Received: 31 March 2023 | Accepted: 16 May 2023

DOI: 10.1111/1751-7915.14276

MINI REVIEW

MICROBIAL BIOTECHNOLOGY Applied Microbiology International

Climate change is not just global warming: Multidimensional impacts on animal gut microbiota

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Abstract

Climate change has rapidly altered many ecosystems, with detrimental effects for biodiversity across the globe. In recent years, it has become increasingly apparent that the microorganisms that live in and on animals can substantially affect host health and physiology, and the structure and function of these microbial communities can be highly sensitive to environmental variables. To date, most studies have focused on the effects of increasing mean temperature on gut microbiota, yet other aspects of climate are also shifting, including temperature variation, seasonal dynamics, precipitation and the frequency of severe weather events. This array of environmental pressures might interact in complex and non-intuitive ways to impact gut microbiota and consequently alter animal fitness. Therefore, understanding the impacts of climate change on animals requires a consideration of multiple types of environmental stressors and their interactive effects on gut microbiota. Here, we present an overview of some of the major findings in research on climatic effects on microbial communities in the animal gut. Although ample evidence has now accumulated that shifts in mean temperature can have important effects on gut microbiota and their hosts, much less work has been conducted on the effects of other climatic variables and their interactions. We provide recommendations for additional research needed to mechanistically link climate change with shifts in animal gut microbiota and host fitness.

INTRODUCTION

Anthropogenic climate change is one of the greatest modern threats facing ecosystems and biodiversity (IPCC, 2021; Kannan & James, 2009). Factors like greenhouse gas emissions, environmental degradation and urbanization have resulted in substantial changes to the climate which have already been linked to shifting geographic distributions of organisms and declines in biodiversity (Fakana, 2020; Nunez et al., 2019). Despite a focus in the literature on the impacts of increasing mean temperature, climate change is multi-dimensional and imposes an array of selective pressures on organisms that go beyond shifts in a single factor. These include altered climatic variability and precipitation patterns, increases in the intensity and duration of extreme weather events, and shifts in seasonality. Further, these effects can act in combination or generate cascades involving indirect pathways such as altered habitat and food availability. Together, these environmental changes will require organisms to respond rapidly, and possibly across a wide range of traits, in order to persist.

When predicting how a species will respond to climate change, most studies make predictions based on physiology, population genetic variation, dispersal ability or habitat requirements (Dunham et al., 1999; Garcia-Costoya et al., 2023; Neel et al., 2021; Urban et al., 2012; Wheatley et al., 2015). However, animals also host a wide array of microbiota and recent work has shown that host-associated microbial communities can affect many dimensions of animal health and fitness and can be influenced by a range of environmental variables (Kau et al., 2011; Kers et al., 2018; Sepulveda & Moeller, 2020; Troyer, 1984; Valdes et al., 2018; Williams et al., 2020). For example, microbial communities can metabolize dietary items to produce energy for the host (Dearing & Weinstein, 2022; Troyer, 1984), support the development of the immune system and exclusion of pathogens (Kau et al., 2011), and mediate endocrine and neurological function (Rutsch et al., 2020; Williams et al., 2020). While climate may affect the microbial communities of other host body regions besides the gut (e.g., the skin or reproductive tract) (Ellison et al., 2019; Ruthsatz et al., 2020; Woodhams et al., 2020), the gut, in particular, is a site of immense microbial diversity, consisting of trillions of bacteria which interact with each other and with their host (Cresci & Izzo, 2019). Climate-driven shifts in host-associated microbiota could exacerbate the negative effects of climate change on hosts or potentially buffer the effects of climate change by enhancing host plasticity (Kolodny & Schulenburg, 2020). Therefore, predicting how climate change will impact animals requires an understanding of how it will affect not only the host but also its microbial counterparts.

Our understanding of how environmental variables drive changes in microbial communities in the animal gut has increased in recent years, yet most studies have focused solely on the effects of mean environmental temperature. Less frequently, studies have examined other environmental variables or their interactions. Here, we summarize some of the key findings and insights from this literature across the major environmental change variables that researchers have considered, with a focus on terrestrial environments, and provide recommendations for future work. We find that additional studies are needed to understand and integrate information about the effects of different dimensions of climate change on animal gut microbiota, and how these changes might impact the survival and evolution of host species across the globe.

