

# Daily Dynamics of an Ant Community in a Mountaintop Ecosystem

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## Abstract

Abiotic conditions have a great influence on the structure of biological communities, especially considering ectothermic organisms, such as ants. In this study, we tested whether the daily temporal dynamics of an ant community in a tropical mountainous ecosystem is driven by daily fluctuations of abiotic factors, such as temperature and humidity. We also investigated whether the strong oscillation in daily temperature leads to high heterogeneity in ant species thermal responses. We have found that air and soil temperatures positively influenced the richness and frequency of foraging ants, while air humidity caused the opposite effect. Ant activity followed daily temperature fluctuations, which resulted in subtle differences in foraging patterns featured by heat-tolerant and heat-intolerant species. Moreover, the studied ant community exhibited broad and highly overlapped thermal responses, suggesting a likely resilience under temperature oscillations. Lastly, identifying how species traits are linked to oscillations in abiotic conditions is a necessary step to predict the effects of future climatic changes on biological community dynamics and ecosystem functioning.

**Key words:** *Campo rupestre*, climate change, temperature, thermal niches, thermal responses

The evaluation of ecological processes involved in the structure and dynamics of biological communities is still considered one of the great challenges of contemporary ecology (McGill et al. 2006, Laliberte et al. 2009, Wittman et al. 2010). A pivotal goal of ecology is to predict changes in community abundance and richness in response to environmental changes, such as climate change and global warming (Kaspari et al. 2019). Recent evidence has revealed the importance of abiotic variables as drivers that modulate the structure and dynamics of biodiversity at different spatial and temporal scales (Lessard et al. 2009, Bishop et al. 2014, Cardoso and Schoederer 2014). For example, the influences of abiotic factors in the daily and seasonal activity patterns of thermally constrained species such as ants are well documented (Calosi et al. 2007, Hoffmann et al. 2013, Diamond et al. 2016). In fact, temperature (Cerdá et al. 1998, Lessard et al. 2009, Arnan et al. 2015), humidity (Kaspari and Weser 2000, Nondillo et al. 2014), and precipitation (Kaspari 1993) are among the main predictors of ant diversity and activity, on both local (e.g., Bujan et al. 2016) and global scales (e.g., Gibb et al. 2015).

Considering the strong dependence of ants on the environmental temperature, it is known that different species have specific thermal responses and tolerances to temperature fluctuations (e.g., Arnan et al. 2015, Boulay et al. 2017). This thermal specificity may reflect

different foraging strategies (Cros 1997, Cerdá et al. 1998). For instance, to avoid stressful temperatures, the activity of some ant species may be restricted to specific periods of the year or day which are thermally suitable (Narendra et al. 2010, Jayatilaka et al. 2011, Fitzpatrick et al. 2014). In fact, the thermal response of ants under climatic fluctuations has been explored (e.g., Cerdá et al. 1998, Lessard et al. 2009, Kaspari et al. 2015). However, most studies have been conducted in temperate regions, in which seasonal patterns strongly differ from those of tropical environments (e.g., Pie 2016), where still there is little evidence (but see Fagundes et al. 2015, Costa et al. 2018). Furthermore, most studies are based on predictions of theoretical data modeling (e.g., Dunn et al. 2009, Gibb et al. 2015), while empirical evidence is still scarce.

Mountainous ecosystems can be ‘natural laboratories’ to test the influence of abiotic factors on the structure and dynamics of biological communities (Sanders et al. 2007, Sundqvist et al. 2013). In general, the daily climatic conditions in mountaintop environments fluctuate widely in a relatively small geographic area (Körner 2007), allowing extrapolations to different spatial and/or temporal scales (Bishop et al. 2014). The *campo rupestre* is a mountainous tropical ecosystem that is thermally stressful in terms of a high incidence of UV light, strong daily and seasonal temperature variations, and

heavy winds (Giulietti et al. 1997, Fernandes et al. 2016, Silveira et al. 2016). It is an extremely diverse ecosystem with a high endemism and diversity of plants (Fernandes et al. 2016), as well as great ant diversity (Costa et al. 2015). However, the *campo rupestre* has been subjected to several anthropogenic pressures and overlooked by public policies related to its conservation (Silveira et al. 2016), and the threatening of habit loss is magnified due to their restrict geographical range size. Furthermore, climatic predictions estimate that by the end of the century, these rocky environments will lose up to 95% of their total area (Fernandes et al. 2016).

