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REVIEW

How does climate change impact social bees and bee sociality?

Madeleine M. Ostwald[1] | **Carmen R. B. da Silva**[2] | **Katja C. Seltmann**[1]

[1]Cheadle Center for Biodiversity & Ecological Restoration, University of California, Santa Barbara, California, USA

[2]School of Natural Sciences, Macquarie University, Sydney, New South Wales, Australia

Correspondence
Madeleine M. Ostwald
Email: mostwald@ucsb.edu

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Abstract

1. Climatic factors are known to shape the expression of social behaviours. Likewise, variation in social behaviour can dictate climate responses. Understanding interactions between climate and sociality is crucial for forecasting vulnerability and resilience to climate change across animal taxa.
2. These interactions are particularly relevant for taxa like bees that exhibit a broad diversity of social states. An emerging body of literature aims to quantify bee responses to environmental change with respect to variation in key functional traits, including sociality. Additionally, decades of research on environmental drivers of social evolution may prove fruitful for predicting shifts in the costs and benefits of social strategies under climate change.
3. In this review, we explore these findings to ask two interconnected questions: (a) how does sociality mediate vulnerability to climate change, and (b) how might climate change impact social organisation in bees? We highlight traits that intersect with bee sociality that may confer resilience to climate change (e.g. extended activity periods, diet breadth, behavioural thermoregulation) and we generate predictions about the impacts of climate change on the expression and distribution of social phenotypes in bees.
4. The social evolutionary consequences of climate change will be complex and heterogeneous, depending on such factors as local climate and plasticity of social traits. Many contexts will see an increase in the frequency of eusocial nesting as warming temperatures accelerate development and expand the temporal window for rearing a worker brood. More broadly, climate-mediated shifts in the abiotic and biotic selective environments will alter the costs and benefits of social living in different contexts, with cascading impacts at the population, community and ecosystem levels.

KEYWORDS

bees, cooperative breeding, functional traits, global change, phenotypic plasticity

1 | INTRODUCTION

Climate represents a major selective force in the evolution of sociality. Climatic conditions can shape developmental rates, physiological performance, biotic interactions and other processes that determine the relative costs and benefits of group formation (Blumstein et al., 2022; Fisher et al., 2021; Menzel & Feldmeyer, 2021; Moss & While, 2021; Wilson, 1971). Social living can give rise to emergent strategies for coping with climatic stressors (Arnold, 1988; Fahrenholz et al., 1989; Klok & Chown, 1999). Observed patterns in global biogeography support hypotheses linking climate to social evolution, with distributions of social organisms falling along gradients of temperature, precipitation and climatic stochasticity (Jetz & Rubenstein, 2011; Lukas & Clutton-Brock, 2017; Purcell, 2011). These interactions between climate and sociality raise important questions about the fate of social organisms and social phenotypes under changing climate.

Climate change is predicted to have major consequences for the survival, health and distributions of organisms globally, including ecologically and economically important animals like pollinators (da Silva et al., 2023; Forrest, 2016; Potts et al., 2010). Bees (Hymenoptera: Apoidea: Anthophila) are the primary animal pollinators of terrestrial ecosystems (Ollerton et al., 2011), and possess some of the richest diversity of social behaviours of any animal taxon, with multiple independent origins of eusociality and a broad range of non-eusocial forms (Michener, 1974; Wcislo & Fewell, 2017). Within the past decade, researchers have increasingly investigated species-level social traits as possible predictors of bee responses to environmental change (Forrest et al., 2015; Hall et al., 2019; Harrison et al., 2018). Social organisation in bees correlates with other behavioural and life history traits, like foraging strategy and phenology, that can influence susceptibility to climate change stressors. However, generalisable patterns linking sociality to climate change vulnerability has remained elusive.

Climate change is also likely to shift the expression and geographic distribution of social behaviours across animal populations. Expected consequences of climate change include not only increasing average temperatures but also increasing climate variability and increasing frequency and severity of extreme events like heat waves and drought (IPCC, 2022). For bees, some of which can flexibly express sociality in response to environmental conditions (Wcislo & Fewell, 2017), the social impacts of these shifts could be particularly profound (Box 1). Nevertheless, very few studies have directly assessed the impacts of climate change on bee social organisation. Still, these effects may be extrapolated from known relationships between bee sociality and local environmental conditions. Drawing from this literature, we make predictions about the consequences of climate change for bee sociality and identify promising directions for future research.

