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Neotropical savanna ants show a reversed latitudinal gradient of species richness, with climatic drivers reflecting the forest origin of the fauna

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Abstract

Aim: To evaluate the extent to which ant species richness in Neotropical savannas varies with macrogeographic variables, and to identify the potential climatic drivers of such variation.

Location: The Cerrado savanna biome of central Brazil, in a region spanning ca. 20° of latitude and 18°of longitude.

Methods: Standardized sampling of the arboreal and ground-dwelling faunas was performed in 29 well-preserved savanna sites using pitfall traps. Species were classified according to their habitat affinities: open-savanna specialists, forest-associated species or habitat generalists. We used generalized linear models to evaluate the importance of geographic (latitude, longitude and elevation) and climatic (mean temperature and three metrics of rainfall) variables as predictors of species richness.

Results: The total number of species recorded at each site varied more than two-fold (from 59 to 144), and latitude was the best geographic correlate of overall species richness. However, contrary to the expected pattern, more species were found at higher than lower latitudes. This reversed latitudinal pattern of diversity occurred for both the arboreal and ground-dwelling faunas, and for the habitat generalists and forest specialists. The savanna specialists showed a mid-latitudinal peak in diversity. Overall, there was a significant positive association between rainfall and species richness, but the strength of this relationship varied with ant habitat affinity.

Main conclusions: The Cerrado ant fauna shows a reverse latitudinal gradient in species diversity, and this can be explained by increasing rainfall during the warmest months of the year (and therefore in plant productivity) with increasing latitude. The sensitivity of Cerrado ant diversity to declining rainfall contrasts with the high resilience to aridity of the Australian savanna ant fauna, and this reflects the contrasting evolutionary histories of these faunas. Our findings highlight the importance of historical processes as drivers of intercontinental contrasts in macroecological patterns.

KEYWORDS
ant communities, Cerrado, latitudinal diversity gradient, Neotropical arid diagonal, species diversity, tropical savanna

1 | INTRODUCTION

A central goal of ecological research is to understand geographic patterns of species diversity, both for its theoretical importance and for setting conservation priorities (Gaston, 2000; Whittaker et al., 2005). One of the best-known patterns of species diversity is the latitudinal gradient of increasing number of species from the poles towards the equator. Despite being an almost universal pattern (Willig, Kaufman, & Stevens, 2003), the causes of this latitudinal diversity gradient are still a matter of debate (Field et al., 2009; Willig et al., 2003), but energy and water availability (which together determine primary productivity) are regarded as key drivers (Hawkins et al., 2003). The relative importance of these drivers is believed to vary with latitude: at high latitudes, where energy inputs are low, temperature is often the most important predictor of species richness, whereas in lower (warmer) latitudes, species richness is most strongly constrained by water availability (Hawkins et al., 2003).

Compared to vertebrates, insects are poorly represented in studies of geographic patterns of faunal species richness (Hawkins et al., 2003). Ants—a major group of insects in most terrestrial ecosystems—have been one of the first faunal taxa to be studied from a macroecological perspective, and have recently been the focus of macroecological analysis based on the compilation and analysis of a collaborative, global ant database (Gibb et al., 2015 and references therein). At global and continental scales, ant diversity is driven primarily by temperature (Dunn et al., 2009; Jenkins et al., 2011; Kaspari, Ward, & Yuan, 2004), and is therefore negatively correlated with latitude (Dunn et al., 2009; Kaspari, O'Donnell, & Kercher, 2000). Ant diversity also often declines with increasing latitude at regional scales (Cushman, Lawton, & Manly, 1993; Gotelli & Ellison, 2002; Chaladze, 2012; but see Pfeiffer, Chimedregzen, & Ulykpan, 2003). Temperature is also a primary predictor of ant diversity along elevational gradients (Sanders, Lessard, Fitzpatrick, & Dunn, 2007; Szewczyk & McCain, 2016). However, the importance of rainfall as a driver of geographic patterns of ant diversity remains contentious. Rainfall is a weak predictor of ant diversity at a global scale (Dunn et al., 2009), and both positive (Parr, Robertson, Biggs, & Chown, 2004; Perez-Sanchez, Lattke, & Viloria, 2013; Vasconcelos, Vilhena, Facure, & Albernaz, 2010) and non-significant relationships (Andersen, Del Toro, & Parr, 2015; Delsinne, Roisin, Herbauts, & Leponce, 2010) between rainfall and ant species richness have been detected at regional scales.