Here, we assessed how the daily temporal dynamics of an epigeal ant community is affected by daily fluctuations of abiotic conditions of *campo rupestre*. First, we tested whether the daily (i.e., 24 h) fluctuations in air temperature, soil surface temperature, and relative air humidity affect the richness and foraging activity of ant fauna, as they are considered good predictors of ant diversity and distribution (Kaspari and Weser 2000, Kaspari et al. 2015). Then, we tested whether the daily temperature oscillations predict the thermal variability of epigeal ant species, as ecosystems with high thermal amplitudes might provide distinct thermal niches for species with different thermal preferences (Arnan et al. 2015, Bishop et al. 2017).

## Methods

### Study Site

We conducted the study in areas of *campo rupestre* located at the Serra de Ouro Branco State Park (20°31'S, 43°41'W) in Minas Gerais State, southeastern Brazil. The Brazilian *campo rupestre* is a megadiverse tropical ecosystem that occurs at altitudes above 900–2,000 m (Alves et al. 2014). It is characterized by a mosaic of vegetation (Silveira et al. 2016) composed mostly of grasslands and shrubs associated with quartzite rock outcrops, poor nutrients, and sandstone soil (Silveira et al. 2016). Additionally, this environment is considered a fire-prone ecosystem, wherein the ant fauna nests in natural cavities of exposed rocks and plants (Fagundes et al. 2015, Costa et al. 2018). The climate regime is mesothermic (Cwb) according to Köppen's classification, with humid summers and dry winters (Alvares et al. 2013). The warmest month is February and the coldest is July. The average annual temperature is 20.7°C and rainfall is around 1,188 mm (data provided by Gerdau-Açominas weather station, placed at 15 km from the studied area).

### Sample Design

We selected three areas of *campo rupestre* (20°50'S, 43°65'W; 20°49'S, 43°66'W; 20°49'S, 43°67'W) that are similar to each other in terms of its vegetational structure (composed mostly by grasses, shrubs, and forbs) and altitude (from 1,250 to 1,350 m a.s.l.). The minimum distance between areas was 1.5 km and the maximum was 5 km. We sampled each area three times during the rainy season, from February to April 2018.

We sampled the epigeal ant fauna using unbaited pitfall traps. The pitfall consisted of a plastic recipient of 77 cm in height and 119 cm in diameter, partially filled with a killing solution comprised of salt, water, and detergent (Cardoso et al. 2010). In each sampling area, we delimited three transects of 100 m, distant from each other by 50 m. In each transect, we installed 10 pitfalls placed at 10 m apart, totaling 30 pitfalls per sampling area.

Before starting our monitoring, over 24 h, we measured the air temperature and humidity with a *datalogger* (mod. 171-DT) positioned 1 m aboveground. The soil temperature was recorded by a chemical thermometer (Incoterm 5005) buried 5 cm belowground.

This preliminary pilot experiment indicated that the abiotic conditions in the study area significantly changed in intervals of 3 h. So, in each sampling day (i.e., 24 h continuous), the pitfalls were monitored eight times in intervals spaced by 3 h, as it represents periods of significant abiotic conditions changes (according to the pilot experiment). In each sampling period, every pitfall was collected, stored, tagged, and replaced with a new killing solution. Hence, to evaluate the influence of abiotic variables fluctuation on richness and foraging activity of ants, we sampled each area three times on three different days (spaced by a minimum interval of 15 d and a maximum of 26 d, all of them during the rainy season).

Thus, pitfall exchange and abiotic variables were monitored from 09:00 h (a.m.) to 06:00 h (a.m.) of the following day in eight periods spaced by 3 h (i.e., 09:00, 12:00, 15:00, 18:00, 21:00, 00:00, 03:00, and 06:00 h). Ants were identified to the lowest taxonomic level as possible using taxonomic keys and genera review articles (compiled in Baccaro et al. 2015). Species identification was confirmed by the taxonomist Dr. Rodrigo Feitosa from the Universidade Federal do Paraná (UFPR), and specimens were deposited in the Laboratório de Genética Evolutiva e de Populações of the Universidade Federal de Ouro Preto (UFOP), Brazil. All permissions for collecting biological data were authorized by the Instituto Estadual de Florestas (IEF—License #079-2017, SISBIO 59834-1).

