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ORIGINAL PAPER

Stingless bees and their adaptations to extreme environments

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Abstract

Nearly half of all terrestrial tropical ecosystems around the globe comprise dry forests, characterised through elevated temperatures all year round, and short rainy seasons at irregular intervals. The consequent water deficit over several consecutive months limits the availability of floral resources to often very brief and unpredictable periods, which poses a challenge to the maintenance of perennial colonies in highly eusocial bees. Thus, only few highly eusocial bees occur permanently in tropical dry forests, among them some highly adapted species of stingless bees (Apidae, Meliponini). In the present review, we discuss the current knowledge on the adaptations to such extreme environments in *Melipona subnitida*, a stingless bee native to the Brazilian tropical dry forest. Key to the success of this species is not so much heat resistance of foragers, as it is the ability to maintain perennial colonies despite extended dearth periods. After several months of drought, *M. subnitida* colonies are capable of re-establishing fully functional colonies from nests containing only few dozens of workers. This surprising resilience is based on a quick reaction to precipitation-driven increase in floral resource availability, mainly owing to selective foraging at high-profit resources and an immediate up-regulation of brood production once food storage conditions improve.

Keywords *Melipona subnitida* · Caatinga · Foraging · Brood production · Colony aestivation

Introduction

The stingless bees (Apidae, Meliponini) are among the most common and abundant native flower visitors in many tropical terrestrial ecosystems, and, thus, are indispensable pollinators in those areas (Roubik 1989). This group of highly eusocial bees, comprising more than 510 species living predominantly in tropical habitats around the globe (Michener 2013; Ascher and Pickering 2018), differs in several biological aspects from the honey bees (Apidae, Apini). (Michener 1974; Sakagami 1982; Engels and Imperatriz-Fonseca 1990). One of these is the gradual and progressive establishment of new colonies in stingless bees, as opposed to the honey bees' swarming behaviour (Michener 1974; Nogueira-Neto 1954). The advantages of this strategy of colony reproduction are a granted food supply during the initial phase of low population size and, if necessary, quick replacement of a lost queen (Engels and Imperatriz-Fonseca 1990). However, owing to the necessity of persistent resource allocation from the maternal to the filial nest, both usually are within short distance of each other, which may cause an overcrowding of nesting sites and limits the possibility of expansion into new territories (Hubbell and Johnson 1977; Roubik 2006).

The limited dispersal ability of the stingless bees may be key to today's taxonomic diversity of this bee group, which is higher than that of all the other corbiculate bees combined (Michener 2007; Rasmussen and Cameron 2010). Origin and distribution of present-day species, presumably, are related to recurrent climate changes during the Pliocene and Pleistocene (Camargo 2013). Particularly, glaciation events in the Northern hemisphere, with cycles of 100,000 years interrupted by short warm periods, led to temporary habitat fragmentation through periodic forest contractions and expansions in South America (Hewitt 1996), therewith creating severe genetic bottlenecks (Alves et al. 2011). The consequent isolation of stingless bee species in often small ecological refuges over several tens of thousands of years have promoted adaptations to very particular environmental conditions.

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Peculiar habitats for eusocial bees are tropical dry forests (Fig. 1). Usually, people associate the Tropics with exuberant rain forests, like the Amazon or the Kongo, that provide food for flower visitors practically all year round (Wilms and Wiechers 1997; Kajobe and Echazarreta 2005). However, 42% of all tropical vegetation types around the globe are dry forests (Murphy and Lugo 1986). These ecosystems are characterised by annual rainfall average of between 400 and 1800 mm distributed over 3–9 months (Murphy and Lugo 1986; Andrade et al. 2017; Silva et al. 2017). The severe water deficit over several consecutive months due to elevated solar radiation and annual mean temperatures of up to 30 °C (Vasconcellos et al. 2010; Andrade et al. 2017) limits the availability of floral resources to often short and unpredictable periods (Machado et al. 1997; Lima and Rodal 2011; Lopezaraiza-Mikel et al. 2014; Quirino and Machado 2014; Maia-Silva et al. 2015, 2018). Recurrent events of supra-annual droughts in tropical dry forests, during which precipitation remains up to 50% below the annual average (Marengo et al. 2017), presumably, impose a high selective pressure upon bees owing to a critically reduced food offer for several years.

For eusocial bees, who rely on a more or less constant food supply to maintain their perennial colonies, long-lasting dry spells and the concomitant shortage of floral resources in the environment pose a threat to colony survival. Thus, when food becomes scarce, tropical honey bees (*Apis mellifera scutellata* and Africanized honey bees, a hybrid of Western and African honey bee subspecies) abandon their nests and migrate into areas of greater resource abundance (Schneider and McNally 1992; Winston 1992). Stingless bees, however, are far less flexible. Because mated queens are unable to fly (Fig. 2), colonies would have to leave their queen behind when abandoning the nest. Consequently, resource-induced absconding, as known from honey bees (Winston 1992) is rare in the Meliponini, and they need to adopt alternative strategies to sustain their permanent colonies during the extended dearth periods they experience in tropical dry forests.

Owing to environmental conditions largely unfavourable for eusocial bees, only few stingless bee species occur in tropical dry forests despite a large bee diversity in adjacent biomes (Zanella 2000; Aguilar et al. 2013; Ayala et al. 2013) (Fig. 1). On the one hand, the colonization by stingless bee species is constrained by the necessity of specific physiological and behavioural adaptations to survive long-lasting dry spells, and only few environmental super-generalists succeed in crossing the border from neighbouring habitats (Zanella and Martins 2003). On the other hand, tropical dry forest-specialists are hardly found outside of their native habitat, resulting in an elevated degree of endemism in these ecosystems (Zanella 2000; Zanella and Martins 2003).

