasitoid of stink bugs. *Insects* **2021**, *12*, 872. [CrossRef]
104. Rodrigues, Y.K.; Beldade, P. Thermal plasticity in insects' response to climate change and to multifactorial environments. *Front. Ecol. Evol.* **2020**, *8*, 271. [CrossRef]
105. Memmott, J.; Craze, P.G.; Waser, N.M.; Price, M.V. Global warming and the disruption of plant-pollinator interactions. *Ecol. Lett.* **2007**, *10*, 710–717. [CrossRef]
106. Bahrndorff, S.; Lauritzen, J.M.S.; Sørensen, M.H.; Noer, N.K.; Kristensen, T.N. Responses of terrestrial polar arthropods to high and increasing temperatures. *J. Exp. Biol.* **2021**, *224*, jeb230797. [CrossRef] [PubMed]
107. Sgrò, C.M.; Terblanche, J.S.; Hoffmann, A.A. What can plasticity contribute to insect responses to climate change? *Annu. Rev. Entomol.* **2016**, *61*, 433–451. [CrossRef] [PubMed]
108. Little, C.M.; Chapman, T.W.; Hillier, N.K. Plasticity is key to success of *Drosophila suzukii* (Diptera: Drosophilidae) invasion. *J. Insect Sci.* **2020**, *20*, 5. [CrossRef] [PubMed]
109. Tepolt, C.K.; Somero, G.N. Master of all trades: Thermal acclimation and adaptation of cardiac function in a broadly distributed marine invasive species, the European green crab, *Carcinus maenas*. *J. Exp. Biol.* **2014**, *217*, 1129–1138. [CrossRef]
110. Powell, S.J.; Bale, J.S. Cold shock injury and ecological costs of rapid cold hardening in the grain aphid *Sitobion avenae* (Hemiptera: Aphididae). *J. Insect Physiol.* **2004**, *50*, 277–284. [CrossRef]
111. Nunamaker, R.A. Rapid vold-hardening in *Culicoides variipennis sonorensis* (Diptera: Ceratopogonidae). *J. Med. Entomol.* **1993**, *30*, 913–917. [CrossRef]
112. Park, Y.; Kim, Y. A specific glycerol kinase induces rapid cold hardening of the diamondback moth, *Plutella xylostella*. *J. Insect Physiol.* **2014**, *67*, 56–63. [CrossRef]
113. Findsen, A.; Andersen, J.L.; Calderon, S.; Overgaard, J. Rapid cold hardening improves recovery of ion homeostasis and chill coma recovery time in the migratory locust, *Locusta migratoria*. *J. Exp. Biol.* **2013**, *216*, 1630–1637. [CrossRef]
114. Simons, A.M. Modes of response to environmental change and the elusive empirical evidence for bet hedging. *Proc. R. Soc. Ser. B* **2011**, *278*, 1601–1609. [CrossRef]
115. González-Aravena, M.; Rondon, R.; Font, A.; Cárdenas, C.A.; Toullec, J.-Y.; Corre, E.; Paschke, K. Low transcriptomic plasticity of Antarctic giant isopod *Glyptonotus antarcticus* juveniles exposed to acute thermal stress. *Front. Mar. Sci.* **2021**, *8*, 761866. [CrossRef]
116. Chu, X.-L.; Zhang, B.-W.; Zhang, Q.-G.; Zhu, B.-R.; Lin, K.; Zhang, D.-Y. Temperature responses of mutation rate and mutational spectrum in an *Escherichia coli* strain and the correlation with metabolic rate. *BMC Evol. Biol.* **2018**, *18*, 126. [CrossRef] [PubMed]
117. McGaughran, A.; Laver, R.; Fraser, C. Evolutionary responses to warming. *Trends Ecol. Evol.* **2021**, *36*, 591–600. [CrossRef]
118. De La Torre, A.R.; Wilhite, B.; Neale, D.B. Environmental genome-wide association reveals climate adaptation is shaped by subtle to moderate allele frequency shifts in loblolly pine. *Genome Biol. Evol.* **2019**, *11*, 2976–2989. [CrossRef]
119. Barrick, J.E.; Lenski, R.E. Genome dynamics during experimental evolution. *Nat. Rev. Genet.* **2013**, *14*, 827–839. [CrossRef] [PubMed]
120. Chaturvedi, A.; Zhou, J.; Raeymaekers, J.A.M.; Czypionka, T.; Orsini, L.; Jackson, C.E.; Spanier, K.I.; Shaw, J.R.; Colbourne, J.K.; De Meester, L. Extensive standing genetic variation from a small number of founders enables rapid adaptation in *Daphnia*. *Nat. Commun.* **2021**, *12*, 4306. [CrossRef] [PubMed]
121. Waldvogel, A.M.; Pfenninger, M. Temperature dependence of spontaneous mutation rates. *Genome Res.* **2021**, *31*, 1582–1589. [CrossRef] [PubMed]
122. Chu, X.-L.; Zhang, D.-Y.; Buckling, A.; Zhang, Q.-G. Warmer temperatures enhance beneficial mutation effects. *J. Evol. Biol.* **2020**, *33*, 1020–1027. [CrossRef] [PubMed]
123. Berteaux, D.; Réale, D.; McAdam, A.G.; Boutin, S. Keeping pace with fast climate change: Can Arctic life count on evolution? *Integr. Comp. Biol.* **2004**, *44*, 140–151. [CrossRef]
124. Troczka, B.; Zimmer, C.T.; Elias, J.; Schorn, C.; Bass, C.; Davies, T.E.; Field, L.M.; Williamson, M.S.; Slater, R.; Nauen, R. Resistance to diamide insecticides in diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae) is associated with a mutation in the membrane-spanning domain of the ryanodine receptor. *Insect Biochem. Mol. Biol.* **2012**, *42*, 873–880. [CrossRef]
125. Foster, B.J.; McCulloch, G.A.; Vogel, M.F.S.; Ingram, T.; Waters, J.M. Anthropogenic evolution in an insect wing polymorphism following widespread deforestation. *Biol. Lett.* **2021**, *17*, 20210069. [CrossRef]
126. Foster, B.J.; McCulloch, G.A.; Foster, Y.; Kroos, G.C.; Waters, J.M. Ebony underpins Batesian mimicry in an insect melanic polymorphism. *bioRxiv* **2022**. bioRxiv:22.06.13.495778. [CrossRef]
127. McCulloch, G.A.; Waters, J.M. Rapid adaptation in a fast-changing world: Emerging insights from insect genomics. *Glob. Change Biol.* **2022**, *00*, 1–12. [CrossRef] [PubMed]
128. Krehenwinkel, H.; Rödder, D.; Tautz, D. Eco-genomic analysis of the poleward range expansion of the wasp spider *Argiope bruennichi* shows rapid adaptation and genomic admixture. *Glob. Change Biol.* **2015**, *21*, 4320–4332. [CrossRef]
129. Snoeck, S.; Wybouw, N.; Van Leeuwen, T.; Dermauw, W. Transcriptomic plasticity in the arthropod generalist *Tetranychus urticae* upon long term acclimation to different host plants. *G3 Genes|Genomes|Genet.* **2018**, *8*, 3865–3879. [CrossRef] [PubMed]