Different ant faunas might show different responses to geographic gradients of rainfall because of differences in their evolutionary histories (Andersen et al., 2015; Delsinne et al., 2010; Jenkins et al., 2011). In the savannas of northern Australia, for instance, high ant species richness is maintained along the entire rainfall gradient from 1,500 to 500 mm/yr, because losses of high rainfall species are matched by gains in arid-adapted taxa (Andersen et al., 2015). This reflects the evolutionary history of Australian savannas in association with the central arid zone, which has an exceptionally diverse ant fauna (Andersen, 2016) from which the savanna fauna is derived. The Australian savanna fauna is dominated by highly thermophilic taxa that do not occur in forest habitats (Andersen, 2000), such that community structure is identical to that throughout arid Australia (Andersen, 2003).

In contrast, several lines of evidence strongly indicate that ants in Neotropical savannas have had a biogeographical and evolutionary association with rainforests. First, savanna is much younger than forest. The flora of the largest block of savannas in South America—the Cerrado—is estimated to have a relatively recent origin of <10 Mya, with most lineages diversifying at about 4 Mya (Simon et al., 2009). This is consistent with other studies that indicate a late Miocene origin of tropical savannas (Beerling & Osborne, 2006). However, the origin and initial diversification of most Neotropical ant taxa took place earlier, during the Eocene, and is coincident with the expansion of tropical forests (Moreau & Bell, 2013; Price et al., 2014). Second, generic composition of the Neotropical savanna ant fauna is very similar to that of rainforest, which is in striking contrast to the situation in Australia (Andersen, 2000; van Ingen, Campos, & Andersen, 2008). The Neotropical savanna ant fauna contains very few arid-adapted elements (Camacho & Vasconcelos, 2015; Campos, Vasconcelos, Andersen, Frizzo, & Spena, 2011; Silvestre, Brandão, & Silva, 2003), and includes a very high diversity of tree-nesting taxa (Campos et al., 2011; Ribas, Schoereder, Pic, & Soares, 2003), which is a feature of forest ant faunas but usually not of those of savannas (Andersen et al., 2015; Campos et al., 2011). Third, phylogenetic analyses of two important groups of Neotropical savanna ants, the turtle ants (genus *Cephalotes*) and the fungus-growing ants, indicate that both originated in rainforest and more recently diversified in dry habitats (Branstetter et al., 2017; Price et al., 2014). Similarly, much of the woody flora from Neotropical savannas have sister groups in more ancient vegetation types such as moist and seasonally dry tropical forests (Simon & Pennington, 2012; Simon et al., 2009). Finally, many ants of Neotropical savannas are widespread forest species that extend into semi-arid habitats (Leal et al., in press), which is in strong contrast to the dichotomous composition of forest and savanna ant faunas in Australia (Andersen, Houadria, Berman, & van der Geest, 2012; Reichel & Andersen, 1996; van Ingen et al., 2008) and South Africa (Slingsby, 2017). Patterns of savanna ant diversity in relation to rainfall remain undocumented in the Neotropics, but marked declines with increasing aridity have been predicted due to the forest affinities of the fauna (Andersen et al., 2015).