MEAN ENVIRONMENTAL TEMPERATURE

One of the primary dimensions of climate change is the documented (and projected) increase in average environmental temperature (IPCC, 2021). Since 1900, human activity has resulted in a global average increase of surface air temperature of approximately 1°C. Continued greenhouse gas emissions are likely to result in a further 0.5–3.5°C increase in mean temperature by the end of the 21st century (IPCC, 2021). The distribution of this warming across the globe has been and will continue to be uneven. For example, the Arctic has warmed at a rate four times that of other regions since 1979 (Rantanen et al., 2022). In addition to this geographic variation in rates of environmental change, shifts in environmental temperature may have opposing effects depending on the thermoregulatory strategy employed by hosts. For example, the rising mean environmental temperature may directly result in an increase in the body temperatures of thermoconforming ectotherms (Neel et al., 2021), but lead to increased energy expenditure for the maintenance of thermal homeostasis in both behaviourally thermoregulating ectotherms and endotherms (Boyles et al., 2011; Huey & Slatkin, 1976). Despite the fact that the degree and implications of mean temperature change differ across these scales of variation, increasing mean temperature has been linked to current and future losses of local species richness (Nunez et al., 2019; Wiens, 2016), and focusing on a global aggregate index like mean environmental temperature can provide a tractable variable to make and test predictions about biological outcomes (Waldock et al., 2018). As a result, many studies have focused on understanding the effects of shifts in mean environmental temperature on host-associated microbiota. We will only briefly summarize this literature as it has already been thoroughly reviewed by Sepulveda and Moeller (2020) and Huus and Ley (2021).

Studies testing the effects of increased mean environmental temperature on microbial communities in the animal gut frequently find a consistent pattern of reduced alpha diversity, as well as a decline in the relative abundance of the bacterial phylum Firmicutes across mammals, reptiles, amphibians and birds (even after short periods of exposure; Huus & Ley, 2021; Sepulveda & Moeller, 2020; but see Williams et al., 2022). Notably, these changes are observed in both ectotherms and endotherms, and it remains unclear whether they are due to direct effects of increased temperature or indirect effects that are mediated through shifts in host physiology or behaviour (Sepulveda & Moeller, 2020). In invertebrates, warming typically results in increases in Proteobacteria and decreases in Actinobacteria (Sepulveda & Moeller, 2020). Further, a recent meta-analysis revealed that warmer mean temperatures impact microbial communities by affecting their phylogenetic diversity and community composition but not dispersion (Li et al., 2023). Beyond illustrating that environmental change can lead to disturbance in microbial communities, it is important to determine the underlying mechanisms by which these changes ultimately impact host fitness (Brüssow, 2020). Many of these temperature-induced shifts in microbial communities have been shown to have significant impacts on host physiology and fitness, including through reductions in digestive efficiency (Fontaine et al., 2018), exacerbation of parasitism (Ingala et al., 2021), increased inflammation and gastrointestinal enteritis (Chen et al., 2019), and altered growth patterns and

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decreased survival (Kikuchi et al., 2016). When taken together, this body of work indicates that increasing mean temperatures alter gastrointestinal microbiota with detrimental outcomes for host health and fitness.

TEMPERATURE VARIABILITY

Even in the absence of climate change, most organisms regularly experience climatic variability. Many habitats display spatial thermal heterogeneity, oscillations between maximum daily and minimum nightly temperatures, seasonal temperature cycles and the occurrence of some baseline rate of heat waves and cold snaps. However, climate change will alter the timing, magnitude, distribution and prevalence of this variation (IPCC, 2021). Although relatively rare, several studies have considered the role of temperature variability—specifically diurnal temperature ranges and the frequency of short-term heat waves—in altering gut microbiota composition.

