



High Temporal Beta Diversity in an Ant Metacommunity, With Increasing Temporal Functional Replacement Along the Elevational Gradient

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Ecological communities vary considerably in space and time and understanding such changes has fundamental relevance for ecology and conservation sciences. Mountains provide an excellent scenario for studies addressing spatial and temporal variation, as they vary in conditions and resources in a small geographic region. Here, we aimed to understand the patterns of variation in ant metacommunity composition across time and along an elevational gradient in a tropical mountain, focusing both on the taxonomic and functional facets of diversity. We used a β -diversity metric and broke it into nestedness and turnover to estimate short-term temporal changes in ant metacommunity composition. We tested the following hypotheses: (i) taxonomic and functional temporal β -diversity increase along the elevational gradient and (ii) turnover is the main component driving taxonomic temporal β -diversity and nestedness for functional temporal β -diversity. Rejecting our first hypothesis, we found that both taxonomic and functional temporal β -diversity did not increase with elevation. Yet, the values were always high, indicating that both species and functional traits are highly variable over time. In accordance with our second hypothesis, we found that turnover was the main component of taxonomic β -diversity. Yet adding complexity to our hypothesis, the contribution of nestedness to functional β -diversity decreased with increasing elevation. These results suggest that at low elevations, the turnover in species composition may then cause changes in trait composition because of the loss of some traits, yet preserving the most common functions (nested functional communities), while at high elevations functional capabilities may change over time (turnover of traits). In the context of global warming, where tropical mountain insects are expected to change their distributional range upwards, it is extremely important to consider the importance of the turnover on the temporal variation in functional traits and functions of ant metacommunity at higher elevations.

Keywords: campo rupestre, metacommunity, beta-diversity, nestedness, species turnover, rupestrian grassland, traits, environmental instability

INTRODUCTION

Understanding how communities are structured in space and time has fundamental relevance in ecology and conservation science (Gaston, 2000; Sutherland et al., 2013). There is abundant evidence in ecological studies that the spatio-temporal patterns we see in nature cannot be disentangled (Schiesari et al., 2019), as individuals and species can move both through space and time, forming metapopulations (Levins, 1969) and metacommunities (Leibold et al., 2004). Knowledge of complex spatial metacommunity dynamics have been advanced by using diversity partitioning analyses (e.g., Bishop et al., 2015; Heino et al., 2015), that partition diversity into local (α), and regional (γ) components, as well as the change among local communities (β) (Crist et al., 2003). However, most studies of this kind are based on one or a few samples in time, creating a gap in our knowledge of the importance of temporal variation of individuals and species in the structuring of metapopulations and metacommunities (Datry et al., 2016; Ruhí et al., 2017). In a changing world (Lewis and Maslin, 2015), there is an urgent need to understand the spatial and temporal distribution of diversity and the underlying mechanisms of these patterns, so we can predict and mitigate the effects of global change on biodiversity, ecosystem functions, and associated services (e.g., Legendre and Condit, 2019).

Since the classic work of von Humboldt and Bonpland (1805), numerous studies have investigated species distributions and the underlying mechanisms of these patterns along spatial and environmental gradients (e.g., Peters et al., 2016). Mountains are central to these studies, because they have significant environmental gradients in a relatively small geographical area (Körner, 2007). The small spatial scale means that all regional species can potentially access the whole gradient, minimizing the effects of the kinds of dispersal limitations seen over larger geographical areas (Longino and Colwell, 2011). Yet, species distribution patterns vary along mountains, with most taxa showing a decline in diversity with increasing elevation and associated changes in species composition (Fernandes et al., 2016; Perillo et al., 2017; Mota et al., 2018; Li et al., 2019). In this context, β -diversity metrics are useful for understanding how species composition changes across habitats or elevations and also attempt to reveal the assembly mechanisms that drive these differences (Bishop et al., 2015; Castro et al., 2019). Differences in habitat and resource use among species determine the spatial structure and maintenance of the β -diversity in mountains, where species turnover among elevations is the dominant component driving taxonomic spatial β -diversity of plants (Mota et al., 2018), birds (Li et al., 2019), termites (Nunes et al., 2017), dung beetles (Nunes et al., 2016), ants (Castro et al., 2020), and benthic invertebrates (Castro et al., 2019).

The abrupt spatial and temporal environmental changes in mountains provide a good experimental setting to study spatio-temporal dynamics of metacommunities. However, most studies on patterns of species and community distributions in mountains focus on the spatial rather than on the temporal dimension (e.g., Fernandes et al., 2016; Lasmar et al., 2020). Yet, the temporal variation in climatic conditions can be just as strong

as the spatial variation, regulating plant resource availability and patterns of animal foraging in seasonal tropical systems (e.g., Basset et al., 2015; Costa et al., 2018; Novais et al., 2019). While the temporal variation in climatic conditions that is driven by seasonal variation could be similar to the variation found at different elevations in mountains (Rocha et al., 2016), it is less clear which drivers shape temporal β -diversity of communities on mountains. We have evidence that although spatial taxonomic diversity at the regional scale (γ -diversity) is mainly caused by differences in species compositions of local communities (β -diversity component), the functional regional diversity (γ -diversity) is mainly driven by patterns of local diversity (α -diversity component; species composition changes along the elevational gradient, but functions do not; Nunes et al., 2016; Castro et al., 2020). In contrast, there is a lack of information on how temporal variation structures communities that are subjected to different climatic conditions at different elevations, both taxonomically and functionally. In other words, we need to explicitly address how the temporal taxonomic and functional β -diversity within metacommunities vary in space, i.e., across the elevational gradient.