### Data Analysis

To evaluate whether the daily oscillation of abiotic conditions influences ant species richness and foraging activity, we built generalized linear mixed-effects models (GLMMs), using 'glmer' package for non-normal data and 'lmer' package for normal data. We considered air temperature, soil temperature, and relative air humidity as predictor variables of fixed effects and the transect varying on the intercept as the random effect (1 | transect). We used the mean records of abiotic conditions registered during each sampling period (spaced by 3-h interval) in each sampling day. Therefore, we evaluated the effect of each abiotic variable in separate models due to their high correlation (Supp Table 1 [online only]). As response variables, we considered the accumulated ants' species richness and frequency sampled in each transect (taking 10 pitfall traps as sample unit) in each sampling period. Thus, the complete data set consisted of nine transects (three per area), monitored at 8 day-periods, in three distinct days, totaling 216 records.

Additionally, we evaluated whether the studied ant species were good indicators of abiotic conditions registered in the day-period in which they were sampled. For this, we used the method of species Indicator Value (IndVal) (Dufrene and Legendre 1997). To determine if a species can be a good indicator, we built an occurrence matrix of each ant species sampled in every day-period. The IndVal ranges from 0 (no indication | specificity) to 1 (high indication | specificity). Thus, species with IndVal above 70% were considered with high specificity, species with IndVal between 45 and 70% were considered detector species, and species with values below 45% were considered species without any specificity for the climatic conditions during the day-periods they were sampled. Detector species were those that could forage in any other day-period if there was any change in abiotic conditions (McGeoch et al. 2002).

Finally, to assess whether daily temperature fluctuations predict the variability of ant thermal responses, we built a thermal niche model (Kühse and Blüthgen 2015). In this analysis, we considered the frequency of occurrence of each species (per transect) and associated these frequencies with the mean air temperature of the period in which they occurred. This weighted approach accounted for the

relative temperature preferences, such as the accuracy (number of observations per temperature), to characterize each species' thermal niche. Hence, the thermal optimum of each species was computed from the weighted average temperature of each species occurrence (i.e., the temperature recorded during the day-period of sampling). To determine the thermal niche breadth of each species, we calculated the weighted standard deviation of the mean temperature. To test whether the foraging activity of each species corresponded to the air temperature in which they were observed, we implemented a null model to estimate the expected thermal response for each species at random temperatures to determine whether it could occur on every transect with the same likelihood in all periods, regardless of the temperature. From the observed optimum thermal and the estimated optimum, we observed whether the species foraging activity significantly deviated from the field sampling conditions. Thus, we performed 1,000 randomizations to calculate how often the expected thermal niche was larger or smaller than the observed temperature for each species activity ( $\alpha = 5\%$ ) (see Costa et al. 2018 for a comparable approach under seasonal variations in temperature).

All statistical analyses were performed using the statistical program R (R Development Team 2018).