The diurnal temperature range (DTR), or the difference between the maximum and minimum temperatures experienced in an average day, is shifting for many species as a result of climate change. In fact, the average global DTR has contracted because daily minimum temperatures have increased more than daily maximum temperatures (0.9°C versus 0.6°C, respectively; Braganza et al., 2004). However, there is substantial regional variation in these changes, with the most significant contractions seen in the northern hemisphere, and with some areas of the southern hemisphere experiencing expansions (Sun et al., 2019).

Changes to the DTR can alter the effects of mean environmental temperature change on organisms (Figure 1). Wide DTRs can interact with mean temperature increases and decrease the fitness of both ectotherms and endotherms (Briga & Verhulst, 2015; Paaijmans et al., 2013; Zeh et al., 2014). Particularly in ectotherms, this response is in part due to Jensen's inequality, where asymmetric thermal performance curves can lead to large performance declines when temperature fluctuations occur near an organism's thermal optimum (Martin & Huey, 2008; Ruel & Ayres, 1999). Despite the established importance of DTRs for host performance, few studies have specifically tested the effects of DTRs on host-microbiota relationships. An exception is work by Higashi and colleagues, who elegantly tested the effect of changes in both mean temperature and DTR (in multiple configurations) on a defensive mutualism in aphids. Under normal climate conditions, the pea aphid (*Acrythosiphon pisum*) is protected from parasitism by wasps through a partnership with its symbiotic microorganism, *Hamiltonella defensa* (Higashi et al., 2020). In some contexts, increases in diurnal temperature variation due to increases in daytime temperature resulted in higher levels of symbiosis breakdown. However, the authors emphasized that increases in night-time temperature, despite leading to contracted DTR, can also be detrimental as nights no longer provide a thermal refuge for host-symbiont recovery. Considering the fine-scale details of temperature changes could alter our predictions of how hosts and their microbiota will respond to climate change, but additional studies are needed to tease apart the independent effects of DTR and mean temperature change.

In addition to shifts in DTR, the frequency and intensity of heatwaves has increased since the 1950s, and these events are projected to increase with further rises in mean temperature (IPCC, 2021). Heatwaves, because of their potential to produce especially severe and acute performance decrements, are perhaps particularly likely to result in acclimatory responses of hosts. It is possible that increasing exposure to heatwaves will lead to heat hardening (thermal tolerance plasticity) which might reduce impacts upon subsequent re-exposures (Renaudeau, 2020). However, many animals, especially those which have evolved in thermally stable habitats, display limited plasticity in response to heat stress (Deutsch et al., 2008; Gunderson & Stillman, 2015; Huey et al., 2018; Stillman, 2003). Therefore, exposure to repeated, high-magnitude heatwaves may ultimately reduce host survival and fitness.

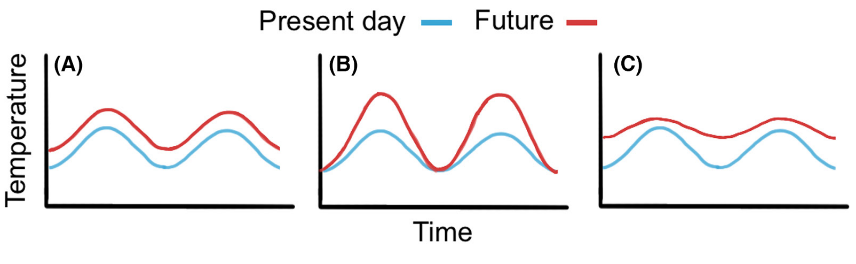

FIGURE 1 Different patterns of change in the daily temperature range can correspond to the same increase in mean temperature. (A–C) All panels show temperature ranges across 2 days, and the differences in mean temperature between present day (blue line) and the future (red line) are the same in each. (A) Increases in mean temperature could occur without changes in diurnal temperature range. (B) Days could disproportionately warm, widening the daily temperature range. (C) Nights could disproportionately warm, shrinking the daily temperature range.