In this study, we explored the spatio-temporal dynamics of metacommunities in tropical mountains by investigating how communities respond to temporal variation in environmental conditions on an elevational gradient in south-eastern Brazil. We collected taxonomic and functional information on ant metacommunity quarterly over 3 years, totalling 12 temporal samplings at each of seven different elevations. We used ants (Hymenoptera: Formicidae) as a focal taxon, because they respond rapidly to changes in environmental conditions, both spatially (Castro et al., 2020) and temporally (Bishop et al., 2014) and perform important ecological functions such as nutrient cycling and seed dispersal (Farji-Brener and Werenkraut, 2017; Magalhães et al., 2018). We investigated how temporal taxonomic and functional β -diversity of ants vary along the elevation gradient and how turnover and nestedness contribute to overall temporal β -diversity. We tested the following hypotheses: (i) the temporal taxonomic and functional β -diversity increase with increasing elevation along the gradient (**Figure 1A**); and (ii) turnover is the main component driving taxonomic temporal β -diversity and nestedness for temporal functional β -diversity (**Figure 1B**). The first hypothesis predicts an increase in temporal β -diversity with increasing elevation because temporal variation in the environment is more pronounced at high elevations than at low elevations. Harsh climatic conditions, climatic instability, and lower resource availability (productivity) at higher elevations are therefore likely to favor higher taxonomic and functional variation of the metacommunity over time [e.g., Costa et al. (2018) for temporal variation in ant species activity among seasons]. With decreasing habitat heterogeneity and resource availability (e.g., during the dry season), we expect to find communities of ants with longer legs, since these communities would be composed mainly by generalist and predator species that usually walk longer distances to forage (Lenoir et al., 2009; Bishop et al., 2016; Fichaux et al., 2019). Accordingly, the communities would be composed mainly by

species with longer mandibles, usually found in omnivore generalist and predator species (Gibb and Cunningham, 2013; Bishop et al., 2015). In addition, in harsher environments or seasons, we would expect higher polymorphism in ant colonies, because this would help colonies to deal with temperature and humidity variation through labor division (Lenoir et al., 2009). The second hypothesis predicts a higher contribution of turnover than nestedness to temporal taxonomic β -diversity, following the spatial pattern found for mountain insects (Nunes et al., 2017; Perillo et al., 2017; da Silva et al., 2018). Moreover, it also predicts a lower contribution of turnover compared to nestedness for temporal functional β -diversity, with communities showing a functional redundancy over time, as demonstrated spatially for insects in mountains (Bishop et al., 2015; Castro et al., 2020).

MATERIALS AND METHODS

Study Area

The study was conducted in the southern part of the Espinhaço mountain range (Figure 2), in the permanent plots of the Long Term Ecological Research Project Campos Rupestres (PELD CRSC/CNPq Project) along a gradient of elevation in the Serra do Cipó region, Minas Gerais State, Brazil (19°22'01"S, 43°32'17"W) (Silveira et al., 2019). The region has marked wet and dry seasons, and the mean annual precipitation is 1,300–1,500 mm, while the mean annual temperature is 20°C (highland tropical Cwb Köppen climate) (Fernandes et al., 2016). The Serra do Cipó region comprises private areas under environmental protection (APA Morro da Pedreira) and a National Park under full protection (PARNA Serra do Cipó), as well as being part of the Espinhaço Range Biosphere Reserve (Domingues et al., 2011; Fernandes et al., 2018). At the study location, soil and vegetation are very heterogeneous, with the core landscape being a vegetation mosaic dominated by *campo rupestre* (rupestrian grassland) intermingled by quartzitic outcrops, surrounding forest patches, gallery forests, and mixing with dry forests and cerrado at the lower elevations (Fernandes, 2016; Silveira et al., 2016; Morellato and Silveira, 2018).

Sampling Design and Explanatory Variables

We distributed our sampling sites every 100 m of elevation on a gradient that ranged from 800 to 1,400 m a.s.l. (Figure 2). At each of these sampling sites, we used three 200 m long transects separated by at least 250 m, totalling 21 transects (three \times seven sampling sites). Within each transect, we placed five pitfall traps separated by 50 m (15 traps per sampling site, 105 in total for each temporal sampling) to collect ants foraging on the ground. Traps consisted of a plastic pot with a diameter of 14 cm and a depth of 9 cm, which was filled with 500 ml of a saline-detergent solution. The pots were set at ground level and covered with a plastic plate (20 cm from ground level) to prevent rain from entering the trap. All pitfall traps remained in the field for 48 h per survey (Bestelmeyer et al., 2000). We sampled quarterly (separated by 3 months), totalling 12 samples between April 2011

and January 2014 (January, April, July, and October); such that the samples spanned the beginning and end of both the wet and dry season each year. The transect represents independent sample replicates because the spacing of 50 m between samples is considered enough to avoid interference related to the foraging range of ants belonging to the same colony (Leponce et al., 2004) and we used five times this distance between transects. We pooled data from the five pitfall traps for each transect and each month (see Castro et al., 2020).