So, what are the adaptations of stingless bees that permit them to survive under the extreme environmental conditions in tropical dry forests? In our review, we try to answer this question analysing the foraging behaviour and brood

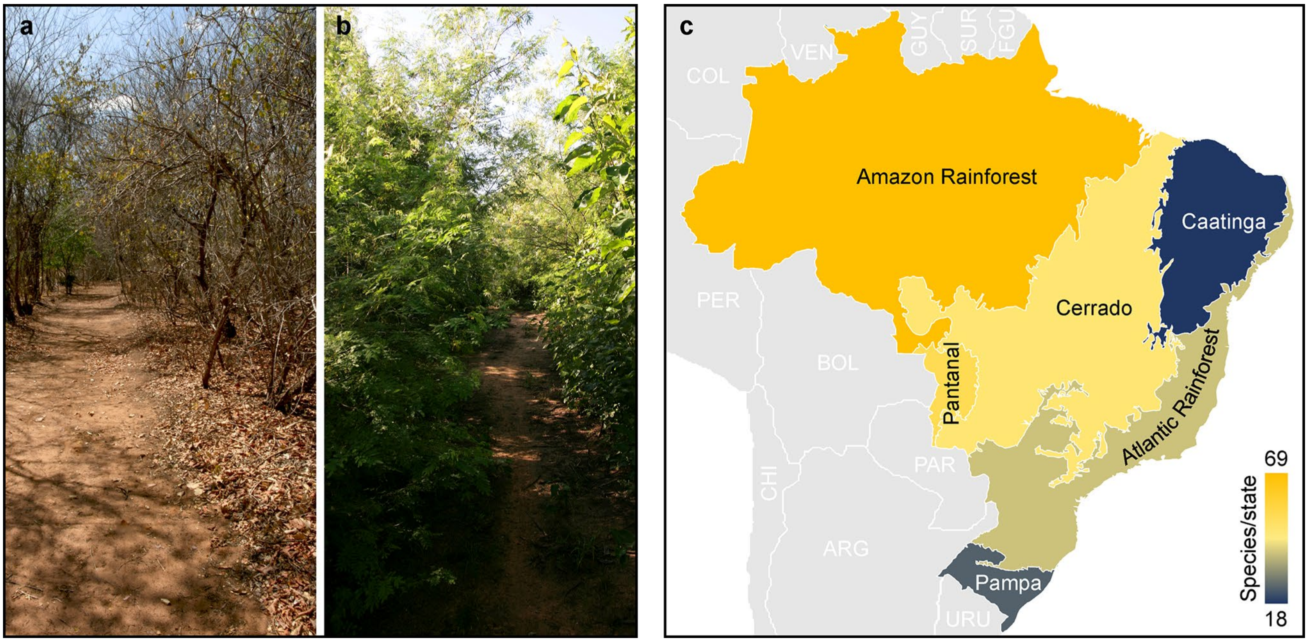

Fig. 1 Caatinga, the Brazilian tropical dry forest. Representative photographs of the vegetation **a** in the dry season, and **b** in the rainy season. **c** Diversity of stingless bee species in Brazil. Given is the average number of species per state comprising the respective biome (data from: Pedro 2014)

Fig. 2 *Melipona subnitida*, a stingless bee species native to the Brazilian tropical dry forest. **a** Physogastric queen on brood comb and worker provisioning brood cell. Note dilated abdomen of the queen, which renders absconding impossible. **b** Top view of nest showing the horizontal brood comb as well as pollen and honey storage pots

production of *Melipona subnitida* (Fig. 2), a stingless bee species native to the Brazilian tropical dry forest in the semi-arid region of northeastern Brazil. In particular, we were interested in (1) how foragers cope with elevated ambient temperatures during food collection, and (2) how colonies successfully overcome the extended periods of drought.

Strategies of stingless bee foragers to avoid overheating

In the Brazilian tropical dry forest, the Caatinga (Fig. 2), mean air temperatures, with annual averages of up to 28 °C in lowland regions, show little variation in the course of a year (Marengo et al. 2017). Daily maxima, however, can reach values close to 40 °C in the shade (Maia-Silva et al. 2015). Most importantly for flower-visiting insects, soil surface temperatures in full sunlight and air temperatures closely above the tree canopy (T_{a-sun}) exceed shade temperatures ($T_{a-shade}$) by up to 15 °C (Souza et al. 2015; Ferreira et al. 2017). Thus, bees foraging in the Brazilian tropical dry forest, even when collecting floral resources well before noon (Fig. 3), may be exposed to temperatures determined as critical (CT) or even lethal (LT) for meliponine species that inhabit cooler regions (*Austroplebeia essingtoni*, northern Australia: CT = 37.2–43.9 °C, Ayton et al. 2016; *Melipona beecheii*, Yucatan Peninsula: CT = 38 °C; Macías-Macías et al. 2011; *Scaptotrigona postica*, southern Brazil: CT = 38.5 °C, LT = 41 °C; Macieira and Proni 2004).