Here, we use results from standardized sampling at 29 sites spanning 20° of latitude and nearly 1,000 m of elevation to identify geographic patterns and their drivers of ant diversity in the Cerrado (savanna) biome of central Brazil. The aim of our study was threefold. First, we evaluate the extent to which savanna ant species richness varies with macrogeographic variables (latitude, longitude and elevation). Second, we examine the importance of climatic variables as correlates of ant species richness. In particular, we test the hypothesis that, in contrast to the arid-adapted savanna fauna of northern Australia (Andersen et al., 2015), the ant fauna of Neotropical savannas shows a marked decline in diversity with decreasing rainfall. Finally, we evaluate the extent to which geographic and climatic drivers of ant diversity vary among different ant functional types relating to nesting stratum and habitat affinity. In particular, we test the prediction that the diversity of species more closely associated with forest than savanna is especially sensitive to increasing aridity. Given that all tree-nesting species belong to forest genera, we also test the prediction that the diversity of arboreal ants is also especially sensitive to increasing aridity. We acknowledge that the effects of rainfall on ant communities are indirect through its influence on primary productivity (Hawkins et al., 2003). However, we focus on rainfall rather than primary productivity to be consistent with previous macroecological studies of ant communities (Andersen et al., 2015; Dunn et al., 2009; Gibb et al., 2015).

2 | MATERIAL AND METHODS

2.1 | Study area

Our 29 sampling sites were spread over a region of approximately 2000 × 1800 km in the Brazilian Cerrado (Figure 1). The Cerrado biome, which harbours the most humid and floristically diverse savannas of the world (Oliveira-Filho & Ratter, 2002), is part of the so-called "diagonal of dry and open formations," which also includes the Caatinga of north-eastern Brazil and the Chaco of Paraguay, Bolivia and northern Argentina. The western and north-western regions of the Cerrado contact the Amazon forest, while the south and south-eastern regions contact the Atlantic Forest.

We restricted our sampling to cerrado sensu stricto which has an open canopy of trees 3–8 m tall, and a dense ground layer composed of grasses, herbs and small shrubs (Oliveira-Filho & Ratter, 2002). Tree and grass cover was relatively uniform among the sites we sampled (Fig. 1). Mean annual temperature at the sites varies from 18.1 to 26.6°C (overall mean = 23.2°C; data obtained from Worldclim; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), and such variation is strongly and negatively associated with both latitude and elevation (latitude: $r = -.750$, $p < .001$; elevation: $r = -.824$, $p < .001$). Mean annual rainfall varies from 860 to 1,830 mm (overall mean = 1,430 mm), and is not correlated with latitude ($r = -.072$), longitude ($r = .282$) or elevation ($r = -.092$). However, there is a positive correlation between latitude and rainfall during the warmest quarter ($r = .839$, $p < .001$), as well as between latitude and rainfall during the driest quarter ($r = .619$, $p < .001$).

2.2 | Ant sampling and sorting

The fieldwork took place between November 2010 and October 2015. Ant collections were performed once at each of the 29 sampling sites. The timing of sampling varied depending on the availability of personnel, funding and access authorization, which was granted in all cases. However, there was no geographic bias with regard to time of sampling (see Appendix S1). Furthermore, studies in the Cerrado show that time of sampling has no significant influence on ant species richness (Camarota, Powell, Vasconcelos, Priest, & Marquis, 2015; Neves et al., 2010), which reflects the fact that the great majority of species forage throughout the year because of constantly high temperatures.

At each site, we established three 380 m transects separated from each other by at least 1 km. Except for sites BJS (7 km) and CUI (19 km; Fig. 1), the maximum distance among transects was 3 km. Along each transect, we marked 20 sampling points (spaced at 20 m intervals), with alternate points used to sample ants that forage on the soil surface (hereafter ground-dwelling ants) and on trees (hereafter arboreal ants). Ants were sampled using pitfall traps, which are considered the most effective method for sampling savanna ants (Andersen, 1991; Lopes & Vasconcelos, 2008; Parr & Chown, 2001). To collect ground-dwelling ants, a set of four pitfall traps, arranged in a square grid of approximately 2.5 × 2.5 m, was installed at each sampling point. To collect arboreal ants, four pitfall traps were fixed on the branches of the tree (>2.5 m in height) that was located nearest to each sampling point. Pitfall traps consisted of a small plastic cup (250 ml, 8.5 cm high and 7.8 cm in diameter) partially filled with water and detergent. The arboreal traps were baited with human urine (diluted 1:2 in water), which is a highly attractive bait for arboreal ants (Powell, Costa, Lopes, & Vasconcelos, 2011). Ground pitfall traps were not baited because this is not necessary for obtaining large catches. Ground and arboreal pitfall traps remained in operation for 48 hours. A more detailed account of the sampling protocol is presented in Vasconcelos et al. (2014).

