


Bumblebee resilience to climate change, through plastic and adaptive responses

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Abstract

Bumblebees are ubiquitous, cold-adapted eusocial bees found worldwide from subarctic to tropical regions of the world. They are key pollinators in most temperate and boreal ecosystems, and both wild and managed populations are significant contributors to agricultural pollination services. Despite their broad ecological niche at the genus level, bumblebee species are threatened by climate change, particularly by rising average temperatures, intensifying seasonality and the increasing frequency of extreme weather events. While some temperature extremes may be offset at the individual or colony level through temperature regulation, most bumblebees are expected to exhibit specific plastic responses, selection in various key traits, and/or range contractions under even the mildest climate change. In this review, we provide an in-depth and up-to-date review on the various ways by which bumblebees overcome the threats associated with current and future global change. We use examples relevant to the fields of bumblebee physiology, morphology, behaviour, phenology, and dispersal to illustrate and discuss the contours of this new theoretical framework. Furthermore, we speculate on the extent to which adaptive responses to climate change may be influenced by bumblebees' capacity to disperse and track suitable climate conditions. Closing the knowledge gap and improving our understanding of bumblebees' adaptability or avoidance behaviour to different climatic circumstances will be necessary to improve current species climate response models. These models are essential to make correct predictions of species vulnerability in the face of future climate change and human-induced environmental changes to unfold appropriate future conservation strategies.

KEYWORDS

adaptation, bumblebees, climate change, desiccation, dispersal, evolutionary potential, heat shock proteins, phenology, phenotypic plasticity, thermoregulation

1 | INTRODUCTION

Bumblebees (genus: *Bombus* Latreille) are large, mostly eusocial bees, encompassing over 265 species worldwide found across a diverse

range of climates, including subarctic, temperate, subtropical, and tropical (Williams & Jepsen, 2020). Bumblebees provide vital pollination services, increasing both crop yield and quality; worldwide, commercial bees alone are estimated to contribute €12 billion per year (Velthuis & van Doorn, 2006) while individual species of wild bumblebees can contribute over \$5000 per hectare (Kleijn et al.,

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2015). Most bumblebees have an annual life cycle, which, in general, starts after a hibernation period when fertilized queens search for a nesting site. These queens start laying eggs which will pass through several larval stages to pupate into workers which will perform work duties for the colony, including foraging on pollen and nectar from a large diversity of flowering plants (Rasmont et al., 2021). Male and fertile female bees are produced later as the season progresses, mostly in the summer. This annual cycle ends in the fall, with the newly produced and fertilized queens searching for an underground shelter to survive the winter while the other remaining bees and the colony will perish (Alford, 1975; Goulson, 2010).

Like many other insects (Wagner et al., 2021), a wide range of bumblebee species experience population declines attributed to various anthropogenic factors, all interacting to varying degrees, including habitat loss and fragmentation, exposure to pesticides, pathogens, and also climate change (e.g. Cameron & Sadd, 2019; Marshall et al., 2018; Rasmont et al., 2015). Climate change is one of the most striking and interactive factors of pollinator decline (see also Halsch et al., 2021; Vasiliev & Greenwood, 2021), and is characterized by rising average ambient temperatures, changes in precipitation patterns, increased CO₂ concentration, higher UV exposure, and increased frequency and intensity of extreme weather events such as heatwaves, cold snaps, or other unseasonable weather (Cornelissen, 2011; IPCC, 2014; Vasiliev & Greenwood, 2021). Most insects evolved under very different environmental conditions in the past and are therefore characterized by species-specific traits selected for those conditions when maintaining the same niche (e.g. Halsch et al., 2021). Several characteristic responses of heat-stressed bees have been described (especially for honeybees, as reviewed in Zhao et al., 2021). However, bumblebees have evolved to thrive under cold (or temperate) conditions (Dehon et al., 2019), with adaptations especially suited to tolerate extreme cold, such as the ability to thermoregulate, and their body covered with long, insulatory setae (Heinrich, 1974; Peat et al., 2005; Ploquin et al., 2013). Derived clades of bumblebees also occur in subtropical and tropical regions, but they are mainly found at higher altitudes (e.g. Ding et al., 2019; Streinzer et al., 2019), and only a few species live and thrive under the conditions expected to be produced by climate change—long, hot and dry summers and short, moderate winters (Rasmont et al., 2008, 2015). As a result, bumblebees are expected to be substantially impacted by ongoing and future climatic changes, and predictions through species climate risk modelling tend to confirm this hypothesis and predict major population, species, and range losses (e.g. Koch et al., 2019; Rasmont et al., 2015; Sirois-Delisle & Kerr, 2018; Vasiliev & Greenwood, 2021). Temperature, in particular, is known to be a critical factor in bumblebee adaptation, since workers must remain active in and outside the colony in the height of summer while queens must tolerate cold winter temperatures (Hines, 2008; Williams, 1998; Woodard, 2017). The effects of climate change can be direct, with an impact on physiology and morphology, such as a shift in freeze avoidance (Owen et al., 2013, 2016) or an increase in body size (Gérard, Marinnet et al., 2020); or indirect,

through changing abiotic and biotic interactions, such as changing land use, induced species competition, spread of invasive plant/insect species, and emergence of new diseases (e.g. Gérard et al., 2020; Marshall et al., 2018; Ogilvie et al., 2017).