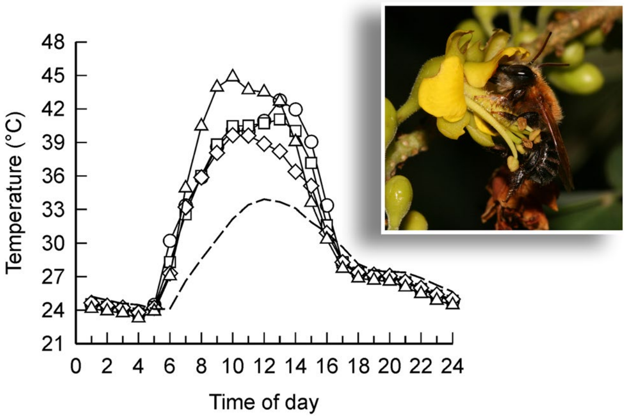

Fig. 3 Elevated air temperatures in foraging areas. Given are average temperatures (*N* = 10 days) measured by a weather station (shade air temperature, dashed line) and at four flower patches (sun air temperature, open symbols) at canopy level of *Libidibia ferrea*, a common tree species in the Brazilian tropical dry forest that provides nectar to flower visitors (original data: Ferreira et al. 2017). *Inset: M. subnitida* forager collecting nectar at a flower of *L. ferrea*

An important first step towards our understanding of the foraging strategies of stingless bees in the Brazilian tropical dry forest is the evaluation of the workers' thermal tolerance. One of the most relevant measures in this context is the critical thermal maximum of individuals, defined as the cease of controlled motoric activity (Lutterschmidt and Hutchingson 1997; Terblanche et al. 2011). Although individuals may recover from this state, their limited mobility hampers the escape from the adverse thermal conditions, which, eventually, results in their death (Mitchell et al. 1993). In experiments subjecting animals to static heat stress, the critical thermal maximum can be inferred from the sudden increase in mortality above certain experimental temperature (Silva et al. 2017). A crucial parameter in this context is exposure time (Chappell 1982; Li et al. 2011). When subjecting *M. subnitida* workers to elevated temperatures for 24 h, simulating constant heat stress within the nest, the critical thermal maxima were 40.0 °C when individuals had access to water, and 38.6 °C without water supply (Silva et al. 2017) (Fig. 4). However, after short-term exposure for 30 min, the average

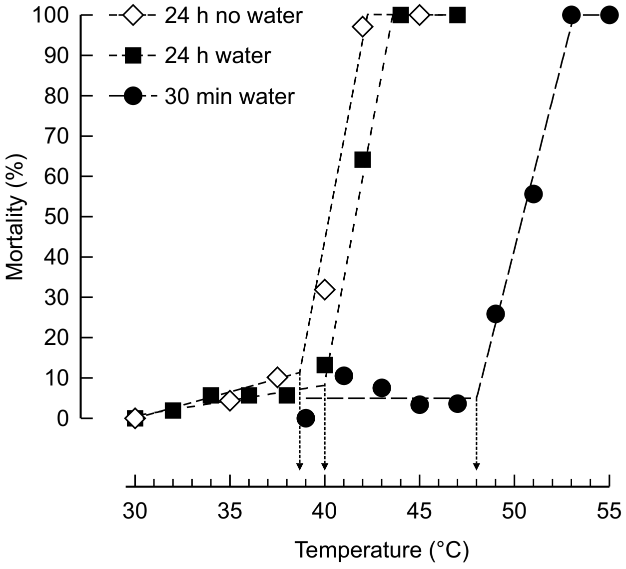

Fig. 4 Thermal tolerance of *M. subnitida* workers. Groups of workers (15–20 individuals per group) were exposed to a given experimental temperature in a BOD incubator either for 24 h without water supply (treatment 1: open diamonds), 24 h with access to water (treatment 2: filled squares), or 30 min with access to water (treatment 3: filled circles). Each symbol represents the mortality rate of one experimental group. Prior to the treatment, bees had been acclimated at 30 °C for 24 h. Subsequently, the temperature in the incubator was increased to the respective experimental temperature (temperature increase: 0.8 °C/min) that was maintained for either 24 h (treatments 1 and 2) or 30 min (treatment 3). At the end of each treatment, the mortality rate was evaluated. Arrowheads indicate the critical thermal maximum for each experiment, indicated by the sudden increase in mortality (three-segment linear regression, dashed lines) (original data from: Ferreira et al. 2017; Silva et al. 2017)

foraging trip time of *M. subnitida* (Pereira 2017), revealed a significantly higher critical thermal maximum of 48.0 °C (Ferreira et al. 2017) (Fig. 4).

On first sight, therefore, *M. subnitida* foragers should have no physiological problem with collecting food even in full sunlight in the Brazilian tropical dry forest. Yet, the critical thermal maximum refers to body temperature, which does not necessarily equal air temperature (T_a). Due to the activity of the flight muscles, the thoracic temperature (T_{th}) of foraging bees usually exceeds ambient temperature (Heinrich and Kammer 1973; Heinrich 1975). In tropical bees, this temperature excess may reach up to 20 °C at ambient temperatures between 20 and 25 °C, yet it decreases to around 5 °C at higher air temperatures (T_a = 35–40 °C) mainly due to conductance of heat from the thorax to the abdomen (Chappell 1982; May and Casey 1983; Stone 1993). In *M. subnitida* collecting sugar syrup at an artificial food source in full sunlight, we observed a very similar pattern (Fig. 5). Surprisingly, at sun air temperatures above 41 °C, T_{th} dropped below T_{a-sun} by up to 5 °C (Ferreira et al. 2017) (Fig. 5). As known from honey bees, this downregulation of the thoracic temperature at high air temperatures may be due to an accelerated heat redistribution from the thorax to the