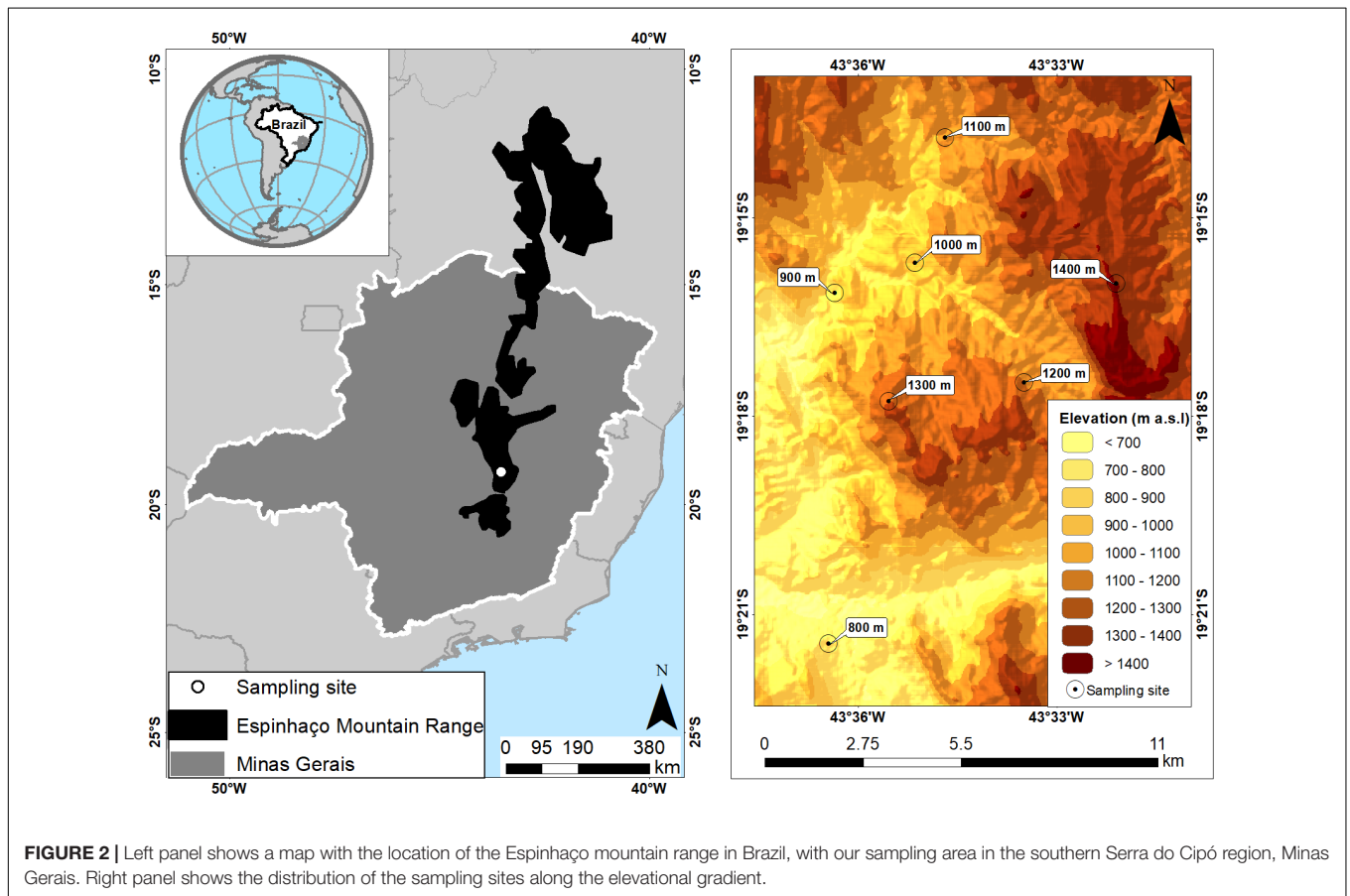
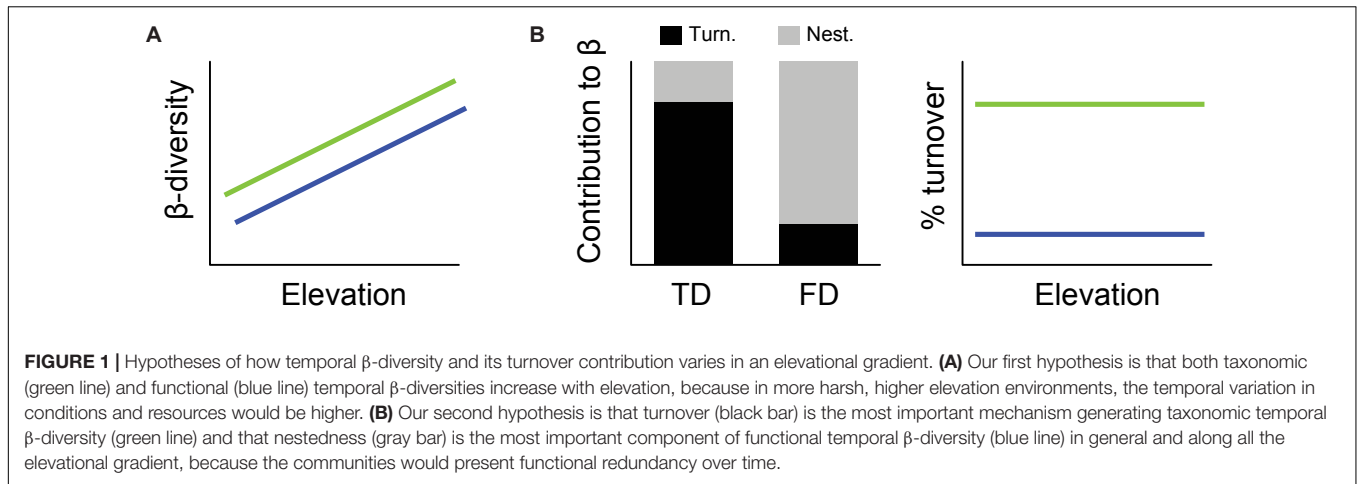
To explore the mechanisms behind the patterns we expected with our hypotheses, we accessed information on climatic and vegetation factors. For climatic factors, we used data from meteorological monitoring towers (equipped with the Onset HOBO® U30 data-logger) located at every 100 m of elevation, adjacent to the sampling sites of the PELD CRSC/CNPq Project (Silveira et al., 2019), between January 2012 and January 2014 (January, April, July, and October). We recorded air and soil temperature, humidity, and precipitation, and we calculated the mean and coefficient of variation of these variables for the whole sample period for each sample site (i.e., each elevation). We also used vegetation data from the same project at each elevation [see Mota et al. (2018) for more details] to assess the total plant richness per sample site.

Identification of Species and Definition of Functional Traits of Ants

To identify ants to species and morphospecies we used a comparison method with the Collection of Formicidae from *campo rupestre* of the Laboratory of Insect Ecology at the Universidade Federal de Minas Gerais, Brazil. In addition, all species were revised by experts of different ant taxa. Classifications were based on Baccaro et al. (2015) and Bolton's Ants of the World catalog (Bolton, 2020) classifications.

