

# How does climate change impact social bees and bee sociality?

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## Abstract

1. Climatic factors are known to mediate the expression of social behaviors. Likewise, variation in social behavior can dictate climate responses. Understanding interactions between climate and sociality is crucial for predicting impacts of climate change on animal populations.

2. These effects 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 impact vulnerability to climate change, and (b) how might climate change impact social organization in bees? In doing so, we generate predictions about the impacts of climate change on the expression and distribution of social phenotypes in bees. Furthermore, we emphasize that social and solitary bee populations could be differentially impacted by climate change due to important behavioral, physiological, and life history differences.

4. We highlight important avenues for investigating evolutionary consequences of climate change for social bees and for bee social organization. Understanding linkages between social behavior and environmental conditions is essential for forecasting vulnerability and resilience to climate change across bee taxa.

## Introduction

Climate represents a major selective force in the evolution of sociality. Climatic conditions can shape developmental rates, nesting strategies, biotic interactions, and other processes that determine the relative costs and benefits of group formation (Blumstein et al., 2022; Fisher et al., 2021; Menzel and Feldmeyer, 2021; Moss and While, 2021; Wilson, 1971). Social living can give rise to emergent strategies for coping with climatic stressors (Arnold, 1988; Fahrenholz et al., 1989; Klok and 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 and Rubenstein, 2011; Lukas and 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). Bees possess some of the richest diversity of

social behaviors of any animal taxon, with multiple independent origins of eusociality and a broad range of non-eusocial forms (Michener, 1974; Wcislo and 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 organization in bees correlates with other behavioral and life history traits, like foraging strategy and phenology, that can influence susceptibility to climate change stressors. However, a unifying pattern linking sociality to climate change vulnerability has remained elusive.

Climate change is also likely to shift the expression and geographic distribution of social behaviors 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 drought, flooding, and wildfire (IPCC, 2022). For bees, many of which can flexibly express sociality in response to environmental conditions (Wcislo and Fewell, 2017), the social impacts of these shifts could be particularly profound. Nevertheless, very few studies have directly assessed the impacts of climate change on bee social organization. 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.

#### Box 1: *Notes on bee social biology and terminology*

The ancestor of bees was solitary, as are the vast majority of extant bee species (Debevec et al., 2012). Nevertheless, diverse forms of social living are known to be found in all currently recognized bee families except the Stenotritidae (Michener, 1974; Wcislo and Fewell, 2017). 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, 1997, 1993; Yagi and Hasegawa, 2012). Social organization in bees takes a diversity of forms, and includes several independent origins of (and reversals from) eusociality (Danforth et al., 2003; Kocher and Paxton, 2014). Among and within taxa, bee societies vary considerably in group size, in the degree of reproductive skew and morphological specialization, and in the genetic relatedness of group members (Michener, 1974; Ostwald et al., 2022b; Wcislo and Fewell, 2017). 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.

The studies we review here vary considerably in their categorizations of social states. 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). We consider communal living as a social category because it entails behaviors and characteristics distinct from solitary living that are relevant to environmental tolerance, for example, by enhancing nest defense from predators and parasites, by generating advantages in nest excavation and initiation, and by enabling social thermoregulatory behaviors. In general, we will broadly compare social groups to solitary individuals, but emphasize that sociality represents a broad spectrum of behaviors with corresponding diversity in their responses to climate conditions.