In this review, we summarize and discuss the different mechanisms that allow bumblebees to cope with, or instead to avoid, a wide range of (changing) climatic stressors. We explore the plastic and adaptive potential of bumblebees in several key traits related to physiology, morphology, behaviour, and phenology. In addition, we also discuss the interaction between adaptation and dispersal processes associated with climatic change, which can be contradictory and could lead to biodiversity loss (Thompson & Fronhofer, 2019). Unravelling plasticity and/or adaptive traits of bumblebees is necessary for a better understanding of their resilience to current climatic and anthropogenic changes. Incorporating potential adaptive responses and resilience into species distribution models will also allow for a better design of conservation strategies to mitigate future environmental changes.

2 | MORPHOLOGY

Bumblebees (Apoidea) are typically medium to large bees with hairy bodies (Alford, 1975; Goulson, 2010). Body size and hairiness are two external characteristics of bumblebees that, in addition to a few other external morphological traits, can play a role in thermoregulation (Figure 1).

2.1 | Body size

Body size is a key morphological trait in bumblebees which exhibits considerable plasticity. Although the members of a bumblebee colony are highly related—all or most workers are offspring from one founder queen and thus full-sibs—extensive size differences can be observed among nestmates (e.g. Goulson, 2010). Their size

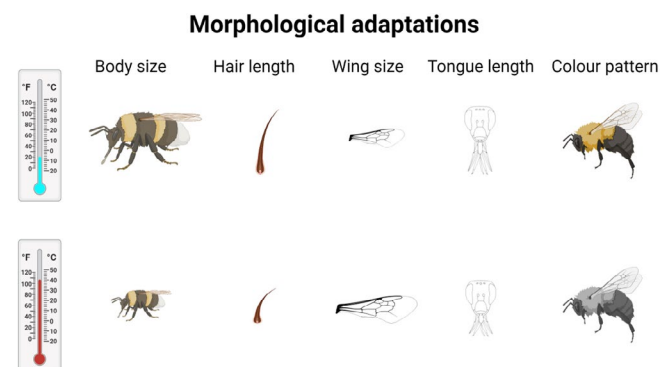


FIGURE 1 Morphology of bumblebees in cold and warm environments. Figure created with Biorender.com, with the drawing of a bumblebee wing and tongue originated from Michez et al. (2019), and are used with permission

is determined by two key factors during development, namely the ambient temperature and their diet/nutrition. Larger bees will develop requiring higher quality/quantity food intake (Chole et al., 2019) and adequate temperature (Vanderplanck et al., 2019). These larger individuals are expected to retain better heat due to surface to volume ratios, and are therefore better suited to cooler environments, a theory known as Bergmann's Rule (Bergmann, 1848). In bees, species-specific body size trends are generally consistent with this rule. Bishop and Armbruster (1999) and De Farias-Silva and Freitas (2020) found that heat generation in larger bees is more efficient, and that thermoregulatory ability correlated with body size. However, bumblebees are an exception to Bergmann's Rule (Gérard et al., 2018), but the evidence has remained unclear, as several studies show results supporting (Peat et al., 2005; Scriven et al., 2016) and arguing against the application of this theory to bumblebees (Gérard et al., 2018; Ramírez-Delgado et al., 2016). Despite the fact that bumblebees are cold-adapted organisms and are prone to overheating during extreme heat waves (Heinrich, 1974, 1979), the evidence suggests that the mean body size of queens of two out of four tested European bumblebee species actually increased over the past 100 years, with the increase in average temperatures (Gérard, Marinet et al., 2020). The response in bumblebees was thus rather species-specific, which prevents generalized predictions for bumblebees as a group. Several theories have been proposed to explain the observed increase in body size, such as (i) the increased season length which may allow for the development of larger queens, (ii) the fact that larger animals have lower rates of water loss and may thus be favoured in extreme temperatures or (iii) the hypothesis that food availability has increased due to longer seasons and lack of winter frost (Ramírez-Delgado et al., 2016). However, non-mutually exclusive factors other than temperature might be also at play, such as agricultural intensification (Gardner et al., 2011; Gérard, Marinet, et al., 2020) or landscape fragmentation (Gérard et al., 2021). The latter hypothesis was strengthened by recent research measuring shifts in body size over an urban-rural gradient which found body size to be correlated to road density as proxy of level of habitat fragmentation due to urbanization (Theodorou et al., 2021). Larger bees would be selected in fragmented areas as they can fly for longer and more easily reach isolated adequate habitat. Local bumblebee sizes are likely a result of phenotypic plasticity, local selection, and habitat matching which all act together, but at different time scales (as discussed in Theodorou et al., 2021). However, the interactive effects of agricultural intensification and landscape fragmentation are not well explored over long temporal and large spatial scales and represent an important future research direction.

2.2 | Pilosity

In addition to body size, other morphological traits, such as hair length, density, and colour are important traits in relation to temperature (Figure 1). Unsurprisingly, bees with longer hair were