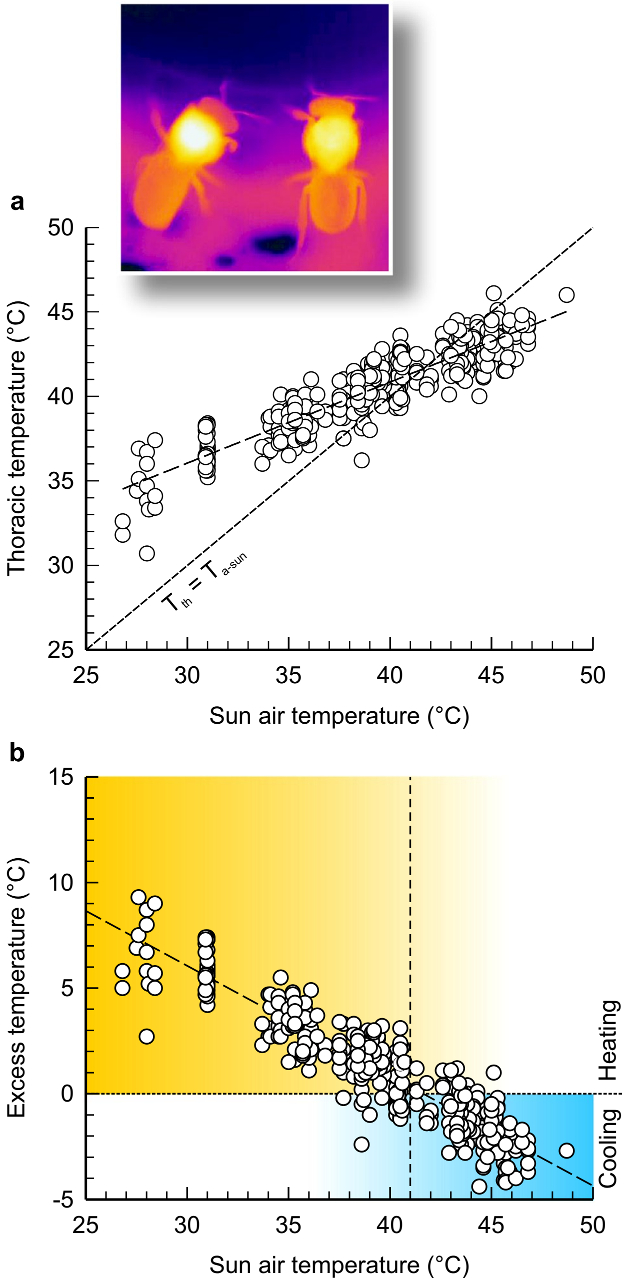

Fig. 5 Thoracic temperature of *M. subnitida* foragers collecting sugar water at artificial feeder in full sunlight. **a** Thoracic temperatures of foragers as function of sun air temperatures at the feeding station ($N = 394$ foragers). Linear regression (dashed line): $T_{th} = 21.7 + 0.48 \times T_{a-sun}$; $R^2_{adj} = 0.83$, $F = 1923{,}8$, $P < 0.0001$. **b** Temperature excess ($T_{ex} = T_{th} - \mathrm{T}_{a-sun}$) as function of sun air temperatures at the feeding station. Linear regression (dashed line): $T_{ex} = 21.7 - 0.52 \times T_{a-sun}$; $R^2_{adj} = 0.85$, $F = 2266.2$, $P < 0.0001$. Note cooling above $\mathrm{T}_{a-sun} = 41$ °C. Temperatures were measured from thermal images (inset) recorded with an infrared camera (Flir SC620) (original data from: Ferreira et al. 2017)

abdomen and the head (Heinrich 1979, 1980) as well as to active evaporative cooling through regurgitation of parts of the honey crop contents (Esch 1976; Roberts and Harrison 2009). Although we do not know yet the exact thermoregulatory mechanism in *M. subnitida*, it efficiently prevents foragers from reaching their critical thermal maximum even at $T_{\text{a−sun}}$ close to 50 °C (Fig. 5).

While foragers collecting nectar or water may easily increase evaporative cooling by regurgitating their crop content, pollen foragers, who leave the nest with only a few microlitres of nectar (Harano and Nakamura 2016), would quickly spend the entire crop content for cooling during food collection at high temperatures (Cooper et al. 1985). Alternatively, they may use their body water reserves, expiring saturated air from the thoracic spiracles (Bailey 1954), thereby risking an increase in haemolymph osmotic concentration (Willmer 1986). Pollen foragers may avoid this physiological stress by abandoning food collection at far lower air temperatures than nectar foragers (Cooper et al. 1985). In *M. subnitida*, accordingly, we observed nectar collection up to $T_{\text{a−shade}} \leq 37$ °C (Maia-Silva et al., unpublished data), whereas pollen foragers stopped their activity already at $T_{\text{a−shade}} \leq 33$ °C (Maia-Silva et al. 2015) under natural conditions in the Brazilian tropical dry forest (Fig. 6).

Interestingly, *M. subnitida*, which are found only in hot semi-arid environments, is far more affected by heat than the honey bee, which presently can be found on every continent except Antarctica from temperate climate zones to desert environments (Michener 2007). The critical thermal maximum of *A. mellifera* is close to 50 °C (Kovac et al. 2014), and foragers are capable of sustaining flight at T_{th} values up to 49 °C (Coelho 1991). In the Brazilian tropical dry forest, correspondingly, Africanized honey bees can be observed foraging in full sunlight even around noon, when *M. subnitida* colonies long ceased food collection (MH, personal observation). However, despite the elevated heat resistance of individuals, the majority of *A. mellifera* colonies abandon the hottest and driest parts of the semi-arid regions of northeastern Brazil as soon as the environmental stress increases (Winston 1992; Freitas et al. 2007), whereas *M. subnitida* colonies persist. Thus, heat tolerance of foraging bees, albeit facilitating food collection in hot climates, is not necessarily associated with a species' capacity to maintain long-lived colonies in tropical dry forests. So, what is the secret of success of *M. subnitida*?