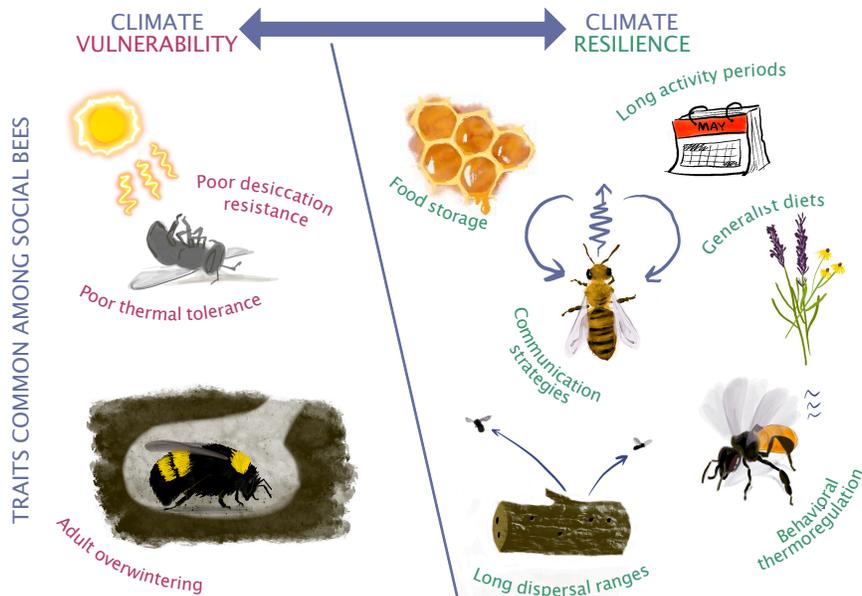


Figure 1: Figure 1. Behavioral, physiological, and life history traits common among social bees, arranged by their tendency to confer vulnerability vs. resilience to changing climate. Importantly, not all social bees possess these traits, and the effect of these traits on climate responses will vary with environmental context.

### 1. How does sociality impact vulnerability to climate change?

Sociality shapes bees' life histories, physiological traits, and behavioral repertoires. These traits can broadly influence how bees respond to climatic variables, and therefore their vulnerability to environmental change (Figure 1). Group living has been proposed to provide buffering effects against environmental variability (Kennedy et al., 2018; Komdeur and Ma, 2021), which may explain why cooperatively breeding animals to thrive in regions characterized by strong climatic variability (Jetz and Rubenstein, 2011; Lukas and Clutton-Brock, 2017; Sheehan et al., 2015). While a considerable body of literature explores effects of climate change on bees that are social, many fewer investigate social effects at the species level, i.e., by assessing social behavior as a predictor variable across bee species. Where data do exist, patterns have been mixed. Some studies have found significant relationships between sociality and climate-relevant functional traits, like desiccation resistance and thermal tolerance (da Silva unpub., Hamblin et al., 2017). 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. Social bees may be less susceptible than solitary bees to urbanization (Banaszak-Cibicka and Źmihorski, 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 trait-related responses to climate change. A promising starting-place to generate predictions for these studies is by examining life history, behavioral, and physiological trait variation between social and solitary bees.

#### *Life history factors*

Known differences in social and solitary bee life histories can offer insights into potential mechanisms of climate resilience. Principal among these differences is the seasonal life cycle of social bees. Solitary bees are active as adults for narrow windows of time, averaging about one month per year, but often for much shorter (Michener, 2007). This restricted activity period could render solitary bees particularly vulnerable

to phenological mismatch as host plants advance their flowering times under climate change (Kudo and Ida, 2013; Visser and Gienapp, 2019). Longer activity periods, however, present other challenges. Social bees are typically multivoltine (i.e., they produce multiple broods per year), with an adult activity period spanning several months (Michener, 1974). The breadth of social bee species' activity windows may increase their likelihood of being impacted by resource gaps (Kaluza et al., 2018; Requier et al., 2020). However, these disadvantages of a long colony lifespan may be counterbalanced by behavioral adaptations common to social species, including polylecty and resource storage, that enhance survival when floral resources are depleted.

Social and solitary bees also differ markedly in their overwintering life cycles. Most solitary bees spend most of the year in diapause in the pre-pupal stage. Eusocial bees, by contrast, typically overwinter as fertilized adult female gynes. Several studies have demonstrated that bees overwintering as adults are more sensitive to increased winter temperatures, leading to increased mortality and weight loss relative to species overwintering in the prepupal stage (Fründ et al., 2013; Kammerer et al., 2021; Slominski and Burkle, 2019). Importantly, not all solitary bees conform to the typical, likely ancestral pattern of prepupal winter diapause, and communal bees exhibit a mix of adult and pre-pupal overwintering life histories. For the eusocial bees, however, many of which are adult-wintering, warming winter temperatures may be disproportionately challenging.