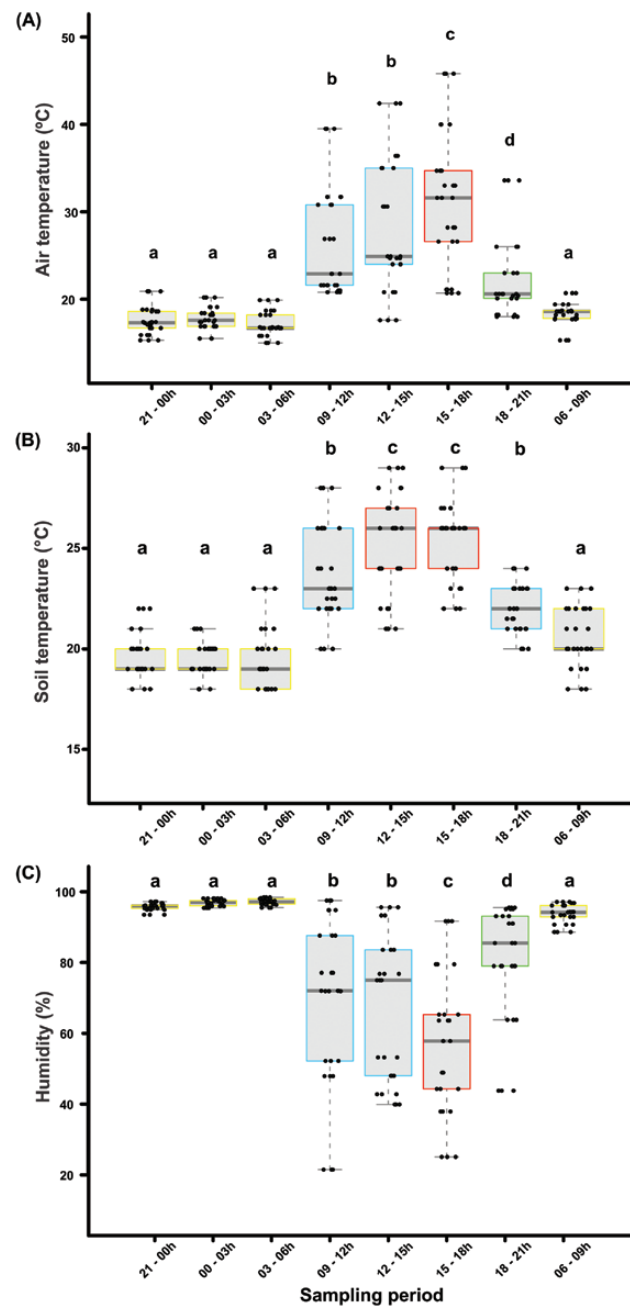
## Results

We sampled 39 ant species from 24 genera and seven subfamilies (Fig. 2). The most representative subfamily was Myrmicinae with 51% species, followed by Formicinae (23%), Dorylinae and Ponerinae (6.9%), Dolichoderinae and Ectatomminae (4.6%), and Pseudomyrmicinae (2.3%). The richest genus was *Camponotus* Mayr (Hymenoptera: Formicidae) (six species), followed by *Pheidole* Westwood (Hymenoptera: Formicidae) (four species). *Eciton* Latreille (Hymenoptera: Formicidae), *Pseudomyrmex* Lund (Hymenoptera: Formicidae), and *Pogonomyrmex* Mayr (Hymenoptera: Formicidae) were the less sampled genus, with only one species each.

The mean air temperature registered during the study was 22.6°C, ranging from a minimum of 15°C to a maximum of 45°C. The observed mean soil temperature was 21.6°C (minimum 11°C, maximum 29°C). For air humidity, we recorded a mean of 81.8% with a minimum of 21.5% and a maximum of 98.4%. Air temperature ( $F = 35.06$ ,  $df = 7$ ,  $P < 0.001$ ), soil temperature ( $F = 43.13$ ,  $df = 7$ ,  $P < 0.001$ ), and relative air humidity ( $F = 34.11$ ,  $df = 7$ ,  $P < 0.001$ ) significantly fluctuated throughout the sampling periods (24 h continuously). The variation of abiotic conditions per day-period and statistically different groups are shown in the Fig. 1.

We have found that the studied abiotic conditions affected the daily temporal dynamics of the epigeal ant community. Increases in air temperature positively influenced ant species richness ( $F = 75.11$ ,  $df = 1$ ,  $P < 0.001$ ) and species frequency ( $F = 20.178$ ,  $df = 1$ ,  $P < 0.001$ ) (Fig. 1). Similarly, soil surface temperature positively affected species richness ( $F = 66.091$ ,  $df = 1$ ,  $P < 0.001$ ) and species frequency ( $F = 18.077$ ,  $df = 1$ ,  $P < 0.001$ ). In contrast, the relative air humidity negatively affected the richness ( $F = 85.8$ ,  $df = 1$ ,  $P < 0.001$ ) and frequency of ants ( $F = 24.273$ ,  $df = 1$ ,  $P < 0.001$ ) (Fig. 2).