found to be able to tolerate colder temperatures before becoming immobile (a behaviour known as chill coma) than bees with shorter hair (Peters et al., 2016). Similarly, Peat et al. (2005) found that the average thoracic setae (hair) length was longer in bee species from cooler climates. Moreover, colour pattern is highly variable both among and within bumblebee species and is known to have a role in thermoregulation due to reflectance and absorption, although the exact mechanics are not well understood (Williams, 2007). As Rapti et al. (2014) noted, black colours frequently occur around the central thorax, where heat is generated during flight. In butterflies, species from cooler environments have dark colouration around the flight muscles, which helps them absorb the heat of solar radiation and allows them to reduce flight costs at lower temperatures (Tsai et al., 2020). A comprehensive study of worldwide colour patterns found that completely and mostly black bumblebee species were found near the equator while paler species were more often found in mid-latitudes (Williams, 2007). However, associations between colour patterns and habitat type were also found, with darker bees strongly associated with broadleaf evergreen forest, and paler colour patterns associated with grasslands probably related to camouflage (Williams, 2007). Stronger associations between habitat, climate, and colouration were described in other bee species; for instance, a darker pigmentation of Eastern honeybees (*Apis cerana*) was strongly associated with cooler, high-altitude regions (Montero-Mendieta et al., 2018), while the dark colour pattern, in combination with basking behaviour, allowed *Xylocopa* bees to warm-up quickly to flight-permissive muscle temperatures (de Farias-Silva & Freitas, 2020). In other insects, such as in *Colias* butterfly populations, levels of wing melanin were found to correlate with thermal tolerance (Kingsolver et al., 2011). In addition, the brightly coloured banding of bumblebees is also a classic example of both aposematism and Müllerian mimicry, with sympatric species tending to converge on similar patterns (Rapti et al., 2014; Williams, 2007), and is driven by changes in *Hox* gene expression (Rapti et al., 2014; Tian et al., 2019).

2.3 | Other morphological traits

Less obviously, wing size and tongue length have also been found to correlate with climatic variables. The minimum temperature at which bees were found to be active was lower in bees with shorter wings relative to their body size (Peters et al., 2016). This is thought to be related to heat loss at wing extremities. For tongue length, the relation with—or rather adaptation to—climate is less obvious. Tongue length in bumblebees is known to relate to the degree of dietary specialization, with generalists typically having a shorter tongue than specialists (Goulson, 2010; Goulson et al., 2005). The tongue length of *B. balteatus* and *B. sylvicola*, two North American species adapted to boreal climates, was found to have decreased by 24.4% since 1966, independent of changes in body size (Miller-Struttman et al., 2015). Bommarco et al. (2012) found that the relative proportion of long-tongued bumblebee species had drastically decreased over the past 70 years, although this was mostly attributed to land

use changes. For Miller-Struttman et al. (2015) the most likely mechanism explaining the observed pattern was evolutionary adaptation; the reduced bloom of alpine flowers due to climate change had encouraged these species to include flowers with shorter corolla tubes into their diet. However, as the authors of this study have not directly measured the effect of tongue shortening on bees' fitness, it is uncertain and rather doubtful that evolutionary rescue allowed these species to escape decline in such short time (see De Keyser et al., 2016). To prove the suggested adaptive hypothesis, research investigating the direct link between tongue length shortening affecting bee fitness is still needed.

Overall, bumblebees can locally adapt to very different climatic conditions due to differences in several morphological traits, such as body size and hairiness, which enable them to reach the crucial body temperatures needed to survive those environmental conditions. However, whether this is due to phenotypic plasticity, directional selection, or an interplay of both mechanisms, is in most cases not yet clear. Future research should focus on disentangling whether plastic response in morphological traits in bees results in evolutionary changes.

3 | PHYSIOLOGY

In addition to their morphology, bumblebees have also various physiological traits that strengthen their resilience to climatic changes, and including variation in their thermal tolerances, and specific traits and mechanisms that help in both cold and heat resistance, as well as desiccation tolerance.

3.1 | Variation in thermal tolerance

Species' critical thermal limits, CT_{MIN} and CT_{MAX} , are the minimum and maximum temperatures at which an animal can maintain muscle control (Oyen & Dillon, 2018). These objective measures are helpful in determining the physiological vulnerability of a species to climate change and to predict species responses to thermal stress (Burdine & McCluney, 2019; Deutsch et al., 2008; Hamblin et al., 2017; Kellermann et al., 2012). However, it seems that thermal sensitivity in bumblebees is species-specific (Hamblin et al., 2017; Martinet, Dellicour et al., 2021; Martinet, Zambra et al., 2021; Oyen et al., 2016; Zambra et al., 2020), and even intraspecific variation between subspecies and castes has been reported (Maebe et al., 2020). Furthermore, Penick et al. (2016) note that the negative effects of temperature extremes can be observed before the limits of CT_{MIN} and CT_{MAX} are reached while selection for thermal tolerance strongly depends on rare but extreme thermal events. More research is necessary to reveal to what extent extreme weather conditions impact the thermal tolerance of bumblebees. Hence, such nuanced data will help to improve models from tolerant/intolerant regions to a gradient of suitability.

3.2 | Cold resistance

Unusually for insects, bumblebees are capable of endothermy, through the shivering of flight muscles and a process known as substrate cycling, which involves the enzymes fructose diphosphatase and phosphofructokinase working antagonistically to 'burn' through ATP to generate heat (Heinrich, 1974, 1979; Surholt et al., 1990). This ability is critical to survival, as their flight muscles will not operate below 37°C (Heinrich, 1974, 1979). This adaptation has allowed bumblebees to thrive in biomes like tundra that would otherwise be inaccessibly cold (Martinet, Dellicour et al., 2021). Given the importance of muscle shivering and enzymes in substrate cycling, genes related to muscle function, thermogenesis and substrate cycling can be expected to be under selective pressure in cold environments. A study in *Drosophila* species found that cold-acclimated populations significantly upregulated myosin chain genes, which are essential for muscle function (MacMillan et al., 2016). Further research is required to confirm whether this is indeed also the case in bumblebees. As with most insects, cold temperatures in bumblebees induce a typical sequence that starts with slowed behavioural responses and impaired coordination before a burst of muscle activity, followed by total paralysis in a chill coma (e.g. Maebe et al., 2020; Oyen & Dillon, 2018). Although the mechanisms for this response have not been investigated in bumblebees, they are likely to be very similar to those described in other insects. In general, due to cold stress, insects first lose their neuromuscular functions and thus enter chill coma, caused by a reduced membrane potential; when the cold stress persists, additional negative effects are caused by the disruption of ion and water homeostasis across membranes and epithelium, eventually leading to insect death (as reviewed by Overgaard & MacMillan, 2017). In *Drosophila* spp. and *A. mellifera*, cold-tolerant populations 'defended' their membrane potentials better than non-tolerant populations (e.g. Andersen et al., 2015; Hosler et al., 2000); and cold-acclimated *Drosophila* populations significantly upregulated both myosin chain genes, which are essential for muscle function, and troponin genes, involved in Ca^{2+} -mediated muscle contraction (MacMillan et al., 2016). Such adaptations might also help bumblebees to protect the resting potentials of muscle cells from depolarization under very cold conditions.