2 | HOW DOES SOCIALITY MEDIATE VULNERABILITY TO CLIMATE CHANGE?

Sociality shapes bees' life histories, physiological traits and behavioural repertoires. These traits can broadly influence how bees respond to climatic variation, and therefore their vulnerability to environmental change. While a growing body of literature explores effects of climate change on bees that are social (Johnson et al., 2023; Kerr et al., 2015; Soroye et al., 2020), many fewer investigate social effects at the species or group level, that is by assessing social behaviour as a predictor of responses to environmental change (Bartomeus et al., 2011; Hamblin et al., 2017). Where data do exist, patterns have been mixed. Some studies have found significant relationships between sociality and climate responses (Hamblin

BOX 1 Notes on bee social biology and terminology

The ancestor of bees was solitary, as are the majority of extant bee species (>75% of species; Danforth et al., 2019; Debevec et al., 2012). Nevertheless, diverse forms of social living are found in all currently recognised bee families except the Stenotritidae (Michener, 1974; Wcislo & Fewell, 2017). Further, the extent of and capacity for social living among bees is likely to be vastly underestimated, given that social strategies may be present at low levels in otherwise solitary populations (Wcislo, 1993, 1997; Yagi & Hasegawa, 2012). Among and within taxa, bee societies vary considerably in group size (2 to >100,000 individuals), in the degree of reproductive skew and morphological specialisation, and in the genetic relatedness of group members (Michener, 1974; Ostwald, Haney, et al., 2022; Wcislo & Fewell, 2017). Social organisation in bees spans a diversity of forms and includes several independent origins of (and reversals from) eusociality (Danforth et al., 2003; Kocher & Paxton, 2014). Eusociality is best known among the corbiculate Apidae, including honeybees (Apini), stingless bees (Meliponini), bumblebees (Bombini) and some orchid bees (Euglossini), and is also found among the sweat bees (Halictidae: Augochlorini and Halictini) and allodapine bees (Allodapini; Michener, 1974). Other social forms (e.g. communal, quasisocial and semisocial) involve nest sharing among same-generation females and are phyletically widespread across the major bee families. Particularly instructive for social evolutionary studies are the many lineages in which social living is a facultative state, which may be determined by environmental conditions. Similarly informative are the lineages in which a diverse range of social forms are represented (e.g. Halictinae, Xylocopinae), which permit comparative analyses within a phylogenetic context (Kocher & Paxton, 2014; Shell & Rehan, 2017). For the purposes of this review, we will define sociality as multi-female group living within a nesting context, with or without reproductive division of labor (sensu Wcislo & Fewell, 2017). No ethical approval was required for this research.

et al., 2017; Kammerer et al., 2021). Others have shown that sociality was weakly or not at all associated with climate change responses, including phenological shifts (Bartomeus et al., 2011; Meiners et al., 2020) and responses to extreme weather events (Graham et al., 2021). More commonly, studies have evaluated sociality as a predictor of responses to anthropogenic landscape change. For example, solitary bees may be particularly susceptible to effects of urbanisation (Banaszak-Cibicka & Żmihorski, 2012; Harrison et al., 2018) and agricultural intensification (Forrest et al., 2015; Hall et al., 2019). While these studies are informative for suggesting general patterns of social resilience to environmental change, more work investigating climate variables specifically is necessary to understand social responses to climate change. A promising starting-place to generate predictions for these studies is by examining life history, behavioural and physiological trait variation across the bee social spectrum.