All ants collected were sorted to morphospecies (subsequently referred to as "species") and, whenever possible, identified using available taxonomic keys. We were able to provide species-level identification for about half of the collected species (see Appendix S2). Cerrado faunal assemblages typically include both Cerrado-endemic species and those also found in adjoining forest biomes (Klink & Machado, 2005; Nogueira, Ribeiro, Costa, & Colli, 2011; Valdujo, Carnaval, & Graham, 2013), and this is the case for ants. Based on published information and on our own field experience, we classified each species as: "savanna specialists" (occurring predominantly in savannas and grasslands), "forest-associated" (occurring primarily in forest), or "habitat generalists" (showing no strong habitat association). We were able to classify most of the named species plus a few of the unnamed species belonging to genera with strict habitat affinities (see Appendix S2). We also classified the collected species according to their main nesting/foraging strata as: "arboreal" or "ground-dwellers". Some ant genera have strict nesting habits (e.g. all species of *Azteca* and *Cephalotes* are arboreal, whereas all *Dorymyrmex* and *Blepharidatta* nest in the soil), and in this case the classification of the individual species was straightforward. For species belonging to genera with mixed nesting habits, species classification was based on the relative frequency with which each species was collected in the arboreal traps versus those placed on the ground. We classified as arboreal those species that were at least twice as frequent in the arboreal traps, and as ground-dwellers those that were at least twice as frequent in the ground traps. A few species ($n = 17$) were found at similar frequencies in both types of traps and were thus classified as "mixed nesting/foraging habits".