However, even under global warming, extreme cold events will occur more frequently (e.g. Cohen et al., 2018, 2020); and such cold snaps will also be a threat to even cold-adapted insects such as bumblebees. In general, insects have two key strategies to cope with the cold: freeze tolerance and freeze avoidance (Storey & Storey, 2012). Freeze-tolerant insects allow for the formation of ice crystals within their cells and cope with the consequences, whereas freeze-avoidant insects prevent freezing through physiological and biochemical means (Storey & Storey, 2012). Bumblebees are known to be freeze-avoidant, though the limits vary by species (Owen et al., 2013, 2016). As common cryoprotectants including glycerol, sorbitol, and trehalose are expensive to produce (Storey & Storey, 2012), they are expected to be under high selective pressure under the

increasing temperatures of climate change. Whether this hypothesis is true has yet to be confirmed by future research.

Another survival strategy of bumblebees, especially of fertilized queens in temperate regions, is to go through a hibernation or overwintering stage (e.g. Goulson, 2010; Heinrich, 1979). For hibernating queens, careful regulation of metabolism, activity levels, and energy reserves are crucial to survive the colder winter months. By lowering the metabolic rate, hibernating queens are able to perform basic cellular maintenance (Hahn & Denlinger, 2007, 2011), but at the same time save their energy reserves for later (Denlinger, 2002). The metabolism-slowness and development-delaying effects of the cold have also been shown by Vesterlund et al. (2014), which found that *B. lucorum* queens lose less fat in cold conditions. A minimum fresh weight of 0.6 g and 0.4 g was found to be necessary for successful hibernation of *B. terrestris* and *B. lucorum* queens, respectively (Beekman et al., 1998; Vesterlund et al., 2014). Given that climate change will likely increase the average winter temperature in the future, this may expose overwintering queens to warmer temperatures, putting those with insufficient reserves at risk. However, even with enough fat reserves, there might be some important fitness costs, as shown in *B. impatiens* where higher metabolic rates were associated with shorter lifespans (Kelemen et al., 2019). Thus, the increase in mean winter temperatures may create excessive energy demands and an increase in metabolic rates, which, in turn, could lead to shorter lifespans of surviving queens. More research should investigate the possible correlation between temperature stress under hibernation and negative fitness effects.

3.3 | Resistance to high temperatures

Several studies suggest important roles for heat shock protein (*hsp*) genes in relation to the queen during hibernation (Kim et al., 2008) and thermal stress in general (Pimsler et al., 2020). For example, *B. huntii* expression levels of *hsp* genes were high in diapausing queens next to the eggs and egg-laying queens, whereas expression levels were low in larvae, pupae, and workers and almost absent in adult drones (Xu et al., 2013). The expression of three *hsp* genes in *B. terrestris* queens showed tissue-specific, differential regulation in relation to hibernation (Kim et al., 2008). Furthermore, small heat shock proteins (*shsp*) were found to be involved in population-specific thermal responses in *B. vosnesenskii* (Pimsler et al., 2020). Although some bumblebee species can limit the potential lethal effects of thermal stress by exhibiting higher levels of natural plasticity (Valladares et al., 2014), the intraspecific variation in activating the transcriptional heat shock response cascade might be a general mechanism that allows bumblebees to adapt to heat stress (Pimsler et al., 2020).

3.4 | Desiccation tolerance

The ability to tolerate desiccation, due to the high temperatures and decreased rainfall, is also relevant to climate change. Most bees,

including bumblebees, are less prone to desiccation than most terrestrial insects, given their ability to collect water (Ferry & Corbet, 1996), their nectar-based diet, and their ability to generate metabolically large amounts of water during flight (Nicolson, 2009). However, Atmowidjojo et al. (1997) showed that water loss rates could still be high in honeybees. By studying the desiccation tolerances across a gradient of urbanization in one representative species of sweat bees, honeybees, and bumblebees, Burdine and McCluney (2019) found that bee species differ in their water content limits, with honeybees being relatively intolerant of desiccation. Although bumblebees were able to maintain their water content, their narrow limits of hydration tolerance may not be enough to cope with droughts and/or heat waves in cities or other urbanized areas (Burdine & McCluney, 2019). Thus, adaptations to improve desiccation tolerance may be also present in bumblebees. The mechanisms behind desiccation tolerance have been well studied in *Drosophila* (e.g. Telonis-Scott et al., 2016), but are still rather unknown for bumblebees. Genes related to cuticle, spiracle, tracheal or respiratory development, and water balance, and homeostasis are likely to be under selective pressure (Chown et al., 2011; Telonis-Scott et al., 2016). Experimental evolution experiments involving *Drosophila* under desiccant conditions found genes related to ion transport, stress sensing, immunity, and neuron differentiation/development under selective pressure (Telonis-Scott et al., 2012, 2016). Some similar patterns are also apparent from studies performed with *Apis mellifera*, which uncovered the importance of temperature-activated transient receptor potential ion channels or thermoTRPs in desiccation tolerance (Chown et al., 2011). While such TRP channels are mostly well conserved across a range of insect taxa, honeybees have several novel TRPs which are likely to be used for temperature sensing (Chown et al., 2011; Matsuura et al., 2009). This implies that they have a fundamentally different mechanism of thermal sensing than most other insects (Kohno et al., 2010; Matsuura et al., 2009). Whether bumblebees or even other bees have similar TRPs is currently unknown and may therefore be an interesting direction for future research.