Strategies of stingless bee colonies to overcome extended drought periods

For social bees, the key to survival in tropical dry forests is not so much the heat resistance of foragers as it is the ability to maintain perennial colonies despite extended dearth periods. Given the restricted ability of stingless bees to migrate temporarily to better foraging grounds (Engels and Imperatriz-Fonseca 1990), species native to these challenging environments have evolved special strategies to overcome several months, or even years, of food scarcity.

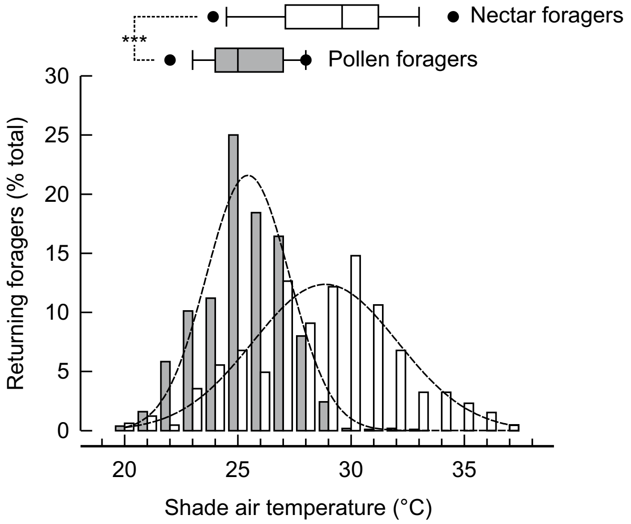

Fig. 6 Thermal foraging window of *M. subnitida*. Given are the relative frequencies of bees returning to the nest with pollen (grey-filled bars; $N = 2{,}311$ foragers; Maia-Silva et al. 2015) and nectar (open bars; $N = 649$ foragers; Maia-Silva et al., unpublished data) at a given ambient temperature. Dashed lines: Gaussian peak regression models: pollen foragers: $R^2_{\text{adj}} = 0.94$, $P < 0.0001$; nectar foragers: $R^2_{\text{adj}} = 0.85$, $P < 0.0001$. Horizontal boxplot indicates the median temperature (line within box), and the temperature ranges in which 50% (box), 80% (whiskers), or 90% of the foragers (outliers) returned to the colonies with pollen (grey-filled box) or nectar (open box). Asterisks indicate significant difference between temperature ranges for pollen and nectar foraging (Mann–Whitney rank sum test: $T = 14{,}736{,}575$, $P < 0.001$)

Selectivity for high-profit food sources

Crucial for sustaining social bee colonies through drought periods is a constant supply of food for both adults and brood. Thus, during periods of resource abundance, meliponine colonies need to collect huge amounts of nectar and pollen and store them within the nest for posterior use (Roubik 1982). Although stingless bees are considered generalist foragers, collecting from a wide array of plants (Roubik 1989; Biesmeijer and Slaa 2006), many species forage predominantly at the most lucrative sources, such as mass flowering trees or plants with poricidal anthers (Wilms et al. 1996; Ramalho 2004). Mass flowering plants, on the one hand, produce a large number of new flowers each day over a short period of time, often less than a week (Bawa 1983; Augspurger 1980). Mostly, individuals bloom synchronously, which results in an excessive supply of floral resources for flower visitors (Bawa 1983). When collecting at this kind of plant, social bees encounter a high spatial density and abundance of a single type of resource and can, thus, quickly replenish or even increase their food stores within the nest (Wilms et al. 1996; Wilms and Wiechers 1997; Ramalho 2004). Flowers with poricidal anthers, on the other hand, produce an excessive amount of pollen that is liberated through small terminal pores or apical slits when vibrated (Buchmann 1983). Here, flower visitors need to be capable of vibrating the flowers efficiently to retrieve the rich floral reward (Buchmann 1983). Among the bees, stingless bees of the genus *Melipona* are well known to perform this so-called "buzz pollination" (Nunes-Silva et al. 2010) and, therefore, can take advantage of these profitable pollen sources when available.

Colonies of *M. subnitida* show a strong selectivity for such high-profit food sources and, consequently, a narrower food niche breadth than *Melipona* species native to other biomes (Maia-Silva et al. 2014). In their natural habitat, *M. subnitida* was found to collect pollen at only few of the pollen sources available during the year (14 pollen types collected, 62 plant species with pollen reward in bloom; Maia-Silva et al. 2015, 2018; for very similar results see). The top six pollen sources, which accounted for more than 90% of the total harvest, were plants with poricidal anthers (Fabaceae, Caesalpinioideae: *Senna obtusifolia, Chamaecrista duckeana*, and *C. calycioides*) and mass flowering trees (Fabaceae, Mimosoideae: *Pityrocarpa moniliformis, Mimosa arenosa*/*M. caesalpiniifolia, Anadenanthera colubrina*) (Fig. 7). Among these, *A. colubrina* is of particular importance for bees in the Brazilian tropical dry forest. Whereas *P. moniliformis* and *Mimosa* spp. bloom in the rainy season, during which pollen sources are abundant, *A. colubrina* produces flowers during a very short time window in the dry season (Maia-Silva et al. 2015), allowing the colonies to replenish part of their pollen reserves.