Many studies which have assessed the effects of mean temperature increases on animal gut microbiota do so through short-term exposure, which can be considered analogous to exposing animals to heat waves (Sepulveda & Moeller, 2020). Therefore, findings from studies of mean temperature change are often informative for understanding the effects of heat waves, especially those that use realistic temperature regimes (e.g., ramping temperatures as opposed to static temperature shifts; Li et al., 2023). A meta-analysis of studies testing increases in mean temperature with ramping regimes showed that longer exposure time does not exacerbate reduction in microbial community diversity but can lead to more substantial community composition divergence compared to control groups (Li et al., 2023). Unfortunately, few studies have tested how the frequency of heatwaves might alter gut microbial communities through repeated exposures. An exception to this is work by Khakisahneh et al. (2020), who tested the effects of three consecutive heat waves on the gut microbiota of Mongolian gerbils. Alpha diversity fluctuated throughout the experiment, with the effects of heat exposure being most apparent after the third heat wave. Heat-exposed groups also showed increasing divergence in community composition across exposures. Different microbial taxa responded differently to repeated exposures, with some consistently shifting in a similar direction and magnitude, others responding more to the first exposure, and others responding most strongly to the third exposure. On each exposure, the degree to which hosts compensated for heat by reducing food intake decreased in magnitude, suggesting a host acclimatory response. It is not surprising that increased frequency of heatwaves can induce plasticity of hosts to warmer conditions, although how this may have been influenced by changes in gut microbiota remains unclear. Nevertheless, this study highlights the importance of measuring biological responses beyond a single exposure to heat stress. To date, there are insufficient data to establish the links between gut microbial community function and heat wave magnitude, duration and frequency. There is thus an urgent need for additional research which uses realistic temperature regimes and explores the effects of repeated heat waves of differing magnitudes on host-microbiota relationships. Moreover, to date, many of the experiments that test the effects of both increases in mean temperature and temperature variability have been conducted in the laboratory or in semi-natural mesocosms. These sorts of studies may have less realism because wild animals can often buffer the effects of changing environmental temperatures through behavioural or physiological compensation (or both). Further work is needed, particularly using field-based experiments in both ectotherms and endotherms, to explore the mechanistic links between changes in environmental temperature, shifts in microbiomes and impacts on host fitness.

PRECIPITATION

Globally, climate change has already resulted in an average increase in heavy precipitation events and droughts (IPCC, 2021). Precipitation patterns are projected to change in a region-dependent manner, with particularly large increases in precipitation projected for high latitudes but decreases projected for parts of the tropics and subtropics (IPCC, 2021). The frequency and severity of droughts will also continue to increase in many regions. Changes in precipitation can have substantial impacts on organismal fitness (Bonebrake & Mastrandrea, 2010; Walls et al., 2013). These impacts include changes to population size (Williams & Middleton, 2008) or offspring growth due to differences in food availability (Groenewoud & Clutton-Brock, 2021) and changes in reproductive phenology driven by water availability (Walls et al., 2013). Similarly, changes in rainfall could affect gut microbial community composition by altering the distribution of microbes in the environment outside the host or by affecting variables like host water intake, diet availability or diet preference (Baniel et al., 2021; Hartmann et al., 2017; Naidoo et al., 2022; Vásquez-Dean et al., 2020).

Precipitation has explained variation in gut microbiota alpha diversity and composition in several taxa (Baniel et al., 2021; Björk et al., 2019; Fan et al., 2022; Liu et al., 2022; Williams et al., 2022). In wild geladas (*Theropithecus gelada*), detailed climatological data alongside longitudinal microbiota sampling has been used to tease apart the independent effects of changes in rainfall and temperature on gut microbial community diversity and composition (Baniel et al., 2021). Rainfall explained most of the temporal variation in gelada gut microbiota, although this likely occurred because of a link between precipitation patterns and food availability. Wet periods increased grass growth and gelada grass consumption, and these shifts were correlated with substantial increases in cellulolytic bacteria. Li et al. (2020) disentangled the direct and indirect effects of precipitation on microbial communities in Brandt's vole by combining feeding trials and faecal transplants in the laboratory with field-manipulations of precipitation. They showed that increased rainfall led to the dominance of a perennial grass (*Leymus chinensis*), increased consumption of this grass by voles, and a resulting increase in vole body mass. Their laboratory feeding trials showed that higher intake of *L. chinensis* resulted in reductions in the prevalence of microbial genes for histidine degradation and increased production of short-chain fatty acids, which are putative pathways through which microbiota can support weight gain. These two studies demonstrated how gut microbial communities may facilitate host plasticity during dietary shifts and nutritional demands induced by precipitation