For all ant species collected, we measured key functional response traits related to diet, nesting ecology, foraging capacity, thermoregulation, and habitat association (Leal et al., 2012; Bishop et al., 2016; Paolucci et al., 2016; Tiede et al., 2017; Fichaux et al., 2019). Specifically, we quantified the following seven traits for each species: Weber's length, femur length, mandible length, predominant color (mesosoma), polymorphism, integument sculpture, and functional groups (six morphological traits and one ecological trait; Table 1).

Morphological measurements were taken following the guide for identification of functional attributes for ants (*The Global Ants Trait Database* – GLAD; Parr et al., 2017), with exception for the variable "color." This trait was obtained from the HSV color model using only the variable V (color brightness), as proposed by Bishop et al. (2016). However, we performed the capture of HSV values of the predominant color on the mesosoma of each specimen, in contrast to Bishop et al. (2016), who considered the predominant color between head, mesosoma, and gaster. Since functional traits are not normally distributed (Arnan et al., 2018; Fichaux et al., 2019), all continuous data, except Weber's length and color brightness, were divided by Weber's length to correct for individual body size.



Imaging was performed using Microscope Digital Camera LC30 OLYMPUS[®] mounted on a stereomicroscope SZ61 OLYMPUS[®]. Measurements were made with a digital capture micrometer (accurate to 0.01 mm) provided in the LC Micro 2.2 OLYMPUS[®] software. All measured specimens were selected at random from our dataset. When possible, at least six individuals were measured, and whenever it was not possible, we measured all the available individuals. Only minor workers were used, and a total of 2103 images

were captured from 701 individuals, with an average of 4.52 individuals per species. Categorical and ordinal morphological traits (i.e., polymorphism and integument sculpture) were attributed using genera/species information available at AntWeb¹ and AntWiki website² (Guénard et al., 2017) and from our own observations.

¹www.antweb.org

²www.antwiki.org

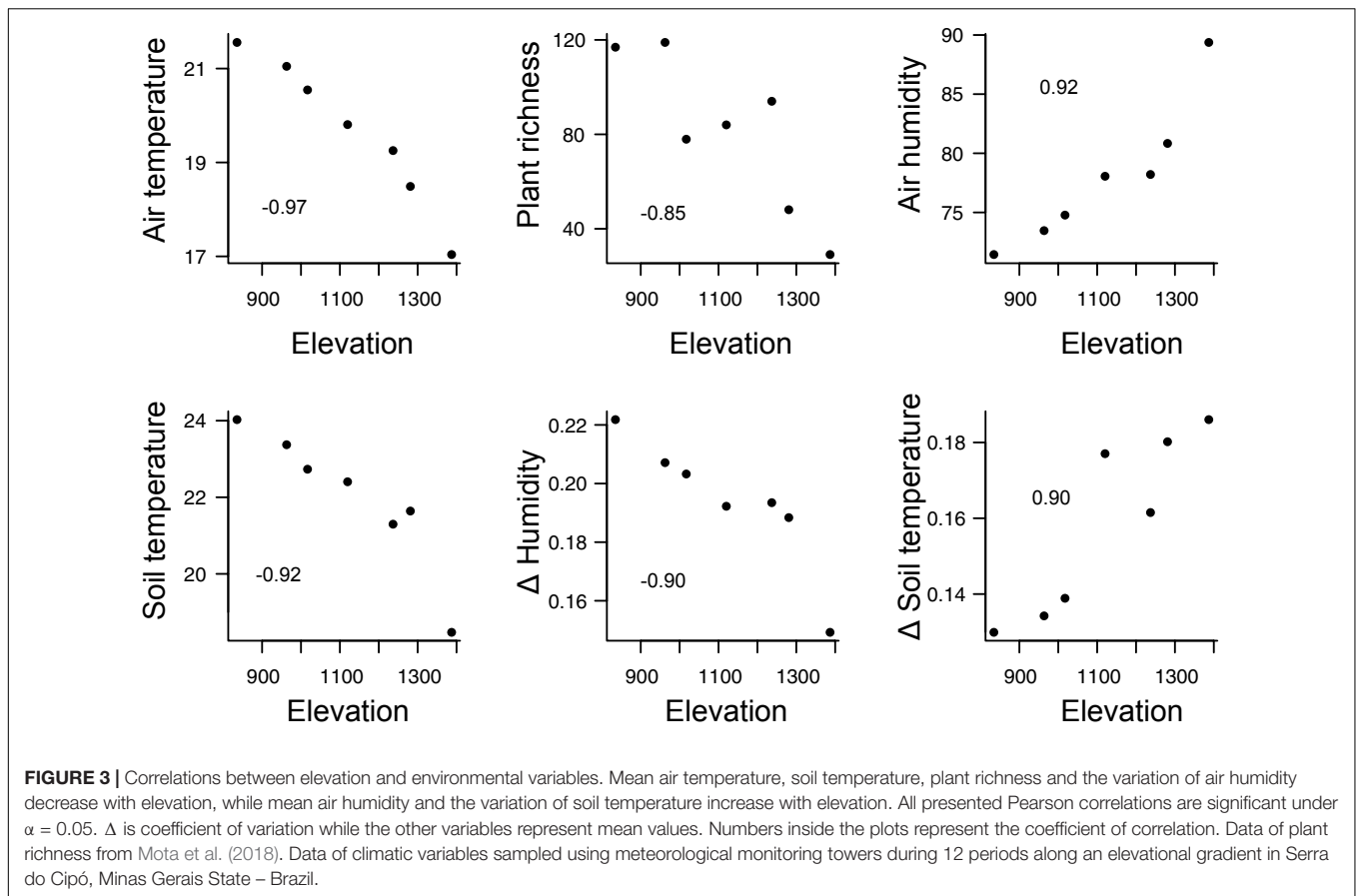
TABLE 1 | List of response functional traits measured (morphological and ecological), their hypothesized ecological functions and the expected response of the traits to environmental change.