2.1 | Resource use and phenological factors

Social living can fundamentally alter bees' seasonal activity patterns. Most solitary bees are active as adults for narrow windows of time, averaging about 1 month per year but often for much shorter (Michener, 2007). The same is generally true for simple social groups comprised of same-generation females (e.g. communal and semisocial). Restricted activity periods may render these bees particularly vulnerable to the effects of unfavourable weather that limits foraging (e.g. extended rainfall) or to phenological mismatch as host plants advance their flowering times under climate change (Kudo & Ida, 2013; Visser & Gienapp, 2019). Eusocial living, by contrast, requires generation overlap, and so eusocial bees are obligately multivoltine with an adult activity period spanning several months (Michener, 1974). In order to support their extended colony life cycles over the course of the flowering season, eusocial bees have broad, generalist pollen diets, while solitary and other non-eusocial bees span a range of nutritional specialisation from host plant generalists to host plant specialists; (Michener, 2007). Narrow diet breadth has been associated with susceptibility to environmental change (Bartomeus et al., 2013; Bogusch et al., 2020; Buckner & Danforth, 2022), whereas generalists may better withstand disruptions to preferred host plant availability (Minckley et al., 2013). Kammerer et al. (2021) examined a long-term bee occurrence dataset in the mid-Atlantic US and found that solitary bees declined in low-precipitation years, whereas eusocial bees did not. Dietary flexibility may be increasingly important as warming temperatures extend activity periods. For example, in urban Britain, *Bombus terrestris* (Linnaeus, 1758) are increasingly active during the winter months, subsisting largely on cultivated plants (Stelzer et al., 2010). Under severe or extended drought, however, specialist (typically solitary) species that can undergo facultative long-term diapause could have competitive advantages over generalist, multivoltine species that cannot wait out unfavourable years (Hung et al., 2021; Minckley et al., 2013).

Sociality can also generate emergent strategies for resource acquisition that may be advantageous as floral resources become scarcer, more patchily distributed and/or unpredictably available under climate change. The highly eusocial bees possess complex communication behaviours (via olfactory, auditory and dance communication) that enable them to adaptively coordinate foraging efforts across large colony workforces (Michener, 1974; Seeley, 1995; von Frisch, 1967). By accurately communicating presence, location and/or quality of food resources, these behaviours enable colonies to more effectively exploit spatially and temporally unpredictable food landscapes (Dornhaus & Chittka, 2004; Hrncir et al., 2019; Maia-Silva et al., 2020). The highly eusocial honey and stingless bees also store food in the nest for adult consumption, buffering against floral dearth periods (Grüter, 2020; Heinrich, 1979; Seeley, 1985). Food storage enables a perennial lifestyle for the highly eusocial bees (e.g. honey bees and stingless bees), and even for annual colonies (e.g. bumblebees), small food stores can provide insurance against short periods of poor foraging conditions (Heinrich, 1979). Many social bees can also share collected food via trophallaxis, even in simpler, facultative societies (Gerling et al., 1983; Kukuk & Crozier, 1990; Sakagami & Laroca, 1971).

Finally, sociality has been associated with increased mobility at the landscape scale, which can confer resilience to habitat loss/fragmentation under climate change. Highly eusocial bees have larger foraging ranges than primitively eusocial and solitary bees (Kendall et al., 2022), enhancing their ability to escape resource-depleted landscapes (Steffan-Dewenter & Kuhn, 2003). Colonies of the African honey bee (*Apis mellifera scutellata* Lepeletier, 1836) and the giant honey bee (*Apis dorsata* Fabricius 1793) will seasonally abscond from their established nest sites, migrating to areas of greater food abundance (Dyer & Seeley, 1994; McNally & Schneider, 1992). Likewise for primitively eusocial bumblebees, long-distance foraging may help colonies overcome seasonal resource declines (Pope & Jha, 2018). In contrast, only a minority of solitary bees are capable of long-distance foraging (Zurbuchen, Cheesman, et al., 2010), which has been shown to decrease offspring production (Zurbuchen, Landert, et al., 2010). Similarly, solitary bees have shorter dispersal ranges than eusocial and facultatively social bees, increasing their susceptibility to effects of habitat degradation (López-Uribe et al., 2019).

2.2 | Physiological and behavioural climate responses

Many social bees possess unique behavioural mechanisms for regulating their microclimates, buffering against thermal stress under climate change. Especially in temperate regions, the eusocial corbiculate bees employ a suite of integrated behaviours to deftly control their nest temperatures, including direct incubation, metabolic heat production, fanning, nest evacuation and evaporative cooling (Heinrich, 1993; Jones & Oldroyd, 2006; Seeley, 1985). These behaviours enable colonies to maintain an optimal thermal set point despite wide variation in ambient temperatures. Coordinated thermoregulatory behaviours can promote recovery from and resilience to extreme heat events. Following intensive water collection to cool the nest under high ambient temperatures, honeybee workers can temporarily store water in their combs and their crops for future distribution, potentially buffering against future emergencies (Ostwald et al., 2016). While these behaviours are best known in the corbiculate bees, thermoregulatory behaviours may exist in other clades. Michener observed fanning at the nest entrance by the primitively eusocial halictid *Augochlorella aurata* (Smith, 1853; 1974). In winter hibernacula, passive clustering of adults could minimise heat loss by reducing the group's collective thermal inertia. For the facultatively social carpenter bee, *Xylocopa sonorina* Smith, 1874, bees that overwintered in groups maintained body temperatures nearly 1.5°C warmer than solitary individuals at the coldest time of day (Ostwald, Fox, et al., 2022). Minor differences such as these could provide survival advantages of social nesting when temperatures approach freezing.