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changes, perhaps helping hosts cope with environmental variation. Studies like this have thus far been conducted in primary consumers, and it remains unclear how changes in precipitation might scale to alter the gut microbial communities of higher order consumers. Additional studies on the impacts of precipitation on gut microbiota composition and function are needed to understand the mechanisms by which climate change-induced changes in rainfall might impact host physiology and fitness. Experiments that include manipulations of precipitation in the field (e.g., rainfall exclusion) or in the lab (e.g., controlled watering conditions) would be especially powerful.

SEASONALITY

The timing and amplitude of seasonal temperature patterns are shifting across the globe (Stine et al., 2009). Over continental areas, the difference between maximum summertime and minimum wintertime temperature has decreased since the 1950s (Stine et al., 2009). In the Northern Hemisphere, summertime temperatures have persisted longer which has resulted in shorter winters (Wang et al., 2021). In addition to temperature, seasons are also characterized by photoperiod, rainfall, wind, humidity and resource pulses (White & Hastings, 2020). Changes in seasonal characteristics like total rainfall or average temperature can exert direct and interacting effects on animals and their gut microbiota. Additionally, changes in seasonal timing can alter the synchronicity of organismal processes or decouple interactions between organisms (Stevenson et al., 2015). Many species have phenological patterns that are triggered by photoperiod, including hibernation, reproduction and migration (Stevenson et al., 2015). Others depend on resources that themselves have phenologies tightly linked to photoperiod (e.g., herbivores which consume seasonal plants; Helm et al., 2013; Huang et al., 2020). Shifts in seasonal timing might elicit phenological mismatches and ultimately reduce organism fitness (Ettinger et al., 2021; Stevenson et al., 2015). Changes in seasonal patterns are a clear example of how understanding and predicting the impacts of climate change requires a consideration of many different dimensions of change.

To date, most studies of seasonal influences on the gut microbiota have been observational in nature and have focused on documenting flux in gut microbiota throughout the year. These studies have demonstrated seasonality in gut microbial communities across a wide range of taxa (Baniel et al., 2021; Cui et al., 2021; Ferguson et al., 2018; Fernandes et al., 2021; Hicks et al., 2018; Liu et al., 2019, 2022; Marsh et al., 2022; Maurice et al., 2015). Seasonal changes in the gut microbiota have been linked to cyclical changes in climatic variables like temperature (Baniel et al., 2021; Fan et al., 2022; Ferguson et al., 2018; Liu et al., 2019; McMunn et al., 2022) and precipitation (Baniel et al., 2021; Fan et al., 2022) or to seasonal shifts in prey or nutrient consumption (Fan et al., 2022; Fernandes et al., 2021; Liu et al., 2022; Wu et al., 2017; Figure 2).

In most cases, it remains unclear what implications these seasonal microbial community shifts have for host physiology and fitness. Several studies in giant pandas have shown that seasonal shifts in dietary nutrients can destabilize the gut microbiota, resulting in dysbiosis and gastrointestinal distress (Williams et al., 2016; Wu et al., 2017). Seasonal transitions and their effects on host immunity through altering the gut microbiota might leave hosts susceptible to infection and increase disease prevalence (Stencel, 2020). Seasonal shifts in temperature can also lead to reduction or loss of mutualistic bacterial taxa in insects (McMunn et al., 2022). However, seasonal changes in gut microbiota could also enable host plasticity and enhance survival in cyclically changing environments. For example, seasonal cycles in microbial communities appear to play a role in digestive plasticity in some species (Amato et al., 2015; Baniel et al., 2021; Hicks et al., 2018; Huang et al., 2022). Amato et al. (2015) found the gut microbiota of howler monkeys could facilitate increased energy production for hosts in the form of volatile fatty acids during periods of low intake of lipids and amino acids. In Siberian hamsters, seasonal and photoperiod induced shifts in gut microbial communities were shown to drive aggressive behaviours that may enhance fitness (Ren et al., 2020; Scotti et al., 2015; Shor et al., 2022). These studies illustrate potential pathways through which the gut microbiota may be able to buffer hosts from some