The mechanisms underlying the selectivity for certain plant species by generalist foragers like stingless bees are largely unknown. One possibility is that the foraging preferences of bees are associated with their olfactory experience during the larval stages (Ramírez et al. 2016). In stingless bees, different from honey bees, brood cells are mass provisioned with larval food from the storage pots prior to oviposition (Michener 1974; Sakagami 1982). During their entire development, therefore, the larvae are constantly exposed to the scents from the larval food within the sealed brood cells, which may trigger a neural bias for these scents as adults (Oleskevich et al. 1997; Ramírez et al. 2016). This may cause a positive feedback, eventually narrowing down the food niche breadth of a colony over the years. In *M. subnitida*, high-profit food sources available during years of extreme drought may constitute the onset of such a feedback cycle: (1) in dry years, or over several years in the case of supra-annual droughts, colonies are able to store food only from plants that bloom even under these severe circumstances; (2) the most abundant food in the storage pots and, consequently, in the larval food is from high-profit food sources that reliably bloom in dry years; (3) the scents of the most abundant plants dominate the olfactory environment

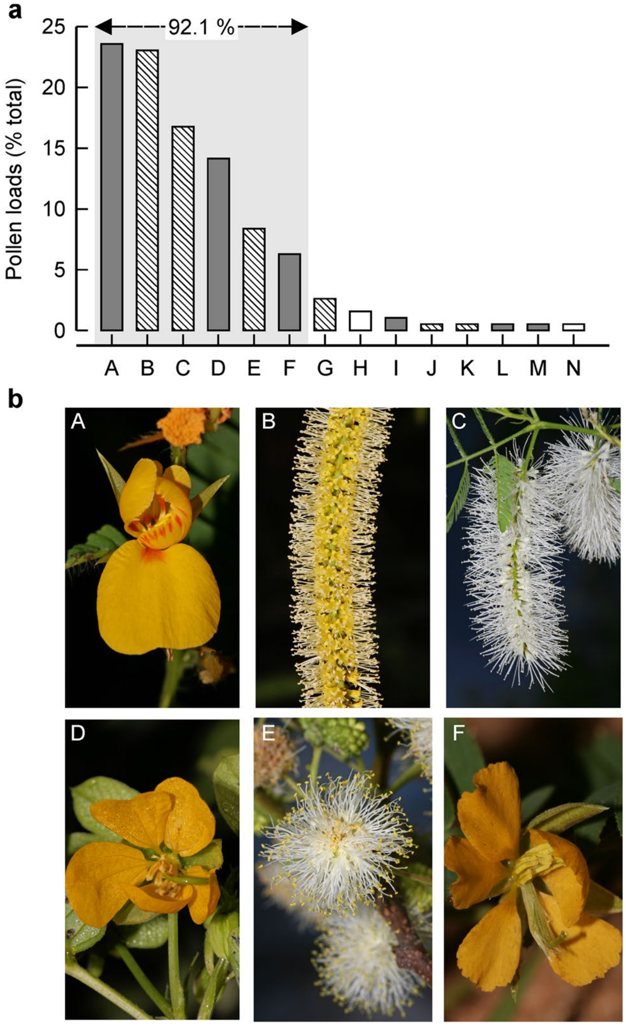

Fig. 7 Selectivity for high-profit pollen sources. **a** Relative frequency of the botanical origin of pollen loads collected from foragers of four colonies o *M. subnitida* during 13 months in an area of native caatinga vegetation ($N=191$ pollen loads analysed; Maia-Silva et al. 2015). A, *Chamaecrista duckeana* (Fabaceae, Caesalpinioideae); B, *Pityrocarpa moniliformis* (Fabaceae, Mimosoideae); C, *Mimosa arenosa*/*M. caesalpinifolia* (Fabaceae, Mimosoideae); D, *Senna obtusifolia* (Fabaceae, Caesalpinioideae); E, *Anadenanthera colubrina* (Fabaceae, Mimosoideae); F, *C. calycioides* (Fabaceae, Caesalpinioideae); G, *M. tenuiflora* (Fabaceae, Mimosoideae); H, *Desmanthus* type (Fabaceae, Mimosoideae); I, *Senna* sp. (Fabaceae, Caesalpinioidae); J, *Eucalyptus* sp. (Myrtaceae); K, *Psidium guajava* (Myrtaceae); L, *S. trachypus* (Fabaceae, Caesalpinioideae); M, *S. uniflora* (Fabaceae, Caesalpinioideae); N, *Turnera subulata* (Turneraceae). Highlighted are the six most frequent pollen types, comprising more than 90% of the total pollen income; grey-filled bars, plants with poricidal anthers; shaded bars, mass flowering trees; open bars, others. **b** Flowers of the six most frequent plant species

in the brood cells; (4) as adults, the search behaviour of the bees is biased towards these reliable high-profit food sources, even in the presence of other resources; (5) an increasing proportion of foragers collect food from at the reliable high-profit source; (6) the relative abundance of food from reliable high-profit sources increases in the storage pots.

Immediate reaction to changes in foraging environment

The Brazilian tropical dry forest is characterised through long, hot dry seasons and equally hot, yet often very short rainy seasons at unpredictable time intervals (Andrade et al. 2017). Since the availability of the vast majority of floral resources is associated with precipitation (Machado et al. 1997; Quirino and Machado 2014; Maia-Silva et al. 2015), stingless bees living in this habitat have to replenish their food reserves within a narrow time window. Owing to the climatic unpredictability, however, it is impossible for bees to foresee beginning and duration of either rainy or dry season. Thus, within sometimes less than 3 months, stingless bees have to hoard sufficient food to sustain their colonies during posterior droughts of unknown length.