| Traits | Measure | Abbrev. /Unit | Ecological functions | Expected response |
|-----------------------------|-------------|--|--|--|
| Morphological traits | | | | |
| Weber's length | Continuous | WL (μm) | Proxy for whole-length, related to metabolic characteristics (Weber, 1938; Kaspari and Weiser, 1999; Bishop et al., 2016). | As temperature decreases, we expect to find a community with larger individuals (e.g., Bishop et al., 2016). |
| Femur length | Continuous | HFL (μm) | Foraging speed indicator, related to habitat complexity (Feener et al., 1988; Yates et al., 2014). | Longer femur let ants move out rapidly, which allow then occurring in harsh environment conditions, as seen in seasonally flooded areas (Fichaux et al., 2019) or desert environments (Lenoir et al., 2009). |
| Mandible length | Continuous | ML (μm) | Diet's indicative (Brandão et al., 2009). Longer mandibles are associated with larger preys in predatory species (Gibb and Cunningham, 2013). | Due to the decrease in the complexity of the environment in the dry and cold season, we expect communities composed by species with larger mandibles; increase in predatory species frequency (e.g., Bishop et al., 2015). |
| Color (Mesosoma) | Continuous | V (%) * | Thermal melanism hypothesis (Trullas et al., 2007); Thermotolerance's indicative and, directly related to temperature variation and solar radiation (Bishop et al., 2016). | Dark ectothermic individuals have a benefit in cool climates compared to lighter ones (Trullas et al., 2007). We expected dark individuals in the dry and cold season (Bishop et al., 2016). |
| Polymorphism | Categorical | 1 = monomorphic; 2 = dimorphic; 3 = polymorphic | Workers' polymorphism, related to the ability to develop different tasks in the colony (e.g., protection, foraging, or activities inside the nest; Wills et al., 2017). | Due to harsh conditions found in mountains, we expect more polymorphic species, which could be able to make labour division at a different time of the day in response to daily temperature variation (Lenoir et al., 2009). |
| Integument Sculpture | Ordinal | 1 = cuticle smooth/shiny; 2 = superficial wrinkles/pits; 3 = surface heavily textured | Integument desiccation protection (Nation, 2008). Thickened cuticles enhanced the dehydration tolerance (Terblanche, 2012). | An intermediate tegument sculpture is expected, due to the lower temperatures during the dry season than the wet season, and due to the thermal amplitude commonly described in mountains between day and night. |
| Ecological trait | | | | |
| Functional Groups | Categorical | AA = Army Ants; AD = Arboreal Dominant; AP = Arboreal Predator; AS = Arboreal Subordinate; CO = Cryptic Omnivores; CP = Cryptic Predators; DD = Dominant Dolichoderinae; EO = Epigeic Omnivores; EP = Epigeic Predators; Hatt = High Attini; Latt = Low Attini; Opp = Opportunist; SC = Subordinate Camponotini SH = Seed Harvester. | Functional groups based on ants' global-scale responses to environmental stress and disturbance. Indicative of ecological tasks, like nesting, foraging, and diet habits (Andersen, 1995; Leal et al., 2012; Paolucci et al., 2016). All groups were based on the classification used by Paolucci et al. (2016). Exception for Seed Harvester group (Johnson, 2015) here represented by <i>Pogonomyrmex naegelli</i> , which was not present in this list. | |

Calculating Temporal β -Diversity

We calculated the variation of the taxonomic (TD) and functional (FD) composition of the ant community temporally using β -diversity (β_{SOR}) (Baselga, 2010). We used the data collected over the 12 sampling periods to calculate temporal TD and FD β -diversity for each transect (21 in total). We also partitioned TD and FD into the components derived from species turnover (β_{SIM}) and species gain/loss or nestedness (β_{SNE}). In this step, we partitioned β -diversity for the whole gradient and for each transect. In all β -diversity calculations, we used

Sørensen dissimilarity index based on a presence/absence species composition matrix. To calculate temporal functional β -diversity, we first generated a distance matrix of species based on their functional traits using the Gower Distance, a useful method for combining categorical and continuous traits (de Bello et al., 2013). We then used this distance matrix to construct a functional space, using Principal Coordinates Analysis (PCoA), which in turn was used to calculate temporal functional β -diversity. We used the "beta.multi" and "functional.beta.multi" functions of the package "betapart" to partition TD and FD β -diversity,



respectively (Baselga and Orme, 2012), in the software R (R Core Team, 2019).

Statistical Analyses

We ran Pearson correlation analyses with all the environmental variables against elevation using the “psych” R package (Revelle, 2017). As elevation was correlated with mean air and soil temperature, air humidity, plant richness and the temporal variation of air humidity and soil temperature (see details in section “Results”), we used elevation as a proxy for all these variables in our analyses. To test our first hypothesis, we ran linear mixed-effect models (LMMs), one with TD β -diversity as response variable and other with FD β -diversity (β_{SOR}), and both had elevation as an independent variable and sampling site as a random variable. To test our second hypothesis, we used the turnover contribution (β_{SIM}/β_{SOR}) as the response variable and also ran separate LMMs for TD and FD, with elevation as an independent variable and sampling site as a random variable. We checked for the error distribution and over-dispersion of the data. All statistical analyses were performed in R (R Core Team, 2019).

RESULTS

We recorded a total of 155 ant morphospecies (species hereafter), belonging to eight subfamilies and 49 genera. Myrmicinae was the

most representative subfamily with 25 of the identified genera, followed by Ponerinae (eight), Dolichoderinae (five), Dorylinae (four), and Formicinae (three). The subfamilies with the highest species richness were Myrmicinae (85 species), Formicinae (23 species), Ponerinae and Dolichoderinae (12 species each). These four subfamilies accounted for 85% of the species sampled. The genera with most species were *Pheidole* with 25 species, *Camponotus* 20 species, and *Solenopsis* with eight species. Across all samples, we recorded 13 doubletons and 23 singletons (23.2%).