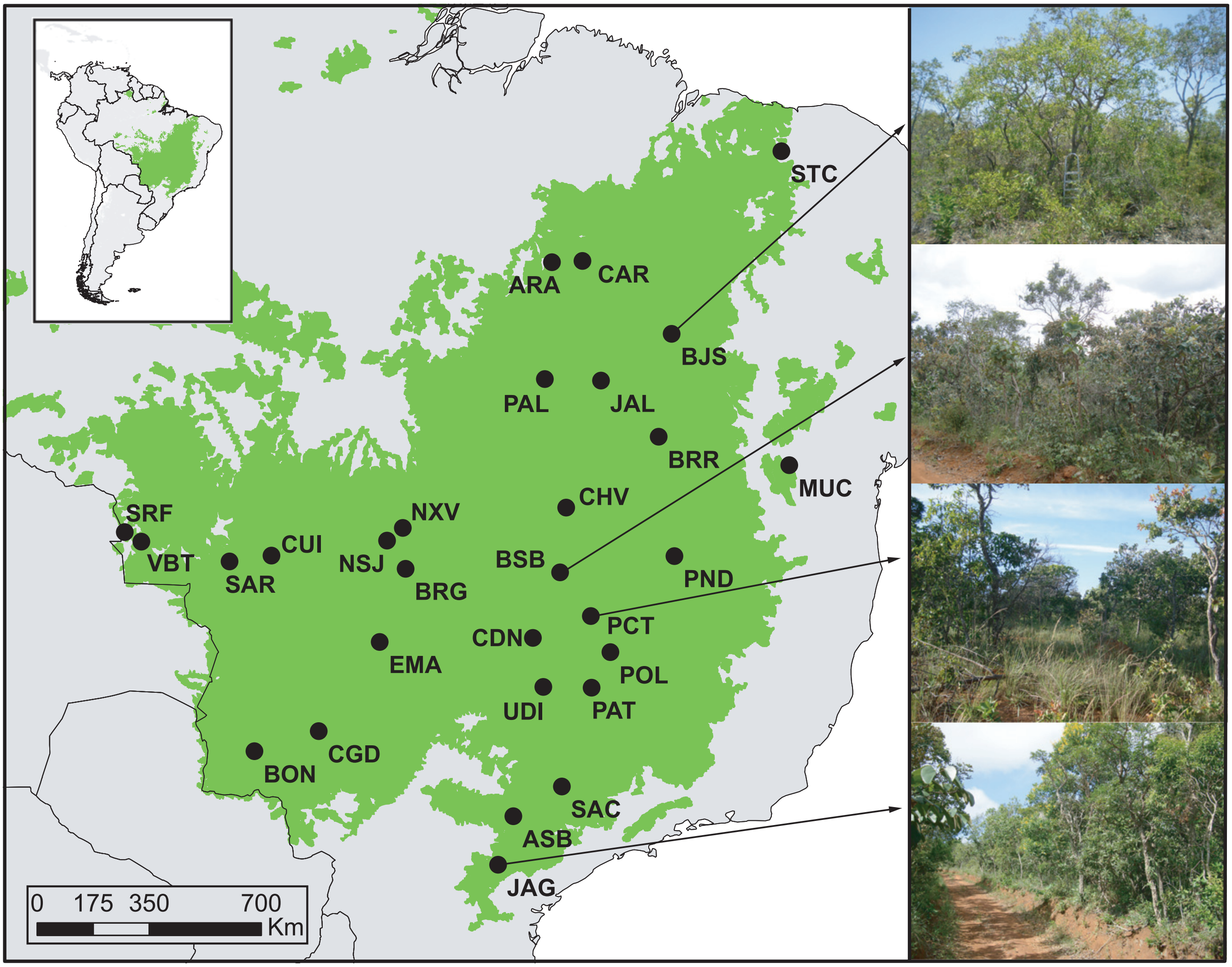

FIGURE 1 Distribution of savanna vegetation within South America with location of the 29 savanna sampling sites in central Brazil (left), and general view of the savanna vegetation in four of the sites (right)

In our analyses, such species were included both in the arboreal and ground-dwellers categories.

Voucher specimens of all collected species/morphospecies are deposited at the Zoological Collection of the Federal University of Uberlândia, in Uberlândia, Brazil, and at the Entomological Collection *Padre Jesus Santiago Moure* (DZUP) of the Federal University of Paraná, in Curitiba, Brazil.

2.3 | Data analysis

For the purpose of the statistical analyses, we pooled ant data for the three transects at each site. Similarly, climatic data extracted for each transect were averaged in order to obtain a single value for each site ($n = 29$ sites). The magnitudes of the geographic and climatic variables were standardized by Z-score transformation prior to analysis.

To evaluate the different geographic variables (latitude, longitude and elevation) as correlates of ant species richness, we built generalized linear models (GLMs) assuming a negative binomial error—as appropriate for overdispersed count data (Hilbe, 2007)—using the R package “mass” (Venables & Ripley, 2002). Visual inspection of the scatterplots suggested that in some cases the relationship between latitude and ant species richness was nonlinear. For this reason, the term latitude^2 was also evaluated in our models. GLMs were also built to evaluate mean annual temperature and three rainfall metrics as correlates of ant species richness. To check for spatial autocorrelation among model residuals, we calculated Moran's I using the default options of SAM 4.0 (Rangel, Diniz, & Bini, 2010).

Temperature and rainfall data were obtained from Worldclim (Hijmans et al., 2005) at 1 km^2 resolution. In addition to total annual rainfall, we obtained data on rainfall during the driest quarter and rainfall during the warmest quarter. These latter measures are not correlated with annual rainfall ($r < .07$), and only weakly correlated with each other ($r = .391$, $p = .036$). Rainfall during the driest quarter is often used as a surrogate of environmental stress, whereas rainfall during the warmest quarter as a surrogate of environmental favourableness (Costa, Nogueira, Machado, & Colli, 2007, and references therein).

To select the best regression models (lowest AICc) that described the relationship between species richness with the geographic or climatic variables, we used a model selection approach based on the Akaike information criterion corrected for small sample sizes (AICc). However, given that in most cases the best models presented a low support value (as indicated by the Akaike weight; w_i), we also performed a model averaging procedure (Burnham & Anderson, 2002). For this, the standardize regression coefficients of each predictor variable were averaged across all models in which the variable was present, and weighting this average according to the w_i value of the model. In addition, we determined the relative importance (or individual contribution) of each variable by summing the w_i values across all models that included that particular variable (Burnham & Anderson, 2002). Multimodel selection and model averaging analyses were performed in R version 3.2.3 (R Core Team, 2015) using the package “MuMIn” (Barton, 2016).