### *Behavioral and physiological factors*

Social bees possess a suite of behavioral adaptations related to resource acquisition that might be advantageous as floral resources become scarcer, more patchily distributed, and/or unpredictably available under climate change. In order to support their extended colony life cycles over the course of the flowering season, the vast majority of social bees have broad, generalist pollen diets (Michener, 2007), which confers resilience to changing floral communities (Bogusch et al., 2020). Highly eusocial bees also possess complex communication strategies (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 behaviors enable colonies to more effectively exploit spatially and temporally unpredictable food landscapes (Dornhaus and Chittka, 2004; Hrcir et al., 2019; Maia-Silva et al., 2020). Many eusocial 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., bumble bees) it can provide insurance against short periods of poor foraging conditions. Social bees can also share collected food via trophallaxis, even in simpler facultative societies (Gerling et al., 1983; Kukuk and Crozier, 1990; Sakagami and Laroca, 1971). Finally, social bees have larger foraging ranges (Kendall et al., 2022) and greater dispersal capabilities (López-Uribe et al., 2019) than do solitary bees, potentially allowing them to escape resource-depleted landscapes. Colonies of the African honey bee (*Apis mellifera scutellata* Lepeletier, 1836) will seasonally abscond from their established nest sites, migrating to areas of greater food abundance (McNally and Schneider, 1992).

These traits can increase social bees' resilience to drought conditions. Several studies have highlighted eusocial bees as ecological "winners" of drought events. Hung et al. found increased representation of eusocial *Lasioglossum* bees in samples collected in Southern California following the severe drought year of 2014 (2021). Similarly, Kammerer et al. 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 (2021). Other findings have highlighted polylecty, a trait that co-occurs with sociality, as a successful strategy under drought conditions. Minckley et al. surveyed bee abundance in the Chihuahuan Desert and found that generalist bees were more abundant in drought years (2013). Alternatively, solitary bee traits may be particularly adaptive in arid regions with unpredictable rainfall. Minckley et al. suggest that under severe drought scenarios, the (solitary) specialist species that can undergo facultative long-term diapause may have competitive advantages over generalist bees that cannot wait out unfavorable years (2013). Indeed, the ability of solitary, specialist, univoltine species to time their active season with short, unpredictable flowering periods represents one hypothesis for why solitary bees are so species rich in desert environments (Danforth

et al., 2019).

Social bees also possess unique behavioral 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 behaviors to deftly control their nest temperatures, including direct incubation, metabolic heat production, fanning, nest evacuation, and evaporative cooling (Heinrich, 1993; Jones and Oldroyd, 2006; Seeley, 1985). These behaviors enable colonies to maintain an optimal thermal setpoint despite wide variation in ambient temperatures. Coordinated thermoregulatory behaviors can promote recovery from and resilience to extreme heat events. Following intensive water collection to cool the nest under high ambient temperatures, honey bee 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 behaviors are best known in the corbiculate bees, thermoregulatory behaviors may exist in other clades. Michener observed fanning at the nest entrance by the primitively eusocial halictid *Augochlorella aurata* (Smith, 1853); (1974). In winter hibernaculae, passive clustering of adults in could minimize 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 1.5degC warmer than solitary individuals at the coldest time of day (Ostwald et al., 2022a). Minor differences such as these could present survival advantages of social nesting when temperatures approach freezing.