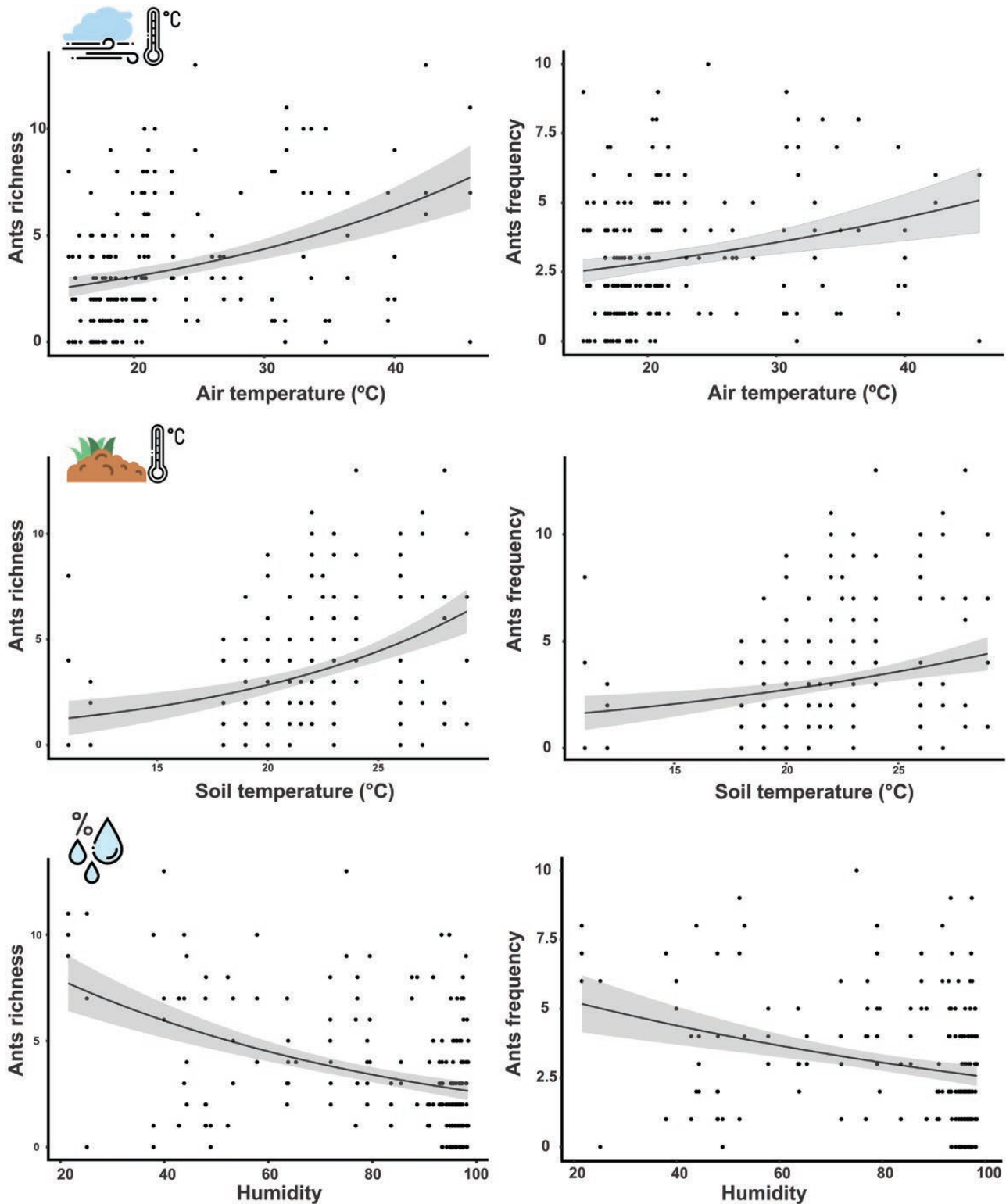
The IndVal analyses showed that most ant species (83.7%) were not specific to the sampling period in which they mostly occurred (i.e., IndVal < 45%) (Fig. 3). Only two species (4.6%) exhibited high specificity for a particular day-period: *Camponotus* sp. 1 and *Camponotus* pr. *scipio* Forel (Hymenoptera: Formicidae) (Fig. 3). Five species (11.6%) were identified as detector species (i.e., IndVal equal to or greater than 45%): *Ectatomma permagnum* Forel (Hymenoptera: Formicidae), *Mycocepurus goeldii* Forel (Hymenoptera: Formicidae), *Camponotus* pr. *personatus* Emery (Hymenoptera: Formicidae),



**Fig. 1.** Abiotic factors measured during the sampling periods. The horizontal line in the box represents the median ( $\pm$ SD) values of the air temperature (A), soil surface temperature (B), and relative air humidity (C) for each sampling period. Different letters above bars and colors indicate similar statistically day-period for abiotic conditions evaluated. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

*Dorymyrmex* sp. 1 Mayr (Hymenoptera: Formicidae), and *Pheidole radoszkowskii* Mayr (Hymenoptera: Formicidae) (Fig. 3).