Being adapted to the environmental uncertainties of the Brazilian tropical dry forest, colonies of *M. subnitida* react almost immediately to ambient factors indicating the availability of floral resources with an increase in foraging effort (Fig. 8). Both the number of returning foragers and the daily collection period were found to increase significantly with rising relative humidity and precipitation (Maia-Silva et al. 2015). As known from other meliponine species, this increase in the colonies' foraging effort was probably due to increase in individual activity (more foraging trips per bee each day) as well as an increase in the number of collecting bees through recruitment of additional foragers (Eltz et al. 2001; Hofstede and Sommeijer 2006; Barth et al. 2008; Schorkopf et al. 2016). As soon as forage availability in the environment declined, however, colonies diminished their food collection to virtually zero (Maia-Silva et al. 2015). This decrease in worker activity, on the one hand, reduces the colonies' energy consumption, thus economizing the stored honey reserves. On the other hand, the longevity of adults increases (Roubik 1982; Biesmeijer and Tóth 1998), which warrants the functioning of the colony for extended time periods and guarantees enough workforce for resuming foraging once floral food becomes available again.

Brood production regulated through pollen offer

In addition to diminishing their foraging activity in periods of resource scarcity, colonies of *M. subnitida* down-regulate their brood production to the minimum necessary for colony maintenance (Maia-Silva et al. 2015). This reaction to environmental adversities is not at all unique to stingless bees from the Brazilian tropical dry forest. Similarly, species occurring in regions with pronounced seasonal changes in southern Brazil decrease or even interrupt their brood production during the cold season yet increase it quickly once the environmental conditions improve (Ribeiro et al. 2003; Borges and Blochtein 2006). In those stingless bees, however, the reproductive diapause is triggered mainly by abiotic environmental factors, like temperature and day length (Ribeiro et al. 2003). In *M. subnitida*, by contrast, changes in brood-cell production are associated primarily with the quantity of stored pollen (Maia-Silva et al. 2016), which, in

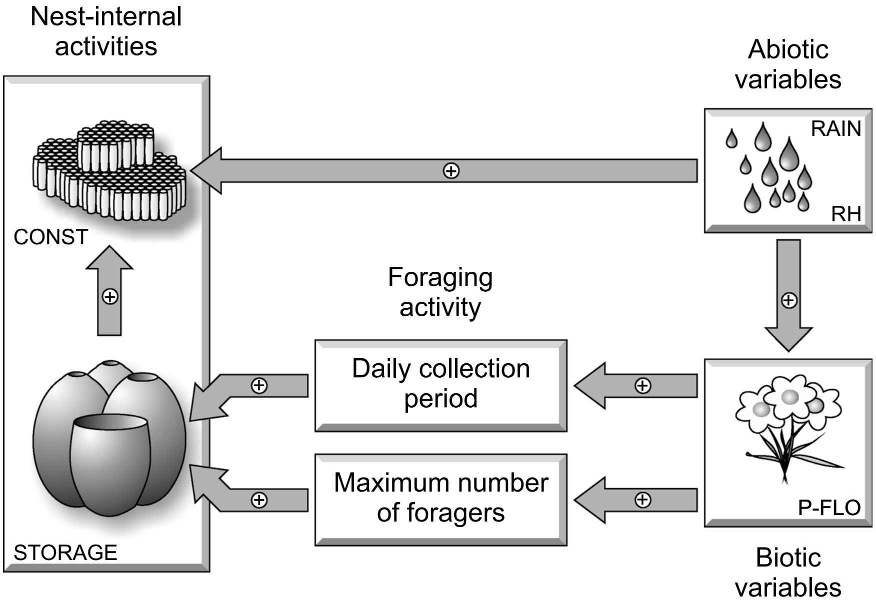

Fig. 8 Influence of environmental factors on the colony activity of *M. subnitida* in the Brazilian dry forest. The monthly variation of abiotic and biotic environmental variables results in variations of the bees' foraging activity, food storage, and brood-cell construction rate. Grey-filled arrows, positive correlations between factors; RAIN, precipitation; RH, average relative humidity; CONST, brood-cell construction rate; STORAGE, food reserves in the nest

turn, depends on the colonies' foraging success (Maia-Silva et al. 2015) (Fig. 8).

This tight link between pollen storage and brood production in *M. subnitida* and other stingless bees (Roubik 1982; Maia-Silva et al. 2016) is due to the mass provisioning of brood cells found in this bee group. A decline in pollen availability within the nest instantly reduces the possibility to provision new brood cells and, thus, results in a decrease of brood production (Roubik 1982; Biesmeijer et al. 1999; Maia-Silva et al. 2016). An increase in pollen storage, on the other hand, triggers the construction and provisioning of new brood cells (Maia-Silva et al. 2016) (Fig. 8). However, once an egg has been laid on top of the larval food, the brood cell is sealed by the workers, and larval development occurs independently of any posterior fluctuations in pollen supply (Michener 1974; Sakagami 1982).