3 | RESULTS

We recorded a total of 455 ant species (and 17,298 species occurrences) from 72 genera in the 29 sampling sites. The most diverse genus was *Pheidole* with 77 species, followed by *Camponotus* (38 species), *Cephalotes* (24 species), *Solenopsis* (24 species), *Pseudomyrmex* (19 species), *Trachymyrmex* (19 species) and *Crematogaster* (18 species) (Appendix S2). Only three species (*Camponotus senex*, *Pheidole fracticeps* and *Pheidole triconstricta*) were found at all 29 sampling sites, whereas 137 (30.1%) were found at just one site. Among the species found, 76.3% were classified as ground-dwellers, 18.7% as arboreal and 3.7% as having mixed nesting/foraging habits (the habits of six species were not determined). Half of the 220 species for which information on habitat affinity was available were classified as habitat generalists, 27.3% as savanna specialists, and 22.7% as forest-associated (Appendix S2).

The total number of species recorded at each site ranged from 59 to 144 ($M \pm SD = 103.6 \pm 24.0$ species) (Appendix S1). Our sampling protocol retrieved 56 to 92.2% ($M = 75.2 \pm 8.4\%$) of the species expected to be found in each site, according to the species richness estimator Chao2. Sampling completeness (ratio between the observed and expected number of species) was not correlated with latitude ($r = .15$) or longitude ($r = .04$), indicating that there was no spatial bias in sampling completeness. There was a strong correlation between the observed and the expected number of species ($r = .92$); consequently, statistical analyses using the species richness estimator Chao2 (results not shown) produced the same results as those using the observed number of species.

Latitude was the best geographical correlate of variation in ant species richness among sites, presenting a much higher coefficient and importance value than longitude and elevation in the regression models involving different ant functional groups (Table 1). In addition, latitude was included as a predictor in all minimum adequate models (i.e. those with the lowest AICc values) (Table 1). Latitude was positively correlated with overall ant species richness, with the richness of both ground-dwelling and arboreal species, and with the richness of species with different habitat affinities (Figure 2). However, for richness of habitat generalists the best regression models also included the term latitude^2 (Table 1), with the rate of increase in species richness with latitude declining after 15°S (Fig. 2d). The term latitude^2 was also included in the best model describing the richness of savanna specialists, which shows that for this particular functional group the relationship with latitude is hump-shaped, reaching a peak at about 15°S and then declining sharply (Fig. 2e). Longitude was included only in the model for forest-associated species, where it was nearly as important as latitude (Table 1). Elevation was included in only one best model, having a weak negative influence on the richness of savanna specialists (Table 1).

The climatic correlates of ant richness varied markedly with ant stratum and habitat affinity. Rainfall during the warmest quarter was the strongest correlate of overall species richness, along with the richness of ground-dwelling ants, arboreal ants and habitat generalists, whereas annual rainfall was the best correlate for forest-associated species and the second best one for habitat generalists (Table 2). No climatic variable was significantly correlated with the species richness of savanna specialists.

Rainfall during the warmest quarter was the only predictor included in the minimum adequate models involving overall ant richness, the richness of arboreal species and the richness of ground-dwellers. In contrast, the richness of habitat generalists was best predicted by both rainfall during the warmest quarter and annual rainfall, whereas the richness of forest-associated species by annual rainfall and rainfall during the driest and warmest quarters (Table 2). In each case, species richness increased with rainfall (Figure 3). Average annual temperature was not included in any minimum adequate model. In addition, the regression coefficients for mean annual temperature were quite low as it was the importance value of this variable in our regression models (Table 2).

Overall, we found no evidence of spatial autocorrelation among the model residuals, except in the case of the model involving ground-dwelling ants for which a negative spatial autocorrelation was detected in distance class 2, and the one involving the forest-associated species for which a negative autocorrelation was detected in distance class 8 (see Appendix S3).