Since water loss in insects is mainly due to cuticular losses (Benoit, 2010), altering the cuticle, mainly in its permeability, by changing the number and composition of cuticular hydrocarbons, could help in reducing water loss (Chown et al., 2011). However, modifying the chemical composition of the cuticle may have unintended consequences, as it affects also other functions such as social communication and mating (Chown et al., 2011; Nicolson, 2009). Future research should investigate whether higher desiccation tolerance is correlated with an improved humidity or thermal sensitivity.

4 | BEHAVIOUR

Bumblebees exhibit specific behaviours that help maintaining colony homeostatic temperature, or that are related to maximizing foraging in (sub-)optimal weather conditions such as built-in circadian foraging rhythms, avoiding undesired climatic conditions through negative thermotaxis, or increasing their dietary choice through generalism.

4.1 | Colony thermoregulation

Bumblebees exhibit contrasting and stereotyped behaviours associated with temperature, both at the individual level and at the colony level (e.g. Heinrich, 1974, 1979; Weidenmüller et al., 2002, 2019; Westhus et al., 2013). Within a bumblebee colony, temperature and CO₂ can reach high levels due to the high metabolic activity of brood incubation. Bumblebee workers can actively ventilate their nest by wing fanning, thereby cooling and reducing the levels of respiratory gases, to maintain their nest temperature between 28 and 32°C (Vogt, 1986; Weidenmüller, 2004; Weidenmüller et al., 2002; Westhus et al., 2013). The large plasticity in task allocation within bumblebee colonies is dependent on response probability, threshold, duration, and experience (Duong & Dornhaus, 2012; Weidenmüller, 2004; Weidenmüller et al., 2019; Westhus et al., 2013). Furthermore, Garrison et al. (2018) showed that nest temperature regulation is both a consistent group response and the result of individual behavioural flexibility. In general, these studies showed that the maintenance of bumblebee nest temperature is mainly due to the large plasticity presence within these social insects.

4.2 | Circadian foraging rhythm

Bumblebees have built-in circadian foraging rhythms that synchronize the colony's foraging pattern with food availability; within this circadian clock, individual bees perform their own temporary tasks according to a diurnal pattern (e.g. Stelzer et al., 2010; Yerushalmi et al., 2006). Although these rhythms are tuned to specific environmental conditions, for example foraging mainly early in the morning and evening in warmer areas to avoid overheating (Stelzer, Stanewsky et al., 2010), bumblebees must also be able to adjust their foraging activity to suddenly changing weather conditions.

4.3 | Negative thermotaxis behaviour

Individual bees exhibit behavioural plasticity in using habitats and can take advantage of thermal heterogeneity in the environment to avoid exposure to undesired thermal conditions (Heinrich, 1974; Huey et al., 2012; Sunday et al., 2014). They will avoid collecting pollen in wet conditions and show limited foraging activity during hot summer days (Peat et al., 2005; Sanderson et al., 2015), with foragers seeking prolonged shelter within the thermoregulated environment of their colony during adverse weather conditions (Heinrich, 1974; Pimsler et al., 2020). Other examples of negative thermotaxis—behaviours seeking escape from extreme thermal conditions to avoid damage—include the use of more isolated, underground nests for colony initiation in cold regions (Goulson, 2010), and aestivation behaviour, a state of inactivity and lowered metabolic rate, in *B. terrestris* queens from hot regions in the Mediterranean (Gurel et al., 2008). Similar behaviours have also been observed in other bees such as in the stingless bee *Melipona subnitida* (Hrncir et al., 2019) and the large carpenter bee

Xylocopa frontalis (de Farias-Silva & Freitas, 2020). Another behaviour associated with heat resilience in bees is nectar dehydration, during which the bee regurgitates the contents of its honey crop—which is normally used to concentrate food—to also induce cooling via evaporation (Bernardino & Gaglianone, 2008; Heinrich & Buchmann, 1986).

Behavioural thermoregulation as a buffer mechanism against harmful thermal conditions is only possible if microhabitats with desired temperature ranges are available and accessible (Huey et al., 2012; Sunday et al., 2014). However, this is not always the case, especially in the anthropogenic human-altered environments in which agricultural conversion, urbanization, and deforestation cause the loss and degradation of suitable habitat (e.g. Wagner et al., 2021). For instance, the ubiquitous impervious surfaces in urban areas, such as asphalt roads, buildings, concrete parking and terraces, etc., will limit nest making not only in underground-nesting bees but also in surface-nesting bees via the absence of cover and necessary nest material (Geslin et al., 2016; Glaum et al., 2017). However, even when such thermal refugia are present and accessible for bumblebees, they can only be used temporarily, as workers will need to leave them to be able to forage. Therefore, like many other insects (see Chapman et al., 2015), bumblebees may try to avoid continuous exposure to such undesirable thermal conditions through migration (Fijen, 2020). Although bumblebees' dispersal over only a few kilometres has been studied for a few common, widespread species (e.g. Carvell et al., 2017; Makinson et al., 2019), altitudinal migration of bees by elevational shifts over time (Pyke et al., 2011, 2012) and mass migration over multiple hundreds of kilometres also occurs, with the latter possibly triggered by a shortage in suitable nesting sites (Fijen, 2020). Investigating whether bumblebees exhibit annual seasonal migration patterns, and if so, which species and why, are interesting research questions that still need to be explored.