Slowing down or even interrupting the production of new brood cells under unfavourable environmental conditions diminishes the use of stored pollen (Roubik 1982). However, it also results in a progressive decline in adult population. This, in return, reduces the consumption of the colonies' energy reserves. Thus, after several months of drought, it is possible to observe *M. subnitida* colonies comprising only a few dozen adults, yet still containing at least one or two pollen storage pots and several honey pots (Hrncir and Maia-Silva, unpublished data). The fact that these colonies recover rapidly as soon as the environmental conditions improve indicates that this bee species is capable of efficiently increasing brood production despite a strongly reduced workforce. Key to this population recovery may be an increased pollen load capacity of the workers at the end of the dry season. In *M. quadrifasciata*, workers from weak colonies were found to carry larger amounts of pollen per unit of body weight than workers from strong colonies (Ramalho et al. 1998). The consequent elevated pollen intake per worker in weak colonies may facilitate the increase in brood production and, thus, colony recovery after long periods of dearth (Ramalho et al. 1998).

Colony aestivation: a key to survival in tropical dry forests

The superorganism concept regards social insect colonies in analogy to individual organisms concerning their organization and evolutionary principles, where groups of interdependent units (insects, cells) cooperate to propagate their genes (Seeley 1989; Moritz and Southwick 1992; Hölldobler and Wilson 2009). The survival and reproductive success of the superordinate unit (colony, organism) relies on the coherent functioning of its subunits (Moritz and Southwick 1992). In line with this view, we can compare stingless bee colonies in tropical dry forest environments to animals that enter a dormant state in response to environmental stress. During dormancy, activity of animals is minimal, and their metabolic rate is reduced to a low level (Withers and Cooper 2010). Although dormancy is frequently associated with hibernating animals in cold temperate climate zones, hypometabolic states also are an important survival strategy for amphibians inhabiting tropical arid and semi-arid environments (Carvalho et al. 2010). During aestivation, these animals sharply reduce their energy expenditure so that supplies may last over the dry period, which, sometimes, may encompass more than a year (Carvalho et al. 2010). Because aestivation in amphibians in semi-arid regions occurs under unpredictable rain patterns, environmental cues, such as increasing levels of soil water potential in response to rainfall, are important for fine tuning the emergence in aestivating amphibians (Tracy et al. 2007). However, endogenous rhythms may play an equally important role, given that aestivating females need to prepare their ovaries prior to the onset of the rains to guarantee reproductive success during the short rainy season (Carvalho et al. 2010).

So far, nothing is known about the contribution of endogenous rhythms to the survival and reproductive strategy of *M. subnitida* or other stingless bees native to tropical dry forests. In any case, colonies should anticipate the end of a dry season and accelerate their brood production rate in time to profit maximally from the increase in floral resource availability. Given that brood development time in *M. subnitida* is more than 35 days (Koedam et al. 2005), colonies would need to boost brood production at least 1 month prior to the onset of the main blooming season in the Brazilian tropical dry forest. Physogastric queens have little influence on this process (Ribeiro 2002). Rather, it is the workers that control the brood production rate by stimulating queens to increase her oogenesis through feeding and increasing brood cell construction (Wheeler 1996; Ribeiro 2002). Environmental cues that may trigger this anticipating boost in brood production are the increase in relative humidity together with initial, light rains at the beginning of the rainy season (Maia-Silva et al. 2015). Thus, in analogy to aestivating amphibians, who increase their metabolic investment prior to emergence (Carvalho et al. 2010), *M. subnitida* colonies presumably increase their brood production rate, using up their remaining food reserves, as soon as they experience the first rainfall. The time lag until the emergence of the new workers is largely compensated for by delays in blooming. Although plants in the Brazilian tropical dry forest react quickly to changes in precipitation, flowering of herbaceous species initiates several days to weeks after the initial rainfalls (Lima et al. 2007), while that of trees may delay even up to 3 months (Machado et al. 1997; Lima and Rodal 2010).

Income breeding, the rapid translation of elevated food abundance into reproductive output, is an adaptive strategy of aestivating animals to optimise their reproduction after extended drought periods (Winnie et al. 2006). In *M. subnitida*, analogously, the production not only of workers but, more importantly, of sexual offspring increases with a gain in food reserves (Koedam et al. 2005). Gynes in *Melipona* species are usually produced all year round (Sakagami 1982; Engels and Imperatriz-Fonseca 1990). The proportion of fertilized eggs that turn into potential queens, between 5 and 20%, is independent of food storage conditions (Koedam 1999; Koedam et al. 2005; Velthuis et al. 2005). Consequently, the increase in gyne number in the rainy season is a by-product of the general gain in female brood under elevated pollen store conditions (Roubik 1982; Velthuis et al. 2005; Maia-Silva et al. 2015). The increase in male production in *Melipona* colonies, by contrast, is mainly due to an elevated laying rate of unfertilized eggs by workers as soon as resource conditions improve (Koedam 1999; Van Veen et al. 2004). In any case, the elevated food supply in the rainy season translates directly into sexual offspring in *M. subnitida* (Koedam 2005), therewith increasing the chances of colony reproduction after several months of aestivation.

The reduction in brood production and adult activity over the dry months reduces considerably the nutritional demands of stingless bee colonies, therewith saving food reserves for colony reactivation at the end of the dry season. A major problem with this strategy, however, is the repeated occurrence of supra-annual droughts in the Brazilian tropical dry forests (Marengo et al. 2017). Owing to the reduced food offer through several years, colonies remain in their state of conservative brood production over extended periods of time, resulting in a progressive population decline down to the point of no return. This, in fact, might be the principal obstacle for stingless bees to colonize tropical dry forests. Here, the capacity of *M. subnitida* to re-establish fully functional colonies from nests containing only few dozens of workers through a quick reaction to precipitation-driven increase in resource availability may give this meliponine species the necessary competitive edge.

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