Altogether, the studied ant community exhibited an thermal optimum of 22.4°C and a niche breadth that ranged from 18°C (*Wasmannia lutzi* Forel [Hymenoptera: Formicidae]) to 45°C (*Pheidole* sp. 3) ( $SD \pm 7.14^\circ C$ ) (Fig. 4, indicated by vertical and horizontal dashed lines, respectively). Most species (74.4%) had thermal responses that corresponded to the average thermal niche of all species sampled (Fig. 4, horizontal dashed line), indicating that the studied community has broad thermal responses with a high level of



**Fig. 2.** Relationship between abiotic factors and the richness and frequency of ant species from *campo rupestre*. The points represent the local mean values in each sampling period. The gray curves are the confidence intervals of the dependent variables. The curves were fitted with parameters from GLMM models.

overlap. Five ant species (11.6%) were more active at lower temperatures than the community average (Fig. 4, blue points in left part of vertical dashed line), and six species (13.90%) were more active at higher temperatures, i.e., above the community average (Fig. 4, red points in the right part of vertical dashed line).

## Discussion

In this study, we demonstrated the direct effect of climatic conditions on the daily dynamics of an ant community present in a mountainous tropical ecosystem. We have found that increases in air and soil temperature positively affected the richness and foraging activity



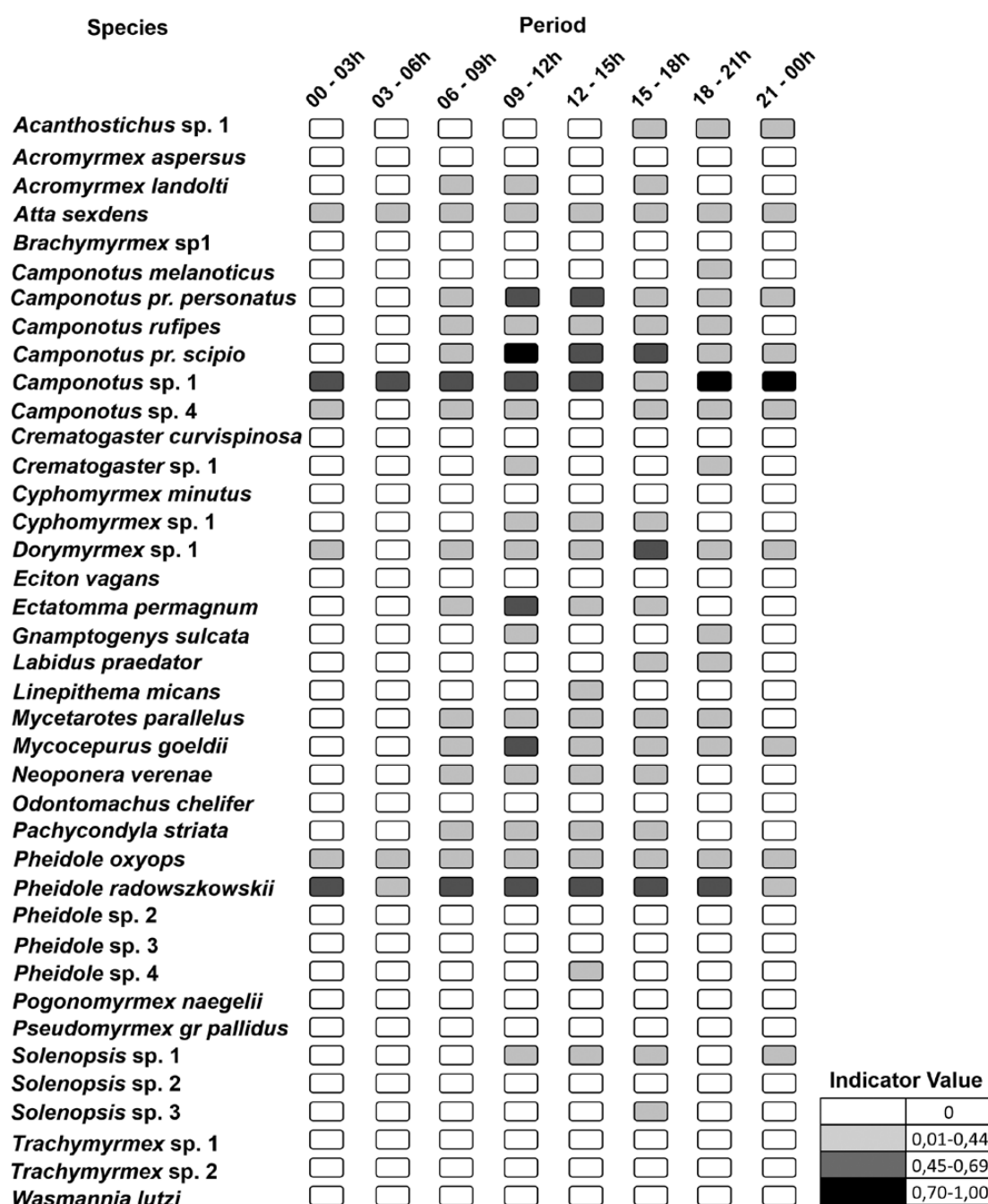
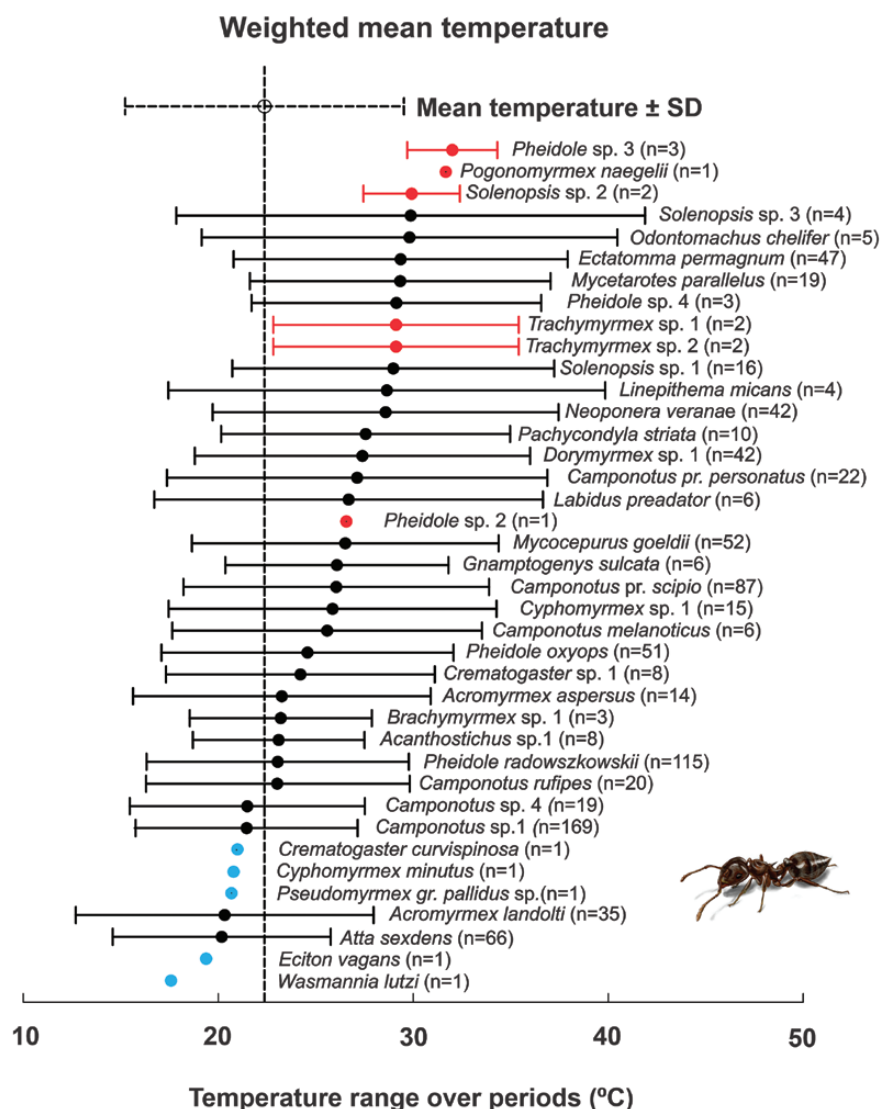


Fig. 3. Indicator value results showing ant species specificity according to day-period in which they occurred. The color intensity indicates the degree of ant specificity in each day-period. White represents no specificity for the sampling period. Light gray indicates a low specificity for the sampling period (IndVal < 45%). Dark gray represents 'detection' for the sampling period (IndVal values between 45 and 70%), and black suggests high specificity for the sampling period (IndVal > 70%).

of ants, while the humidity had an opposite effect. Our results suggest that despite the strong daily amplitude of abiotic conditions in the *campo rupestre* (see Fig. 1), the studied ant community exhibited broad and highly overlapping thermal responses, indicating a likely tolerance of this ant community under climatic fluctuations. Furthermore, the studied ant community presented low specificity for the daytime period, indicating that the daily amplitude of abiotic conditions in the *campo rupestre* does not restrict ant species occurrence.