We found that mean air and soil temperatures, plant richness, and coefficient of variation of air humidity were negatively correlated with elevation, whereas mean air humidity, and coefficient of variation of soil temperature were positively correlated with elevation (Figure 3 and Supplementary Table 1). That is, mean air and soil temperature, plant richness and the temporal variation of humidity decrease with increasing elevation, while air humidity and the temporal variation of soil temperature increase with increasing elevation (Figure 3). We also found that precipitation dropped from ~ 170 mm to close to 0, while mean air temperature dropped from 21.1 to 17.2°C in the beginning of the wet season to the beginning of the dry season, respectively (Figure 4). Air and soil humidity mirrored this pattern of decrease from the wet to the dry season (Figure 4).

The main driver of temporal taxonomic β -diversity was the turnover component (β_{SIM}) with 86% of contribution. In contrast, nestedness (β_{SNE}) was the main component to temporal

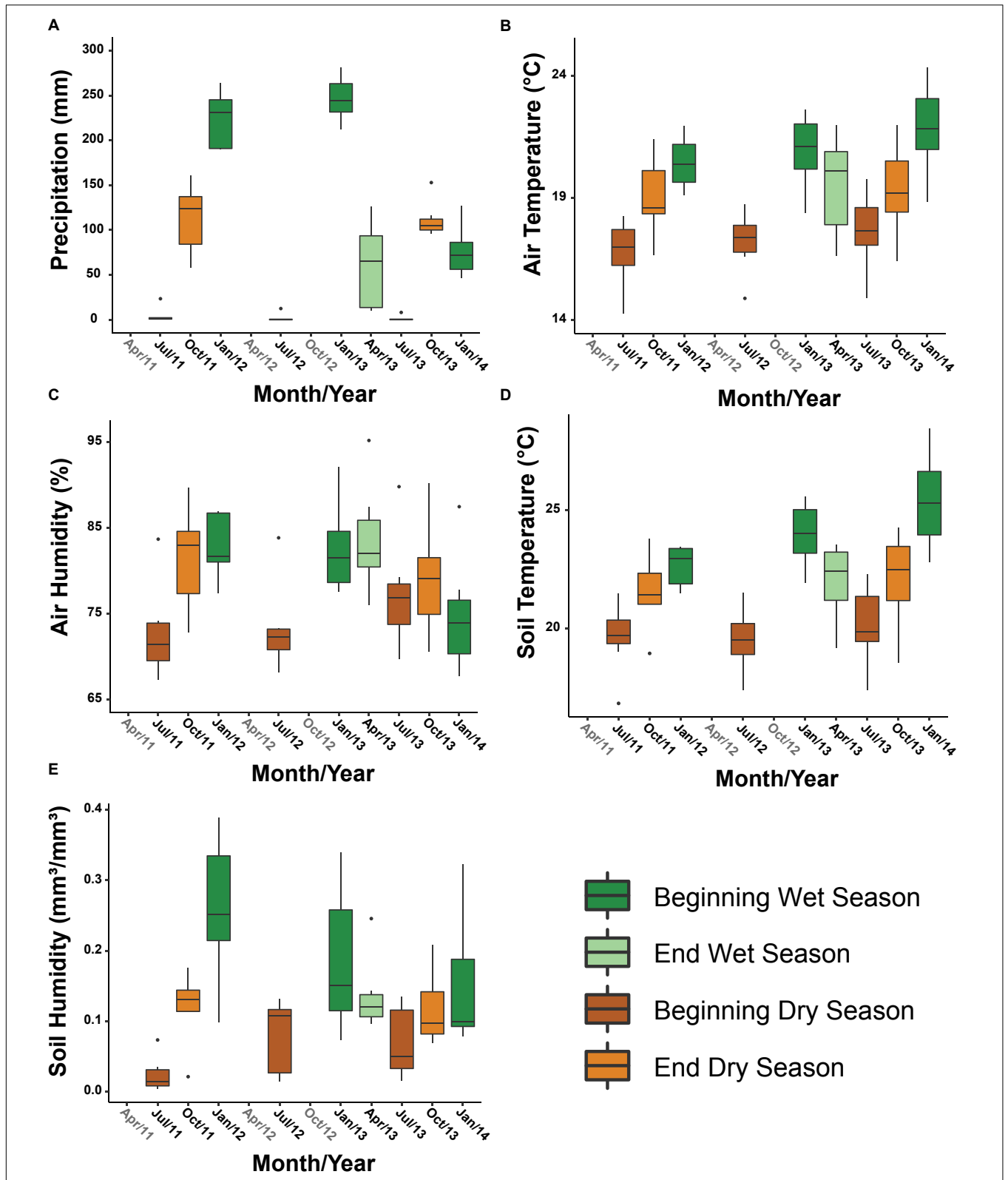
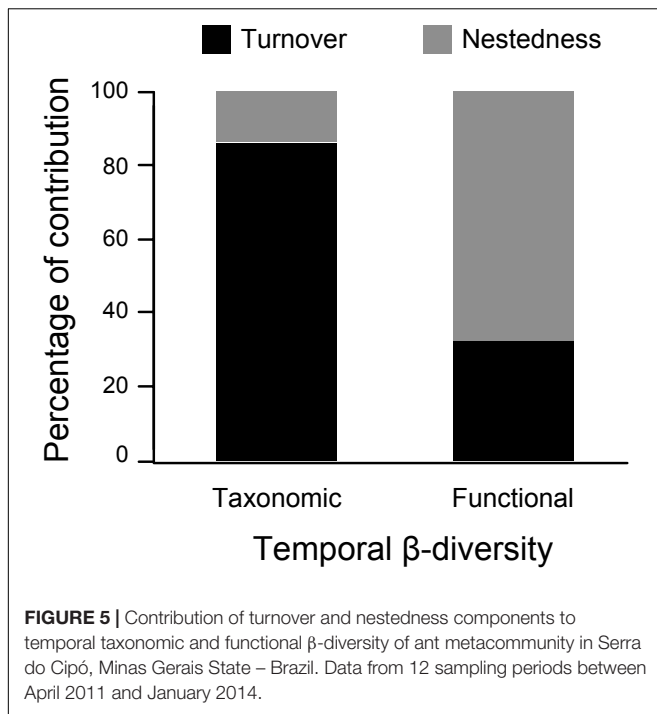