4.4 | Generalism in diet

Generalist bumblebees can forage on multiple plants while specialist species are more restricted in their choice and forage on only a few specific plant species (Laverty & Plowright, 1988). This generally makes generalists less vulnerable to food shortages. Since climatic change can render preferred food resources unavailable, being able to forage on multiple food resources is then an advantageous mechanism to avoid food shortage. Such polylectic bees could even broaden their diet to other native and invasive plant species (Drossart et al., 2017; Tiedeken et al., 2016). However, there is a downside as these new floral resources can be toxic or have negative fitness effects (Brochu et al., 2020; Wang et al., 2019). As described by Vanderplanck et al. (2018), it is a trade-off between nutritional requirements and toxicity.

5 | PHENOLOGY

As recently reviewed by Gérard, Vanderplanck et al. (2020), climate change is also affecting the phenology of bumblebees.

Environmental temperature can have an impact on the number of generations per year (i.e. voltinism) and the pace of the life cycle. These shifts have strong implications on the specific interactions between bumblebees and their food resources.

5.1 | Voltinism

Bumblebees normally have one generation per year (univoltinism) in which there is a hibernation or aestivation stage to allow queens to hide from cold or hot environmental temperature extremes (Goulson, 2010). Their annual life cycle has evolved to synchronize their phenology with food resource availability (e.g. Kearns et al., 1998; Ollerton et al., 2011). Bumblebees are known to exhibit plastic responses in their life cycle to take advantage of (sub-) optimal weather conditions and to cope with temperature extremes. In cold climates, post-diapause queens accelerate the development of their ovaries by an upregulation of abdominal temperature and also raise their body temperature when incubating brood (Woodard, 2017), which helps capitalizing on the narrow window of permissible temperatures. While bumblebees can also have naturally occurring multiple generations per year due to warmer winter months (Rasmont et al., 2008). Interestingly, instead of undergoing diapause, an increasing number of winter-active colonies of *B. terrestris* queens have been reported in the United Kingdom (Stelzer et al., 2010). Several mechanisms have been proposed to explain the increase in winter activity, such as increased floral resources due to exotic plants import, introgression with continental bivoltine subspecies, or plastic response to the increasing winter temperatures (Owen et al., 2016; Stelzer, Chittka et al., 2010), although winter activity seems unlikely to be caused by interbreeding with managed conspecifics (Hart et al., 2020). While Beekman et al. (1999) found that the ability to start a colony without diapause has some genetic component, and thus can be selected for, the maintenance of bivoltinism can have fitness costs, such as non-hibernating queens producing fewer workers (Beekman & Van Stratum, 2000). On the other hand, there are also fitness consequences for queens that still choose to hibernate in warmer winters, with queens 'burning' through their fat reserves sooner under warmer conditions than under cooler regimes (Vesterlund & Sorvari, 2014). Future research should investigate the fitness cost and impact on colony initiation of increased thermal fluctuations during queen hibernation.

5.2 | Pace of the life cycle

It is known that with increasing ambient temperature, the emergence date of bees and pollinator foraging period decrease; with an on average 10.4 days per decade earlier emergence of North American bee species (which included two bumblebee species; Bartomeus et al., 2011), and on average a 2 days shorter flight period and 6 days earlier average flight day in European pollinators over the past six decades (Duchenne, Thébault, Michez, Elias et al., 2020). Timing of queens

emerging from hibernation is also known to be controlled largely by temperature (Alford, 1969; Stemkovski et al., 2020). In honeybees, specialization to the local environmental conditions determines the success of the colony, through dictating the pace of development, close timing of worker emergence with floral resources, and weather-dependent behaviour thresholds, such as colony-fanning during hot periods (Le Conte & Navajas, 2008). Climate change can potentially cause mismatches between these adaptations in phenology and the environment (Le Conte & Navajas, 2008). Induction of diapause is also expected to be affected by climate change; photoperiod, temperature, temperature cycles, and other circadian rhythms are known to affect diapause initiation in insects, which may also delay or advance diapause in bumblebee queens (Gallinat et al., 2015; Jaworski & Hilszczański, 2013; Saunders, 2014).

5.3 | Impact of shifts in phenology on bumblebee-plant interactions

Shifts in phenophases of bees and their resources can go synchronically; both apple and bee populations were advancing their phenology at approximately synchronous rates (Bartomeus et al., 2013), or antagonistically, with an earlier community flowering phenology, but no synchronic shift in North-American bumblebees' phenology over a 33-year period (Pyke et al., 2016). This desynchronization can cause 'mismatches' in plant-pollinator interactions (Gérard, Vanderplanck et al., 2020; Renner & Zohner, 2018). Ogilvie et al. (2017) found evidence that populations of three bumblebee species were affected indirectly and species-specific through the changing and asynchronous phenology of floral communities. Although it is modelled that biodiversity could theoretically buffer the community-level against pollinator species-specific phenological shifts (Bartomeus et al., 2013), phenology mismatches have also been shown at the community level (Duchenne, Thébault, Michez, Elias et al., 2020; Duchenne, Thébault, Michez, Gérard et al., 2020), reducing the functional complementarity of the partners within the plant-pollinator network and might ultimately threaten ecosystem functioning (Duchenne, Thébault, Michez, Elias et al., 2020; Gérard, Vanderplanck et al., 2020).