The thermoregulatory behaviors of social bees may have important implications for their physiological tolerance limits. Eusocial bees are highly adept at controlling nest temperatures, and they are particularly sensitive to deviations from their optimal thermal ranges. European honey bees tightly regulate the temperature of their broodnests within the range of 33-36degC, even as ambient temperatures drop below freezing or soar to extreme highs (Fahrenholz et al., 1989; Seeley, 1985). Brood reared at even a single degree below this range (32degC) experience significant learning deficits (Jones et al., 2005; Tautz et al., 2003). Solitary bees, in contrast, may tolerate a much wider range of temperatures during development and throughout their adult lives (Earls et al., 2021; Frund et al., 2013; Park et al., 2022), during which they may be poorly buffered from environmental temperatures. This variation in the thermal experiences of social and solitary bees might help to explain corresponding variation in their heat tolerance or ability to survive in arid environments. For example, the climatic variability hypothesis proposes that species that experience greater environmental variability should have greater phenotypic plasticity (ability to shift underlying physiology with changes in environment) than species that experience little environmental variability (Janzen, 1967). In contrast, organisms that evolve in highly variable environments are also expected to have broad physiological tolerances and limited plastic responses to changes in climate (Gabriel, 2005). However, there are examples of species that have plastic physiological responses to changes in temperature and broad thermal tolerances (da Silva et al., 2019; Healy and Schulte, 2012). Thus, if solitary bees are evolving in stochastic and variable environmental conditions, we would expect them to either have broader thermal tolerances, greater plasticity in their thermal performance, or both, compared to social bees which are expected to evolve in more stable environmental conditions. Indeed, determining whether social or solitary bees are more vulnerable to climate change will require an understanding of their physiological tolerances and the microclimates that they inhabit (i.e., social species are less heat tolerant, but also experience lower extreme thermal environments). For example, many solitary and communal species live in stem nests that are exposed to a great deal or climatic variability or, alternatively, live in underground tunnel nests, which are much more thermally stable (da Silva et al., 2019; Healy and Schulte, 2012). Eusocial lineages (e.g., Apini and Meliponini) often nest in cavities, which we would expect to experience an intermediate amount of thermal variability compared to stem nests or underground tunnel nests. Thus, microclimate variability is likely to be influenced by both sociality and nesting strategy, which in turn could shape the evolution and plasticity of physiological tolerances.

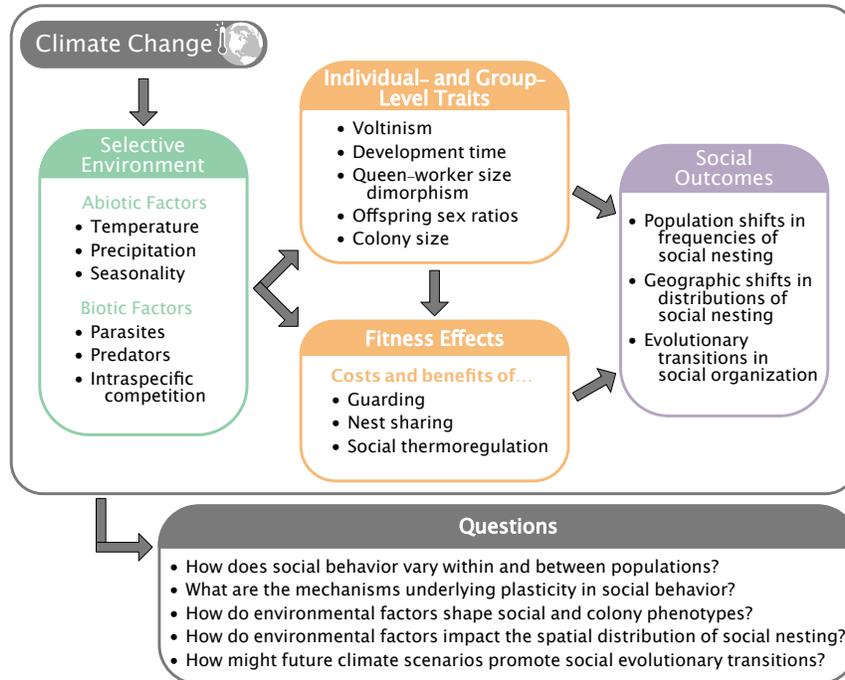


Figure 2: Figure 2. Summary of the impacts of climate on sociality, as mediated by changes in the selective environment and resulting impacts on social traits and fitness. Arrows indicate directions of influence.