FIGURE 4 | Variation of (A) precipitation, (B) air temperature, (C) air humidity, (D) soil temperature, and (E) soil humidity over 12 periods in the beginning and end of wet and dry seasons. The boxplots represent the variation of the mean values of the seven sampling sites (different elevations) in each month/year. Data sampled using meteorological monitoring towers along an elevational gradient in Serra do Cipó, Minas Gerais State – Brazil.



functional β -diversity with 67% of contribution across the entire gradient (Figure 5).

Neither temporal taxonomic nor functional β -diversity were influenced by elevation [TD: $\chi_{(1,19)} = 1.02$, $p = 0.31$; FD: $\chi_{(1,19)} = 1.86$, $p = 0.17$; Figure 6A]. Turnover (β_{SIM}) was the main driver of temporal taxonomic β -diversity with a consistent pattern along the entire elevation gradient [contribution always higher than 80%; $\chi_{(1,19)} = 0.24$, $p = 0.62$; Figure 6B]. In contrast, temporal functional turnover contribution increased with elevation [$\chi_{(1,19)} = 5.22$, $p < 0.05$, pseudo- $R^2 = 0.22$], going from less than 20% in lower elevations to more than 50% in higher elevations (Figure 6B).

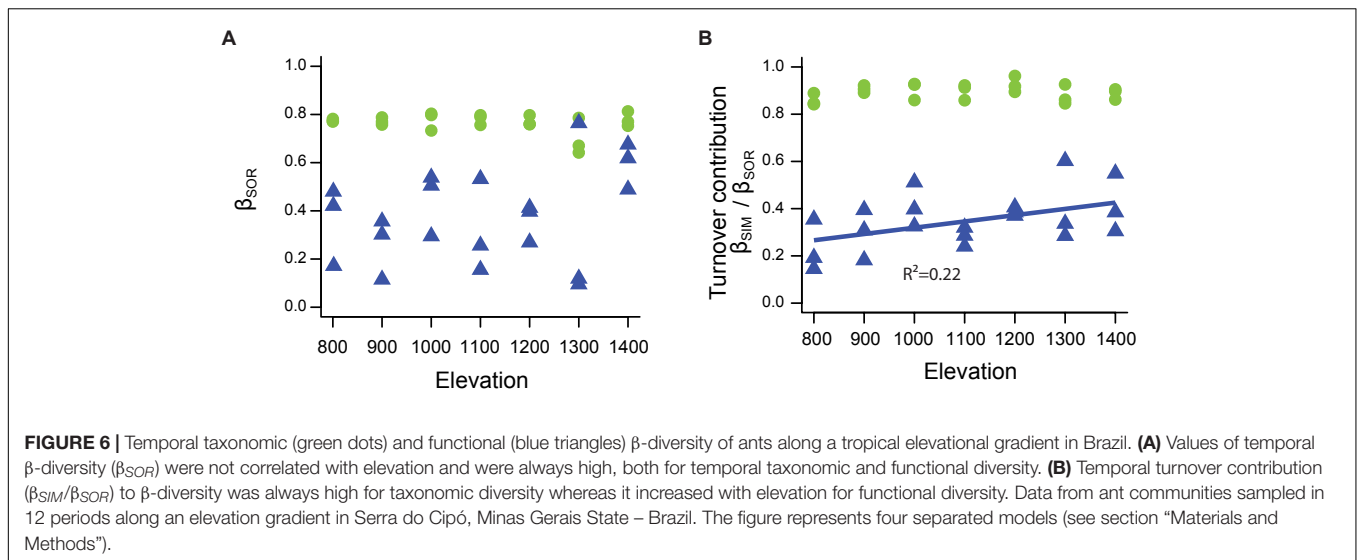
DISCUSSION

We found that ant communities had remarkably high temporal taxonomic and functional β -diversity. Contrary to our first hypothesis, values of temporal taxonomic and functional β -diversity are high irrespective of their position along the elevational gradient. Partially in line with our second hypothesis, turnover was the main component of temporal taxonomic β -diversity along the gradient (above 80% of contribution). However, the contribution of nestedness to temporal functional β -diversity decreased significantly with elevation. We propose that ant activity is very sensitive to temporal variation in environmental conditions, and mainly temperature (Costa et al., 2018; Castro et al., 2020). The effect on ant community composition is then the same along the elevational gradient, with both species and functional traits highly variable over time at all elevations. Although ant metacommunities are changing over time, at low elevations the turnover in species composition

may cause changes in trait composition because of the loss of some traits, but probably preserving the most common functions (nested functional communities). In contrast, at higher elevations, the turnover in species composition cause changes in the set of functions performed over time (i.e., temporal turnover of traits).