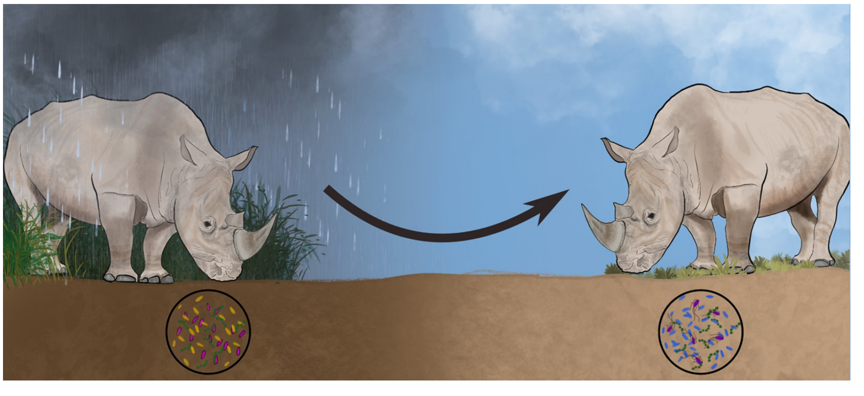

FIGURE 2 Seasonal changes (e.g., wet season versus dry season) encompass shifts in many variables including temperature, rainfall, resources and day length. These changes may alter water availability, environmental microbiota and host diet.

of the negative the effects of climate change. It is difficult to generalize the results of these studies to all animals, as the temporal stability of the gut microbiota and the degree to which host physiology is influenced by seasonality varies among species (Yao et al., 2019; Zoelzer et al., 2021). Nevertheless, some attention has been paid to characterizing the relative magnitude and synchronicity of different species' gut microbiota shifts across seasons (Björk et al., 2019; Marsh et al., 2022; Xue et al., 2015). These studies suggest that there is variation in how responsive the gut microbial communities of different species are to seasonal changes and how synchronized these changes are within individuals.

While prior research has shown that seasonality can drive shifts in gut microbiota and that in some cases this scales up to impact host health and fitness, additional studies are needed to: (1) understand the factors that govern sensitivity of different species' microbial communities to seasonal shifts, (2) characterize the independent and interacting effects of seasonal variables, (3) link these changes to shifts in host physiology and fitness, and (4) use these findings to predict the effects of seasonal shifts under climate change.

MOVING TOWARDS A MULTIDIMENSIONAL UNDERSTANDING OF CLIMATE CHANGE IMPACTS ON GUT MICROBIAL COMMUNITIES AND THEIR HOSTS

Understanding and predicting the impacts of climate change requires a consideration of many different dimensions of change, such as shifts in mean temperature, temperature variability, precipitation and seasonality. The effects of these variables on animals will be, at least in part, mediated through gut microbiota (Figure 3). Climatological variables can alter gut microbial community diversity, composition and function, potentially leading to cascading effects for animal health, including altered digestion, thermal tolerance or disease susceptibility. In contrast, climate-driven shifts in gut microbial communities can also be beneficial to the host, serving as a mechanism for adaptive plasticity. Nevertheless, the majority of gut microbiota studies have focused on the role of increasing mean environmental temperature alone. Of those studies that have investigated other sources of climate-related stress, very few have considered interactive effects between stressors. While investigating the effects of each climate variable independently is understandable as it has enabled us to reveal the mechanistic links between gut microbiota and particular climate variables, the examination of combinations of these variables might lead to unexpected outcomes that could not be predicted by studies of individual factors in isolation. Indeed, Rillig et al. (2019) investigated the effects of several global-change related stressors both independently and in combination on soil microbial communities and found that single-effect responses could not be used to predict the outcomes of combined stressors. To our knowledge, studies like this have not been conducted to evaluate combinatorial climatological stressors on the gut microbiota in any animal species.