6 | DETECTION OF UNDERLYING GENETIC ADAPTATIONS

Although the presence of habitat and climate-related local adaptations have already been described in different bumblebee species (Ings et al., 2005; Peters et al., 2016), modern genomic approaches such as Restriction-site-Associated DNA sequencing (henceforth RADseq) and transcriptomics (RNAseq), in combination with physiological and/or environmental data can now be used to identify genes or gene expression responses, associated with environmental factors (e.g. Jackson et al., 2018; Jaffé et al., 2019; Montero-Mendieta et al., 2018; Pimsler et al., 2020). These techniques thus specifically enable the screening of the adaptability of bee populations to the

stressor of interest, such as forest cover, elevation, precipitation, and temperature. For example, Theodorou et al. (2018) compared pairs of urban and rural populations of *B. lapidarius*, and found that despite low population structure and few barriers to gene flow, directional selection still occurred, with 176 loci being identified as candidates for selection. Populations have also been found to adapt to local climate factors, such as in Jackson et al. (2020), who reported that in *B. vosnesenkii* and *B. Vancouverensis*, precipitation and temperature were linked to genes related to cuticle and tracheal development, and neural function, respectively. By associating physiology with RNAseq data, Pimsler et al. (2020) found a strong link between the thermal minima tolerated by populations of *B. vosnesenkii* and the climate from which they were sampled from; further analysis of gene expression revealed that heat shock proteins, cell-membrane-related proteins, and neurogenesis and muscle function-related genes were differentially expressed among populations of cooler origins.

More generally, climate change is expected to impact the genetic diversity of populations. Initial response to unpredictable and unseasonable environmental conditions will be based on plasticity, the ability and extent of which have genetic and epigenetic foundations (Chown et al., 2010; Gautier et al., 2019). A range of potential long-term effects on population genetics have also been described. Leading edge range shifts, depending on dispersal and migration patterns, may be accompanied by founder effects, bottlenecking the ability of future populations to adapt further (Hill et al., 2011). Although genetic population structure occurs among European bumblebee populations (Ghisbain et al., 2021; Lecocq et al., 2017; Maebe et al., 2020), species that have wide distributions are less vulnerable to climate change, as individual populations are exposed to different climatic parameters, and thus overall the species will have genes/variants appropriate to diverse environmental conditions for selective pressure to act upon (Bonebrake & Deutsch, 2012; Kingsolver & Buckley, 2017). Recent research associated the intraspecific heat tolerance among bumblebees with species' diversity in habitat occupation (Martinet, Dellicour et al., 2021). Furthermore, Hill et al. (2011) predicted that climate-change-induced habitat fragmentation is also likely to reduce genetic diversity, 'eroding' the genetic diversity of populations without causing extinction. However, this pattern

has not been observed in bumblebees, in fact the opposite—genetic diversity, at least in European and North American bumblebees, has been relatively stable over the past 100 years (Lozier & Cameron, 2009; Lozier et al., 2011; Maebe et al., 2015, 2016). Future research should focus on investigating bumblebees' adaptability to the individual and combined stressors they face within human-altered environments, to identify the underlying genomic make-up, and to assess the impact of these stressors on population genetic diversity.

7 | DISPERSAL VS. ADAPTATION

Under climate change, populations may be maintained by adapting to new environmental conditions; alternatively, they may track suitable climate conditions through dispersal (Nogués-Bravo et al., 2018). These contrasting responses to climate change can be in conflict; if individual dispersal rates are quicker than local population adaptations, then the chance of adapting to new climate conditions is repressed (Norberg et al., 2012). Alternatively, in a situation where local adaptation is rapid, then the species adapting to the new conditions can limit the success of newly arriving species through competition (Thompson & Fronhofer, 2019). The degree to which these eco-evolutionary interactions influence bumblebee responses to climate change is still poorly understood. Comparisons of historical data with modern surveys have found that, both in Europe and in North America, bumblebee populations across multiple species have shown range contractions in line with increasing temperatures (Cameron et al., 2011; Kerr et al., 2015). In higher elevation areas, some bumblebees have also been observed shifting their ranges further up hill in response to environmental changes (Fourcade et al., 2019; Marshall et al., 2020; Ornos et al., 2017; Ploquin et al., 2013; Pyke et al., 2016). However, studies suggest that at the leading edges of their ranges and elevations, bumblebees may not be able to track climate changes freely (Kerr et al., 2015; Ploquin et al., 2013). The traits and adaptations necessary to maintain bumblebee populations are likely to contrast between those at the leading and trailing range margins, and physiological adaptations are more likely in populations at the trailing edge while traits important for dispersal and colonization may be more prevalent at the