The *campo rupestre* has two well-defined seasons: a wet season that is also hot (~170 mm/month and mean temperature of 21.1°C), and a dry season that is cold (close to 0 mm/month and 17.2°C). The changes in temperature and humidity impose changes in plant productivity (Rocha et al., 2016) and animal activity (especially the ectothermic animals; e.g., Costa et al., 2018). Indeed, temporal changes in temperature, humidity and resource availability are known to influence ant foraging activity (Calazans et al., 2020) and consequently the diversity and composition of communities. However, we found high levels of species and trait composition changes along the entire elevation gradient, contrary to our expectations. We propose two non-exclusive hypotheses to explain this result: (i) the sensitivity of ant communities in tropical mountains to changes in environmental conditions (Longino and Colwell, 2011; Castro et al., 2020; Lasmar et al., 2020) are enough to impose drastic changes in species and trait composition; ii. ant communities are regulated by the minimum humidity at low elevations, while the highland ant communities are regulated by the minimum temperature, consistent with our finding that the variation of temperature increases with elevation, while the variation in humidity decreases. Bishop et al. (2017) found that ants are constrained more by the critical thermal minimum temperature (CTmin) than by the maximum in a southern African mountain. Accordingly, Calazans et al. (2020) found, in a study in *campo rupestre*, that ant activity increased with temperature, but most species were not active under 20°C. Although highland ants would probably have a lower CTmin, the higher variation on temperature at high elevations could filter different species and traits in different seasons.

We found that turnover was the main mechanism generating temporal taxonomic β -diversity, as expected based on the spatial pattern for ants and many other organisms (Perillo et al., 2017; da Silva et al., 2018; Kaltsas et al., 2018; Castro et al., 2020). The spatial variation in conditions and resources provide an environmental filter for species that have pre-adaptations to survive in different places (Heino and Tolonen, 2017; García-Llamas et al., 2019) leading to high rates of turnover of species. In this sense, the same processes would be occurring to generate the temporal pattern but related to ant activity: environmentally filtering ant species to be active in different seasons along all the elevational gradient. In contrast, functional β -diversity is generated by a higher contribution of nestedness in spatial patterns (Nunes et al., 2016, 2017; Castro et al., 2020) especially on elevational gradients, showing high functional redundancy. In our study, at lowlands the temporal pattern mirrors the spatial and nestedness contributes 80% of functional β -diversity (i.e., 20% turnover, Figure 6B). However, the importance of turnover in functional diversity increases with elevation, reaching more than 50% in some highlands. The changes in species composition, caused by a change in the set of active species, lead to creation



of subsets of traits among seasons, with a more complete set in hot and dry season and a subset of the most common traits in dry and cold season. However, at higher elevations on the gradient, increasing trait turnover can create a greater variation in trait combinations over space and time. This means that lower elevation ant metacommunities are more functionally resistant to changes in species composition, having greater functional redundancy over time while higher elevation metacommunities are more functionally sensitive to changes in species composition across the seasons.

Contextualizing our results within the metacommunity framework, we can propose that ant diversity is explained by a combination of the species sorting and the mass effect models (Leibold et al., 2004; Sojininen, 2014). We found a high β -diversity and turnover contribution in our study, showing that environmental conditions and resources are filtering the species comprising the ant metacommunity (i.e., species sorting; Leibold and Chase, 2018). Due to high environmental heterogeneity across the elevational gradient, if we are looking at different sites (e.g., different elevations or different habitats) or different times (e.g., different seasons) we expect to find different ant species compositions. Conversely, generalist ant species may have access to different habitats with different conditions through dispersal and can establish long term populations (e.g., Neves et al., 2020), maintaining the mass effect. Therefore, although environmental filters are strong in spatially and temporally regulating the ant metacommunity (species sorting), some ant species can disperse, overcoming local niche limitations and establish populations in different sites following close-to-optimal conditions (mass effects). In both cases, we observe a greater importance of environmental than dispersal-related factors, a pattern expected when there is high environmental heterogeneity (e.g., He et al., 2020).

Implications for Conservation

Our study builds on growing evidence that montane tropical insects are highly sensitive to local climatic and environmental

changes (e.g., Longino and Colwell, 2011; Lasmar et al., 2020). The studied ant metacommunities are highly variable over time along the entire elevational gradient. Montane insect assemblages are thought to be very vulnerable to global warming (Laurance et al., 2011), because with increasing temperature, these organisms are expected to shift their elevational ranges, leading to mountaintop extinctions (Colwell et al., 2008). As there is growing evidence that climate change affects both temperature and precipitation regimes (e.g., Romero et al., 2020) and also the occurrence and intensity of extreme climatic events (e.g., Fischer and Knutti, 2015; Patricola and Wehner, 2018), we may expect that such increase in climatic variation and instability will drastically affect ant metacommunities. With this higher temporal variation in conditions and resources, we might lose the rarer and specialized species (Davies et al., 2004) that cannot survive the new environmental filter, leading to the homogenisation of the metacommunity (Newbold et al., 2019). In plants, generalist species tend to be functionally closer, i.e., have high functional redundancy (Denelle et al., 2020), and in assemblages with homogenized species composition we may observe a loss of functional traits and consequently, ecological functions (Newbold et al., 2019). In addition, species that show temporal shutdown in their activity, are likely to be more active year-round as the climate warms (Costa et al., 2018), potentially increasing competition, although the outcome of competitive interactions will likely be influenced by the prevailing combination of temperature and humidity. Furthermore, as we identified an increasing importance of functional temporal turnover along the elevational gradient, we expect that the higher climatic variation associated with climate change (Fischer and Knutti, 2015) will favor generalist species within communities. This, in turn, will result in the homogenisation of the set of functions performed in different seasons. With mountaintop extinctions, elevational range shifts, and taxonomic and functional homogenisation of assemblages, ecosystem functions provided by ants

will be severely jeopardized in tropical mountains under global climatic changes.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

CAN, FN, SP, and RS: study design. GF and FN: project funding. HB and FC: data collection. CAN, FC, and FN: data analyses. CAN, FC, HB, SP, RS, GF, and FN: writing the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2020.571439/full#supplementary-material>

Supplementary Figure 1 | Community weighted mean (CWM) values of continuous traits of ant metacommunities during four periods of the year: the beginning and end of wet and dry seasons.

Supplementary Table 1 | Correlations between environmental variables.

Supplementary Table 2 | Functional traits and temporal data used in data analyses.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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