The effects of climate change go beyond the environmental variables we have discussed here. Climate change is also associated with increases in the

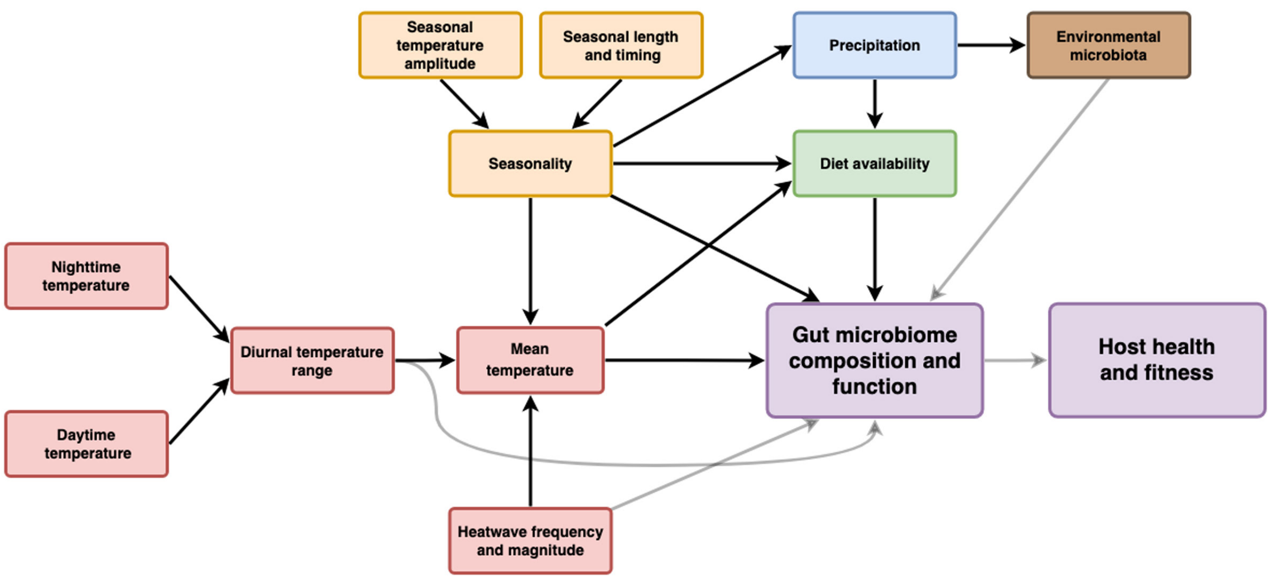

FIGURE 3 Many types of climatological variables (grouped by colour) can alter gut microbial community composition and ultimately impact host fitness through both direct and indirect pathways. To date, some pathways have more empirical support (black arrows) than others (grey arrows). Only a subset of possible variables and pathways are indicated here.

frequency of storms and wildfires, glacial retreat and sea level rise, and other indirect impacts on ecosystems. We lack research into the roles played by many of these phenomena in altering microbial communities in the animal gut. To improve our understanding of the effects of climate change on the gut microbiota of animals with the goal of developing more accurate climate-impact forecasts, we require (1) mechanistic studies, examining direct and indirect mechanisms through which microbiota might mediate the effects of climate stressors on animals, in part through using approaches that survey gut microbiota function (see Greenspan et al., 2020; Li et al., 2020), and (2) studies exploring the outcome of combined stressors on microbial communities and the fitness of their hosts.

AUTHOR CONTRIBUTIONS

Claire E. Williams: Conceptualization (lead); visualization (lead); writing – original draft (lead); writing – review and editing (equal). **Candace L. Williams:** Supervision (supporting); visualization (supporting); writing – review and editing (equal). **Michael L. Logan:** Conceptualization (supporting); supervision (lead); writing – review and editing (equal).

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

FUNDING INFORMATION

No funding information provided.

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How to cite this article: Williams, C.E., Williams, C.L. & Logan, M.L. (2023) Climate change is not just global warming: Multidimensional impacts on animal gut microbiota. *Microbial Biotechnology*, 00, 1–9. Available from: https://doi.org/10.1111/1751-7915.14276