4 | DISCUSSION

Our study uses results from standardized sampling from throughout Brazil’s Cerrado biome to identify the drivers of geographic patterns of ant diversity in Neotropical savannas. Our first aim was to evaluate the extent to which ant species richness varies with the large-scale geographic variables latitude, longitude and elevation. Our results show that ant species richness in Cerrado varies strongly with latitude. However, contrary to the expected pattern, more species were found at higher than at lower latitudes. Although several exceptions to the typical latitudinal diversity gradient exist (e.g. Buckely, Miller, Ellison, & Gotelli, 2003), these usually involve

TABLE 1 Standardized regression coefficients and relative importance (within parentheses) of macrogeographic variables used to model the species richness of different ant functional groups across the savannas of central Brazil. Reported are the coefficients obtained in the average model (weighted by w_i). Also shown are the variables included in the minimum adequate model (ΔAICc = 0), the relative weight (w_i) of the model and the amount of variance explained

	Minimum adequate model			Averaged coefficients (relative importance)			
Functional group	Model	w_i	Pseudo-R^2	Latitude	Latitude^2	Longitude	Elevation
All ants	Lat	0.335	0.482	0.254 (0.81)	−0.215 (0.38)	0.024 (0.24)	−0.030 (0.25)
Ground-dwellers	Lat	0.300	0.479	0.283 (0.79)	−0.247 (0.45)	0.023 (0.24)	−0.027 (0.24)
Arboreal	Lat	0.360	0.233	0.210 (0.78)	−0.256 (0.32)	0.033 (0.21)	0.007 (0.20)
Habitat generalists	Lat + Lat^2	0.274	0.444	0.370 (0.77)	−0.363 (0.50)	0.040 (0.26)	−0.042 (0.27)
Savanna specialists	Lat + Lat^2 + Elev	0.300	0.319	0.617 (0.60)	−0.651 (0.60)	0.074 (0.34)	−0.090 (0.43)
Forest-associated	Lat + Long	0.447	0.449	0.225 (0.81)	0.055 (0.18)	0.206 (0.74)	−0.112 (0.31)