## 2. How might climate change impact social organization in bees?

Climatic selective pressures have been implicated in social evolutionary transitions across animal taxa (Guerra and Avilés, 2015; Jetz and Rubenstein, 2011; Liu et al., 2020; Lukas and Clutton-Brock, 2017). These patterns support the hypothesis that sociality can facilitate the colonization 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 and Rehan, 2018; Kocher et al., 2014). The same selective forces that have historically shaped the evolution of social behavior in bees could likewise influence social behavior under climate change.

The bees most likely to experience transitions in social organization in response to climate change are facultatively social bees with some degree of social plasticity because they already possess the behavioral flexibility to express multiple social states. Facultative sociality is best known among the Halictidae and Xylocopinae (Michener, 1990; Shell and Rehan, 2017), but may be widespread across bee taxa when one considers communal nesters and the many typically solitary species that may have some capacity for communal nesting (Wcislo and Tierney, 2009). Additionally, climate change may influence colony demography and social traits (e.g., colony size, reproductive skew, sex ratios) across bee species more broadly, including the obligately social species. Importantly, these demographic shifts can impact the social environment, which can in turn promote changes in social organization and complexity (Figure 2).

### *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 and Field, 2018a; Hunt and Amdam, 2005). For this reason, some socially polymorphic species exhibit intraspecific variation in social behavior 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 and Field, 2016; Eickwort et al., 1996; Packer, 1990; Sakagami and Munakata, 1972). Similarly, *Ceratina* are more likely to be social in tropical regions, where long breeding seasons permit bivoltinism, and suggest that dispersals to temperate regions prompted evolutionary reversions to solitary living (Groom and Rehan, 2018).

The extent to which social polymorphism is determined by phenotypic plasticity will dictate how individual species and populations respond to changing climate. Transplant and common garden experiments represent promising tools for disentangling genetic and plastic effects on social strategy. For example, Davison and Field transplanted *Lasioglossum calceatum* Scopoli, 1763 foundresses from a solitary, high latitude population to a lower-latitude site where conspecifics are typically eusocial (2018). Nine of ten transplanted foundresses retained a solitary lifestyle despite the extended breeding season, suggesting that the social polymorphism in this species may be largely genetically determined. In contrast, reciprocal field transplants of *Halictus rubicundus* Christ, 1791 across a latitudinal gradient induced social behavior in foundresses from typically solitary populations and solitary behavior in foundresses from social populations (Field et al., 2010). Schürch et al. used climate projections to predict that the social phenotype in *H. rubicundus* will appear at higher latitudes than previously observed, as increasing average temperatures extend the breeding season (2016). Importantly, the extent to which sociality is plastic varies even within species; North American populations of *H. rubicundus*, for example, show stronger genetic differentiation between social and solitary populations than do European populations (Field et al., 2010; Soucy and Danforth, 2002). These considerations suggest that social responses to climate change will be strongly heterogenous 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 the allopapine bee *Exoneura robusta* Cockerell, 1922, faster brood development times at lower latitude, probably due to warmer temperatures, enabled social nesting via the production of a second brood (Cronin and Schwarz, 1999). Because emergence order can determine social dominance for *Exoneura* (Schwarz and Woods, 1994), accelerated development could also have consequences for social organization, if warmer temperatures reduce variation in emergence time. 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 and 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 and Willmer, 1989). In some contexts, warming temperatures could increase the thermal activity window for foraging, enabling foundresses to rear larger broods. Schürch et al. demonstrated that the number of provisioning trips completed and the number of offspring provisioned increased with temperature for *Halictus rubicundus* foundresses (2016). Combined, these mechanisms may account for the association between warmer climates or years and increases in colony size (Cronin and Schwarz, 1999; Field et al., 2010; Packer and Knerer, 1986; Richards and Packer, 1995). Alternatively, in environments characterized by hot summers that regularly exceed bees' optimal foraging temperatures, 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, for example, by shaping the within-group distribution of female body sizes. Body size in social bees is strongly associated with reproductive dominance (Brothers and Michener, 1974; Richards, 2011; Smith et al., 2008). Specifically, larger females are better able to physically coerce offspring or other nestmates into worker behaviors like foraging; and these dominance behaviors seem to be important in inhibiting worker ovarian development (Brothers and Michener, 1974; Michener and Brothers, 1974). Environmental impacts on body size thus