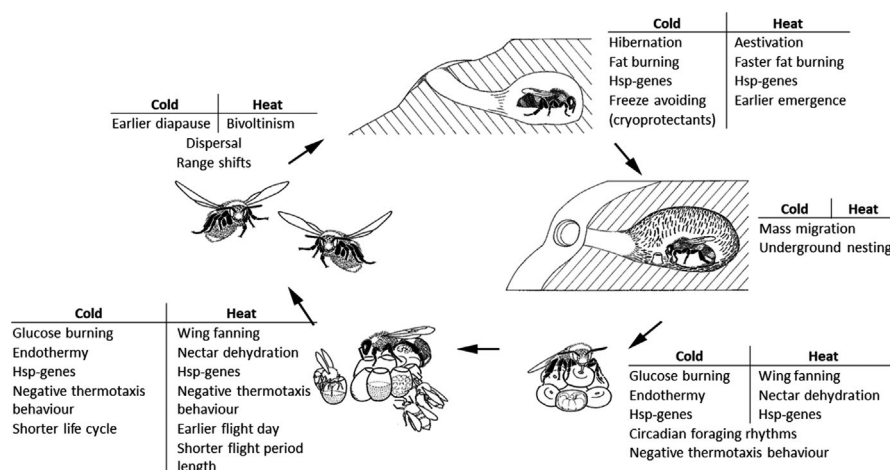


FIGURE 2 Bumblebee adaptive traits to cold and heat at different stages during their life cycle. Life cycle consisting out of five stages: a queen hibernating, a queen nesting, a colony developing, workers foraging, new queens, and males emerging. (Drawing of bumble bee life cycle originates from Michez et al. (2019), and is used with permission)

leading edge (Diamond, 2018). Furthermore, the dispersal ability of most bumblebees is not known (Mola & Williams, 2019). Therefore, the conflict between the pressure to adapt to climate change or to track suitable climate conditions is difficult to quantify and represents an important future line of research. Two closely related bumblebee species (Cameron et al., 2007), which have shown increases in range limits, may have specific adaptations that facilitate rapid range shifts. Crowther et al. (2019) associate rapid range expansion of *B. hypnorum* in urban areas of the UK with short foraging distances, high nest density, and increased polyandry. In particular, polyandry may be higher in expanding populations, facilitating colonization through larger effective population sizes (Brown et al., 2003; Crowther et al., 2019). Additionally, range expansion in *B. haematurus* seems to indicate an ability to track suitable climate conditions (Biella et al., 2020) but is also likely associated with a high tolerance for temperature extremes (Martinet, Dellicour et al., 2021).

Several studies based on empirical and species distribution data have projected the impact of climate change on the future distribution ranges of bumblebees (Giannini et al., 2020; Lee et al., 2019; Marshall et al., 2018; Rasmont et al., 2015; Sirois-Delisle & Kerr, 2018). These projections assume that the modelled habitat suitability represents a fundamental climate niche of the species but in practice it is often a representation of the contemporary realized niche (Veloz et al., 2012). Furthermore, most predictive models do not account for adaptations, population demographics, or biological interactions; this means there is a lot of room to improve projections of climate change impacts on bumblebees. Spatially explicit eco-evolutionary models demonstrate that having high genetic variance alongside limited dispersal may result in lower risks of extinction (Norberg et al., 2012), and the degree to which dispersal will provide spatial insurance will likely depend on competition between species (Thompson & Fronhofer, 2019). This would suggest that bumblebees that demonstrate considerable plasticity, capacity to adapt, and have been relatively stable in their distribution are those most likely to persist in the future. However, comparing simulated vs. real data has been shown to provide conflicting results (Valladares et al., 2014). Therefore, as more information becomes available regarding the adaptive capacity and dispersal rates of bumblebees, modelled future projections of bumblebees should include estimates of physiological adaptations alongside range-limiting traits to provide more robust and accurate scenarios (Diamond, 2018). Allowing for adaptation to new climate conditions may decrease the severity of projected range losses and shifts (Bush et al., 2016).

8 | CONCLUSIONS AND AVENUES FOR FUTURE RESEARCH

Climate change is an important driver of insect population drift across many taxa, including bumblebees. In addition to their abundance, it affects their distribution, multiple aspects of their phenology, and alters a range of morphological and physiological traits (e.g. Gérard, Vanderplanck et al., 2020; Marshall et al., 2018; Figures 1

and 2). As Fourcade et al. (2019) concluded, so far, climate change has had an overall negative impact on bumblebees.

To survive climate change, bumblebees must exhibit a high degree of plasticity and adaptation (Sgró et al., 2016). Generalist species will be favoured under climate change, as they are more adaptable (Hill et al., 2011). Given that bumblebee populations are already shrinking due to factors such as agricultural intensification and land use change, and that the likelihood of negative effects such as inbreeding is increasing in these declining populations, maintenance of high genetic diversity can be a critical factor in escaping this extinction vortex, since natural selection can only act on a population with enough standing variation (Frankham, 2005; Goulson et al., 2008; Rasmont et al., 2015; Zayed, 2009; Zayed et al., 2005). Important future lines of research would be (i) to test trait responses in-situ (in ecologically relevant fluctuating thermal regimes as mentioned by Kellermann and van Heerwaarden (2019)), (ii) to assess whether these adaptive hypotheses around bumblebee traits affect fitness, (iii) and/or genetic diversity levels, (iv) to understand the interactive effects of climate and land use change, (v) to study, in situ, the combined effects of climate change, land use change, disease, competition, etc., and thus to separate the impact (on adaptive responses) of climate change from that of other drivers in 'real-life' experiments, and (vi) to include physiological limits, behavioural plasticity, biotic interactions and phenological shifts into biodiversity forecasts under climate change (e.g. distribution models), with varying degrees of dispersal ability to see how these factors interact, and how important it is for species to track climate changes (e.g. González-Tokman et al., 2020).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTION

KM and GS conceived this review. KM and AFH developed and wrote the initial manuscript. LM, DM, and NJV participated in the revisions. All authors have read and approved the final manuscript.

DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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