The thermoregulatory behaviours of social bees may have important implications for their physiological tolerance limits. While highly eusocial bees are highly adept at controlling nest temperatures, they are particularly sensitive to deviations from their optimal thermal ranges. European honeybees, for example, tightly regulate the temperature of their broodnest within the range of 33–36°C, even as ambient temperatures vary as widely as 10 to 60°C (Kronenberg & Heller, 1982; Lindauer, 1954; Seeley, 1985). Brood reared at even a single degree below the optimal range (32°C) experience significant learning deficits (Jones et al., 2005; Tautz et al., 2003). Other bees tolerate a much wider range of temperatures during development (Earls et al., 2021; Fründ et al., 2013; Park et al., 2022), during which they may be poorly buffered from environmental fluctuations. Variation in thermal experiences with sociality might help to explain observed variation in heat tolerance and warming margins (the degrees distance between a species' upper thermal limit and maximum environmental temperature), both of which may be reduced in eusocial species compared with sympatric solitary species (da Silva et al., unpub.; Burdine & McCluney, 2019).

3 | HOW MIGHT CLIMATE CHANGE IMPACT SOCIAL ORGANISATION IN BEES?

Climatic selective pressures have been implicated in social evolutionary transitions across animal taxa (Guevara & Avilés, 2015; Jetz & Rubenstein, 2011; Liu et al., 2020; Lukas & Clutton-Brock, 2017). These patterns support the hypothesis that sociality can facilitate the colonisation of unpredictable environments, or can expand species' ranges (Brooks et al., 2017; Cornwallis et al., 2017). In bees, climatic factors have shaped the diversification and distributions of social lineages (Brady et al., 2006; Groom & Rehan, 2018; Kocher et al., 2014). The same selective forces that have historically shaped the evolution of social behaviour in bees could likewise influence social behaviour under climate change.

The bees most likely to experience transitions in social organisation in response to climate change are facultatively social bees with some degree of social plasticity because they already possess the behavioural flexibility to express multiple social states. Facultative sociality is best known among the Halictinae and Xylocopinae (Michener, 1990; Shell & Rehan, 2017), but could be widespread across bee taxa when one considers the many typically solitary species that have some capacity for communal nesting (Wcislo & Tierney, 2009). Additionally, climate change might influence colony demography and social traits (e.g. colony size, reproductive skew and offspring sex ratios) across bee species more broadly, including the obligately social species. These demographic shifts can impact the social environment, which can in turn promote changes in social organisation and complexity (Table 1).

3.1 | Phenological and thermal effects

Some of the best-known impacts of climate on bee social strategy relate to seasonal constraints. Because eusociality requires adult generation overlap, eusocial colonies can only form where breeding seasons are sufficiently long to permit the rearing of a worker brood prior to a reproductive brood (Davison & Field, 2018a; Hunt & Amdam, 2005). For this reason, some socially polymorphic species exhibit intraspecific variation in social behaviour along environmental gradients in breeding season length. This is the case for several temperate halictine species, for which solitary populations are found at high latitude or high-altitude portions of their range (where short breeding seasons preclude the production of a worker generation), and eusocial populations are found at lower latitude or altitude (Davison & Field, 2016, 2018a; Eickwort et al., 1996; Field et al., 2010; Packer, 1990; Purcell, 2011; Sakagami & Munakata, 1972). As warming temperatures extend the breeding season, some temperate facultatively social bees may increasingly produce two broods annually, such that eusocial colonies occur more frequently and at higher latitudes and altitudes than previously observed, as Schürch et al. predicted for *Halictus rubicundus* Christ, 1791 under future climate scenarios in Great Britain (2016).