represent an avenue through which climate change might impose shifts in social organization. Richards and Packer found that favorable conditions (warm, dry years) led to primitively eusocial *Halictus ligatus* Say, 1837 queens producing larger-bodied workers than they did in unfavorable 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 favorable conditions, workers were relatively large and more likely to reproduce. Conversely, under unfavorable conditions, queens and workers were more dissimilar in size and worker reproduction was rare, leading to more strongly eusocial colony organization (Richards and Packer, 1996). Similarly, for the facultatively social, subtropical small carpenter bee, *Ceratina australensis* Perkins, 1912, unfavorable 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 can shape colony demography through shifts in offspring sex ratios. Female-biased broods early in the reproductive season create opportunities for social nesting via worker recruitment (Boomsma, 1991; Trivers and Hare, 1976). Yanega found that warmer temperatures were correlated with increasing male bias in the first brood of *H. rubicundus*, which led to a population-level decrease in the frequency of eusocial nesting (Yanega, 1993). Future work tracking first brood sex ratios in flexibly social bees will be particularly instructive for predicting impacts of warming on colony demography and the frequency of social nesting.

#### *Precipitation effects*

Social strategies can also help mitigate environmental stressors associated with precipitation and water availability. Many of these effects are intrinsically bound to thermal effects, working in concert with temperature variation to determine whether conditions are favorable or unfavorable for foraging and brood rearing. 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 time window to produce a second brood (2016). Likewise for *Halictus ligatus*, high rainfall created conditions unfavorable for worker production, with consequences for social organization (Richards and 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. 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 favors 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 behavioral consequences of dry soil excavation remain to be tested empirically.

#### *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 and Michener, 1972; Wcislo and Fewell, 2017). Climate change will impact the distribution and abundances of diverse com-

munities of bees' competitors and natural enemies, with variable consequences for bee social behavior. In populations under strong selective pressure from parasitism or predation, sociality can enable bees to forage without leaving their nests unattended. Active defensive behavior 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 parasitized 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 characterized 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 and 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 and 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 Fiji has no native stem-nesting bees, low competition for nesting substrate in their introduced environment may have expanded opportunities for egalitarian sociality (2016). Finally, nests may be limiting not due to a shortage of substrate, but due to costs of exploiting that substrate. For large carpenter bees (*Xylocopa*), the high metabolic costs of wood nest excavation may favor sociality via nest inheritance strategies (Ostwald et al., 2021). Indeed, for one population of *Xylocopa virginica* Linnaeus, 1771, high-density conditions led to an increase in social nesting due to saturation of available nests (Vickruck and Richards, 2021). Under climate change, as species are redistributed in time and space (phenological and geographic shifts), we expect social evolutionary consequences of these changes in selective pressures related to parasitism, predation, and intraspecific competition.

## Conclusions

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 and Ma, 2021; Menzel and Feldmeyer, 2021). In many contexts, changing climate will favor social bees with long activity periods, generalist diets, and behavioral adaptations (e.g., communication and thermoregulatory strategies) that facilitate survival in stochastic environments. In other cases, extreme climate conditions may select for life history patterns and expanded physiological tolerances common to solitary bees. 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 behavioral data), which will enable meta-analyses of the traits co-occurring with sociality and their impacts on climate change responses. Beyond these differential impacts, climate change can also shape 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 local climatic variability and the extent to which plasticity governs responses to environmental change. 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. 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.

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### Author Contributions

MMO led the writing of the original draft. All authors contributed to conceptualization and editing.

### Conflict of Interest

The authors declare no conflict of interest.

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