In the tropics, seasonal temperatures vary slightly but widely fluctuate throughout the day (Ghalambor et al. 2006, Esch et al. 2017).

Here, we have observed that local climatic conditions vary strongly over a day, a similar pattern already registered for other regions in the same ecosystem (Fernandes et al. 2016, Costa et al. 2018). In fact, the maximum daytime air temperature and the minimum nighttime air temperature ranged by approximately 30°C. Likewise, we registered large daily amplitudes for soil temperature (ca. 18°C) and air humidity (ca. 77%). These findings reaffirm the stressful conditions imposed by local climatic factors that may impose differences in the physiological responses and foraging strategies of associated organisms (Sheriff et al. 2012, Sunday et al. 2014, García-Robledo et al. 2018).



**Fig. 4.** Thermal response of the ant community from the *campo rupestre*. The points indicate the thermal optimum where each species occurred, i.e., the mean temperature in which each species occurred. The horizontal dashed lines represent the weighted standard deviations of temperature in which each species occurred (niche breadth). Species in red are more heat tolerant, while species in blue prefer lower temperatures than the average sampled during the study. The numbers after species names (*n*) represent the number of different temperatures in which each species was sampled, i.e., occurrence in transects monitored at distinct temperatures. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

Indeed, the high daily range of climatic conditions in the studied *campo rupestre* influenced the richness and foraging activity patterns of epigeic ant species. The community showed greater richness and foraging activity in daytime periods that coincided with periods of highest temperature, followed by decreased activity after twilight and nighttime. This positive effect of temperature may indicate some tolerance of ants to handle higher temperatures. Moreover, our results indicate that the studied ant fauna do not show preferences for foraging in specific periods during the day (see Fig. 3). Thus, despite the high daily amplitude of abiotic conditions in the *campo rupestre*, temperature ranges did not constrain the occurrence and activity of ground foraging ants. The inclined tolerance of ants under climatic fluctuations has already been documented for ants foraging on the vegetation throughout seasonal oscillations in abiotic conditions (Costa et al. 2018). It is worth mentioning that the increased activity of ants under temperature and precipitation enhances may have a maximum tolerance limit that once achieved, may prompt to descendent physiological performances reducing ants' growth and survival (Kaspari et al. 2019).

We have found low variability in ant fauna thermal responses, as most species exhibited broad and highly overlapping thermal niches. This low variability of thermal responses suggests that this diverse ant community has similar physiological performances, being able to forage in a broad spectrum of temperature throughout the day. The thermal niche of organisms may determine their susceptibility to climate warming (Diamond et al. 2012, Nelson et al. 2018). The broad and overlapped thermal response of *campo rupestre* ants, associated with the positive effect of temperature on ant diversity suggests that this community is likely able to track certain temperature increases (Arnan et al. 2015, Kaspari et al. 2019). A recent study found similar results wherein ants' activity tracked temperature seasonality variation, likely being able to endure climatic fluctuations (Costa et al. 2018). Combined, these findings indicate that *campo rupestre* ants' paths in a warming scenario are somewhat predictable. Alternatively, we must consider a thermal performance limit that might predicts nonlinear increases in ants' diversity, followed by declined performances after to a certain point of heating (Kaspari et al. 2019).

Overall, our study points that daily variations in abiotic conditions in a mountainous tropical ecosystem shape the temporal dynamics of an epigenic ant community. Daily fluctuations in air temperature, soil temperature, and humidity in the *campo rupestre* modulated the richness and foraging activity of ants. As already known, climatic conditions can be considered determinant factors that drive the distribution and dynamics of organisms (Gibb et al. 2015 and references therein). Our study provides evidence that the studied ant community can be widely tolerant with respect to temperature, corroborating other studies that suggest a potential resilience of ants under environmental changes (see Costa et al. 2018, for temperature and fire, and Kaspari et al. 2019, for temperature). But it is important to note that we tested the thermal responses of ants with respect to local air and soil temperature in a controlled altitudinal range (i.e., 100 m). As follows, we must be careful to infer on the tolerance, resilience, and adaptability of ants to environmental heating, processes that would be even stronger in altitudinal shifts (Kinzner et al. 2019). The understanding of climate influence on organisms' distribution has important implications for species persistence in a warming world. In this context, further assessments of species thermal tolerances are fundamental, as they allow the comprehension of organisms adaptability toward climate change, the consequences for the services they provide and subsequent ecosystem functioning.

## Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

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