Importantly, these shifts will depend on the extent to which local environmental conditions govern the expression of social phenotypes. For example, latitudinal variation in sociality is known in *Exoneura robusta* Cockerell, 1922 but not the sympatric *Exoneura angophorae* Cockerell, 1912, which is multivoltine across its range (Bernauer et al., 2021; Cronin & Schwarz, 2001). Even within a species, populations may vary in their social plasticity: North American populations of *Halictus rubicundus*, for example, show stronger genetic differentiation between social and solitary populations than do European populations, for which social behaviour is strongly determined by local environmental conditions (Field et al., 2010; Soucy & Danforth, 2002). These considerations emphasise that social

TABLE 1 Summary of predicted effects of climate change on bee social organisation.

Climate effect	Mechanism	Predicted social consequences	Support
↑ temperatures	Longer active seasons permit rearing of multiple broods	↑ social nesting	Halictidae:Halictini: Eickwort et al. (1996), Field et al. (2010, 2012), Davison and Field (2016), Davison and Field (2018a), Schürch et al. (2016); Soucy and Danforth (2002), Sakagami and Munakata (1972) and Kocher et al. (2014) Apidae: Ceratinini: Groom and Rehan (2018)
	Decreasing brood development time permits rearing of multiple broods	↑ social nesting	Apidae:Allodapini: Cronin and Schwarz (1999) Halictidae: Halictini: Hirata and Higashi (2008)
	Longer active seasons and daily activity windows increase provisioning opportunities	↑ colony size	Halictidae:Halictini: Field et al. (2010); Packer and Knerer (1986); Richards and Packer (1995) and Schürch et al., 2016 Apidae:Allodapini: Cronin and Schwarz (1999)
	Increasing male bias in first brood	↓ social nesting	Halictidae:Halictini: Yanega (1993) and Kamm (1974)
↑ variability in temperature and precipitation (incl. drought, extreme rainfall, extreme temps)	Favourability of foraging conditions influences provisioning opportunities	↓↑ social nesting	Halictidae:Halictini: Schürch et al. (2016) Apidae:Ceratinini: Dew et al. (2018)
		↓↑ colony size	Halictidae:Halictini: Packer (1990)
	Favourability of foraging conditions influences the degree of queen-worker size dimorphism, which determines the effectiveness of worker reproductive policing by queens	↓↑ worker reproduction	Halictidae:Halictini: Richards and Packer (1996)
	Drought increases the cost of nest excavation through dry, hard soils	↑ social nesting	Halictidae:Halictini: Bohart and Youssef (1976) Andrenidae:Perditini: Danforth (1991) and Danforth et al. (1996)
Resource and community effects (i.e. downstream effects of ↑ temps and ↑ variability)	Shifts in abundances and distributions of parasites, predators, and conspecific competitors influence the costs/benefits of having a nest guard	↓↑ social nesting	Halictidae:Halictini: Abrams and Eickwort (1981) Apidae:Ceratinini: Rehan et al. (2011) Apidae:Xylocopini: Hogendoorn and Velthuis (1993)
	Shifts in availability and durability of nests and nest substrate influence pressure for social nesting	↓↑ social nesting	Apidae:Allodapini: Silberbauer and Schwarz (1995) and da Silva et al. (2016) Apidae:Xylocopini: Ostwald et al. (2021) and Vickruck and Richards (2021)

responses to climate change will be strongly heterogeneous across and even within socially polymorphic species.

Phenological effects on sociality are tightly linked to thermal effects. Temperature not only influences the temporal window in which bees can rear brood; it also directly impacts development time. These factors interact to determine the capacity for completing two broods in a single breeding season. For *Exoneura robusta*, faster brood development times at lower latitude, probably due to warmer temperatures, enable social nesting via the production of a second brood (Cronin & Schwarz, 1999). Remarkably, even microclimate variation within a single site might be sufficient to drive variation in social phenotype. Hirata and Higashi demonstrated that intra-population social dimorphism in *Lasioglossum baleicum* Cockerell, 1937 depends on local temperature differences (2008). Brood developed faster in nests located in sunny areas due to increased soil temperature, permitting a second brood to be reared before the end of the breeding season (Hirata & Higashi, 2008). The effects of temperature on development time could be compounded by increases in foraging rate with temperature. In temperate climates, foraging activity is limited by the threshold temperature required for flight initiation (Stone & Willmer, 1989). In some contexts, warming temperatures could increase daily thermal activity windows for foraging, enabling foundresses to rear larger broods. For example, the number of provisioning trips completed and the number of offspring provisioned increased with temperature for *Halictus rubicundus* foundresses (Schürch et al., 2016). Combined, these mechanisms could account for the association between warmer climates or years and increases in colony size (Cronin & Schwarz, 1999;

Field et al., 2010; Packer & Knerer, 1986; Richards & Packer, 1995). Alternatively, in environments characterised by hot summers that regularly exceed bees' optimal foraging temperatures (e.g. southern Australia), warming could constrain second brood provisioning by limiting activity windows (Jaboor et al., 2022).

Thermal effects on colony demography can also impact within-group social dynamics by shaping the distribution of female body sizes. Body size in social bees is strongly associated with reproductive dominance (Brothers & Michener, 1974; Richards, 2011; Smith et al., 2008). Specifically, larger females are better able to physically coerce offspring or other nestmates into worker behaviours like foraging; and these dominance behaviours seem to be important in inhibiting worker ovarian development (Brothers & Michener, 1974; Michener & Brothers, 1974). Environmental impacts on body size thus represent an avenue through which climate change might impose shifts in social organisation. Richards and Packer found that favourable conditions (warm, dry years) led to primitively eusocial *Halictus ligatus* Say, 1837 queens producing larger-bodied workers than they did in unfavourable conditions (cool, rainy years), likely due to enhanced foraging opportunities (1996). When the body size differential between queens and workers is low, queens may be less successful at policing worker reproduction. Indeed, under favourable conditions, workers were relatively large and more likely to reproduce. Conversely, under unfavourable conditions, queens and workers were more dissimilar in size and worker reproduction was rare, leading to more strongly eusocial colony organisation (Richards & Packer, 1996). Similarly, for the facultatively social, subtropical small carpenter bee, *Ceratina australensis* Perkins, 1912, unfavourable years (hot, dry years) produced smaller-bodied brood (Dew et al., 2018). Because *C. australensis* females that found social nests tend to be larger-bodied, climate-mediated body size variation may impact year-to-year variation in the frequency of social nesting (Dew et al., 2018).

Finally, temperature could shape colony demography through shifts in offspring sex ratios. Female-biased first broods create opportunities for sib-rearing and eusocial colony organisation (Boomsma, 1991; Trivers & Hare, 1976). Warmer temperatures have been associated with increasing male bias in offspring of halictine bees (Kamm, 1974; Yanega, 1993), resulting in population-level decreases in the frequency of eusocial nesting (Yanega, 1993), though the mechanism underlying these patterns is unclear. Future work investigating interactions between temperature, offspring sex ratios and social organisation will help clarify impacts of climate warming on colony demography, particularly for bees that express intraspecific variation in both sex allocation and social organisation (Cronin & Schwarz, 1997; Smith et al., 2019).

3.2 | Precipitation effects

Social living may equally be shaped by precipitation and water availability. Many of these effects are intrinsically bound to thermal effects, working in concert with temperature variation to shape floral resource availability and foraging windows. Annual variation in precipitation can dictate activity periods, either by inhibiting foraging in times of extended rainfall or by creating floral dearth periods in times of drought. Indeed, for the facultatively eusocial *Augochlorella aurata*, drought conditions reduced brood sizes by two to three offspring (Packer, 1990). Conversely, Schürch et al. suggest that an increase in spring rainfall under climate change could reduce the frequency of social nesting in *Halictus rubicundus*, by delaying provisioning and reducing the temporal window to produce a second brood (2016). Similarly, for *Halictus ligatus*, high rainfall created conditions unfavourable for worker production, with consequences for social organisation (Richards & Packer, 1995). Finally, precipitation can pose direct survival risks that may affect the frequency of social nesting. Heavy rainfall and flooding threaten brood survival, which can reduce worker recruitment, decreasing colony size and restricting opportunities for social nesting.

Precipitation can also alter features of the physical environment that determine the costs and benefits of social nesting (McCorquodale, 1989). For ground nesting bees, nest excavation may be particularly costly when soils are hard, especially during drought. Danforth suggests that the high energetic costs of excavating dry, hard-packed soils favours communal nesting for the desert-adapted bees *Perdita portalis* Timberlake, 1954 (1991) and *Macrotera texana* Cresson, 1878 (1996). Drying of soils is a predicted consequence of climate change in many regions, which may raise the costs of nest excavation for ground nesting bees, thereby increasing the benefits of cooperative nest excavation. Indeed, Bohart and Youssef observed an increase in the incidence of social nesting during drought conditions for the typically solitary sweat bee *Lasioglossum lusorium* Cresson, 1872 (1976). In addition to energetic costs, excavation of dry soils could entail increased cuticular wear, potentially increasing risk of desiccation. However, the physiological and behavioural consequences of dry soil excavation remain to be tested empirically.

3.3 | Predation, parasitism and competition

For many bee lineages, sociality may have arisen as a strategy for mitigating the effects of inter- and intraspecific interactions, especially parasitism, predation and intraspecific competition (Lin & Michener, 1972; Wcislo & Fewell, 2017). Climate change will impact the distributions and abundances of diverse communities of bees' competitors and natural enemies, with variable consequences for bee social behaviour. In populations under strong selective pressure from parasitism or predation, sociality can enable bees to forage without leaving their nests unattended. Active defensive behaviour by guard bees, or even simply the presence of a bee in the nest, can successfully deter natural enemies (Kukuk et al., 1998; Mikát et al., 2016; Zammit et al., 2008). Abrams and Eickwort observed cleptoparasitic bees (*Nomada*, Apidae) entering solitary nests of the sweat bee *Agapostemon virescens* Fabricius, 1775 (Halictidae), but never communal nests, which were continuously guarded (1981). Similarly, solitary *Ceratina australensis* nests were more severely parasitised by chalcid wasps (*Eurytoma* sp.) than social nests of the same species (Rehan et al., 2011). Importantly, social nesting can also provide insurance against nest failure in the event of foundress mortality (Gadagkar, 1990; Queller, 1994). In one study of the facultatively eusocial sweat bee *Megalopta genalis* Meade-Waldo, 1916, adults in the nest successfully defended brood against raiding ants, but orphaned brood all succumbed to ant predation (Smith et al., 2003).

Similarly, in environments characterised by strong intraspecific competition, sociality can provide strategies for securing and safeguarding limiting resources, especially food and nesting substrate. Social nests of the facultatively social carpenter bee, *Xylocopa pubescens* Spinola, 1838, contain a non-reproductive guarding female and a reproductive forager (Gerling et al., 1981). In one study, the presence of a guard in the nest prevented pollen robbing by conspecifics and also allowed the dominant reproductive to complete longer foraging trips (Hogendoorn & Velthuis, 1993). Importantly, the relative costs and benefits of tolerating a guard (i.e. a reproductive rival) in the nest depended on local resource availability and therefore the intensity of pollen robbing (Hogendoorn & Velthuis, 1993). Competition over nests is also a driver of social evolution in some bees, especially when nest substrate is limited or costly to exploit. Shifts in nest substrate availability may even drive social evolutionary transitions, as for one stem-nesting allodapine bee, *Braunsapis puangensis* Cockerell, 1929. The recent introduction of *B. puangensis* to Fiji accompanied by a shift to communal nesting from the ancestral strategy of reproductive queueing (da Silva et al., 2016). Because native stem nesting bees are very rare in Fiji (Dorey et al., 2024), low competition for nesting substrate in their introduced environment may have expanded opportunities for egalitarian sociality in *B. puangensis* (da Silva et al., 2016). Finally, nests may be limiting not due to a shortage of substrate, but due to properties of the substrate itself such as durability and excavation costs. In one study of the facultatively social allodapine bee *Exoneura nigrescens* Friese 1899, Silberbauer and Schwarz found that more durable nesting substrates were associated with a higher incidence of social nesting, perhaps because nest longevity creates opportunities for generation overlap (1995). For large carpenter bees (*Xylocopa*), the high metabolic costs of wood nest excavation may favour sociality via nest inheritance strategies (Ostwald et al., 2021). Indeed, for one population of *Xylocopa virginica* Linnaeus, 1771, high population density led to an increase in social nesting due to saturation of available nests (Vickruck & Richards, 2021).

4 | DISCUSSION

Sociality has repeatedly arisen as an adaptive response to extreme and variable environments. The same features of sociality that have enabled its evolutionary success in these conditions may render social organisms particularly resilient to climate change (Blumstein et al., 2022; Fisher et al., 2021; Komdeur & Ma, 2021; Menzel & Feldmeyer, 2021). In many contexts, changing climate could favour social bees with long activity periods, generalist diets and behavioural adaptations (e.g. communication and thermoregulatory strategies) that facilitate survival in stochastic environments, particularly where floral resources become increasingly fragmented and unpredictable (Bartomeus et al., 2013; Bogusch et al., 2020; Kammerer et al., 2021; Minckley et al., 2013). In other cases, especially in arid regions, effects of extreme drought and heat waves may select for life history patterns (e.g. facultative long-term diapause) and expanded physiological tolerances common to solitary bees (Danforth et al., 2019; Minckley et al., 2013; da Silva et al. unpub.).

Our understanding of these effects is currently data-limited and should be expanded in part through open sharing of bee functional trait data (especially physiological tolerance and social behavioural data), which will enable meta-analyses of the traits co-occurring with sociality and their impacts on climate change responses (Ostwald et al., 2023). In particular, efforts to expand the geographic, behavioural and taxonomic breadth of this research will be crucial. Currently, our understanding of bee responses to climate change is dominated by studies of eusocial honeybees and bumblebees, especially in temperate regions. Understanding how tropical bees respond to climate change is particularly urgent given the vulnerability of tropical ectotherms to climate stressors, due to their relatively narrower physiological tolerance breadths (Hoffmann et al., 2013; Tewksbury et al., 2008). Importantly, the diversity of social bees is greatest in the humid tropics, where longer flowering periods support extended colony life cycles (Danforth et al., 2019). The concentration of eusocial species (especially Meliponini) in the tropics suggests important challenges for tropical eusocial bees under climate change, during which they may increasingly rely on behavioural thermoregulation to protect sensitive brood. In contrast, solitary bees are most species-rich in deserts, where they are adapted to cope with unpredictable flowering events, a strategy that will be increasingly tested under extended drought.

Future work should also address gaps in our understanding of the many bees that are neither eusocial nor solitary, many of which may facultatively shift social organisation in response to changing climate. As the studies highlighted here emphasise, these groups can share some behaviours with eusocial groups (e.g. nest guarding, simple forms of behavioural thermoregulation), but in many respects behave similarly to solitary species (e.g. short active seasons, lack of complex foraging communication, limited foraging ranges) and may be expected to respond similarly to climate change. Accounting for this behavioural variation in community-level studies of bee responses to climate change will be essential for understanding the interplay between sociality and climate responses.

Beyond these differential impacts, climate change may also influence social evolution itself by shifting the abiotic and biotic selective pressures that determine the fitness outcomes of different social strategies. The direction of these shifts will be largely heterogeneous within and across taxa, depending on such factors as the local pace of climate change and the extent to which plasticity governs climate change responses (Loarie et al., 2009; Martin et al., 2023). Experimental studies of socially polymorphic bee species (e.g. common garden experiments, reciprocal transplants, and studies manipulating environmental conditions) will extend our understanding of these evolutionary consequences (Davison & Field, 2018b; Field et al., 2010). In many contexts, warming temperatures may broadly increase the frequency of eusocial nesting as extended active seasons coupled with shorter brood development times increase the probability of rearing multiple broods in a year (Hirata & Higashi, 2008; Kocher et al., 2014; Schürch et al., 2016). Simultaneously, increasing climate variability and associated shifts in competition, predation, parasitism and nesting resources will alternately favour social and solitary strategies based on ecological context and the magnitude of the climatic stressors (Bohart & Youssef, 1976; da Silva et al., 2016; Hogendoorn & Velthuis, 1993; Rehan et al., 2011; Silberbauer & Schwarz, 1995; Vickruck & Richards, 2021). Future work in this area has the potential to clarify interactions between climate change and sociality at multiple levels and timescales, from shifting distributions of social bees to evolutionary transitions in social organization (Hirata & Higashi, 2008; Kocher et al., 2014; Schürch et al., 2016).

AUTHOR CONTRIBUTIONS

All authors (Madeleine Ostwald, Carmen da Silva and Katja Seltmann) contributed to study conceptualisation and manuscript editing. Madeleine Ostwald led the literature search and writing of the original draft.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Our study is a review of existing published data.

ORCID

Madeleine M. Ostwald https://orcid.org/0000-0002-9869-8835
Carmen R. B. da Silva https://orcid.org/0000-0003-0160-5872
Katja C. Seltmann https://orcid.org/0000-0001-5354-6048

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