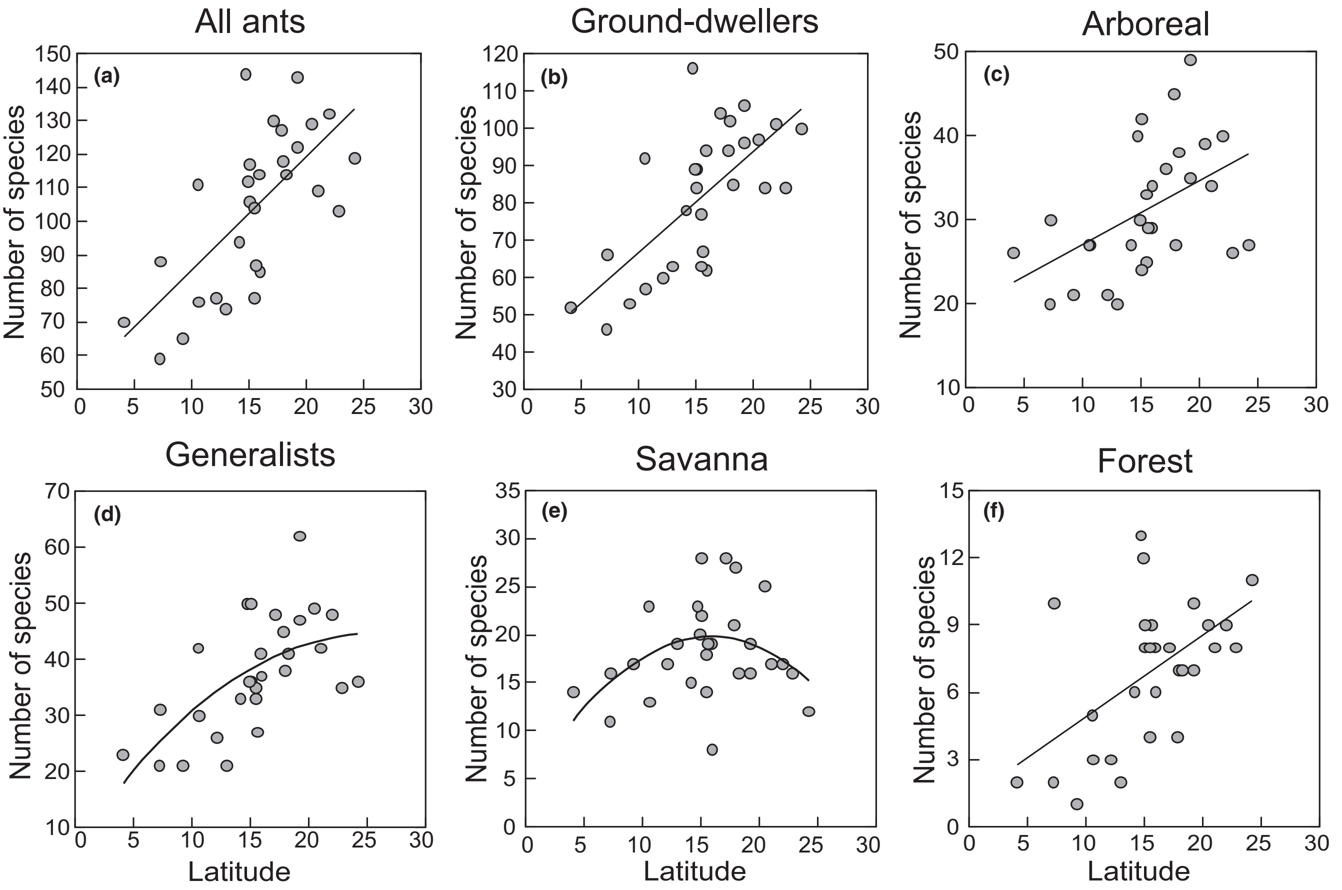

FIGURE 2 Latitudinal variation in ant species richness. (a) Overall species richness (b) ground-dwelling ants, (c) tree-dwelling ants, (d) habitat generalists (e), savanna specialists, (f) forest-associated. Lines represent simple regression lines

relatively small latitudinal extents (reviewed in Willig et al., 2003), rather than encompassing over 20° of latitude as in our study.

The other two large-scale geographic variables analysed here—elevation and longitude—had a much smaller influence on species richness than did latitude. As expected, ant species richness was negatively correlated with elevation. However, such correlation was weak (as revealed by the low average regression coefficients; Table 1), and this was true even for the savanna specialists, the only group in which elevation was included as a predictor in the minimum adequate model. Contrary to previous studies (e.g. Sanders et al., 2007), we did not analyse elevational changes in species richness along a given mountain range. Rather, our sampling sites were spread over a large biogeographic region, and so the potential effect of elevation (mediate by climate) on species richness is likely to have been confounded or minimized by other factors (e.g. latitude). In fact, although temperature declines on average 6°C for each

TABLE 2 Standardized regression coefficients and relative importance (within parentheses) of four climatic variables used to model the species richness of different ant functional groups across the savannas of central Brazil. Reported are the coefficients obtained in the average model (weighted by w_i). Also shown are the variables included in the minimum adequate model (ΔAICc = 0), the relative weight (w_i) of the model and the amount of variance explained

	Minimum adequate model			Averaged coefficients (relative importance)			
Functional group	Model	w_i	Pseudo-R^2	Rainfall warmest quarter	Annual rainfall	Rainfall driest quarter	Mean annual temperature
All ants	RWQ	0.307	0.375	0.147 (0.98)	0.060 (0.49)	0.013 (0.20)	−0.032 (0.24)
Ground-dwellers	RWQ	0.297	0.310	0.146 (0.98)	0.060 (0.50)	0.016 (0.21)	−0.036 (0.25)
Arboreal	RWQ	0.349	0.238	0.123 (0.91)	0.054 (0.36)	−0.027 (0.24)	−0.007 (0.21)
Habitat generalists	RWQ + AR	0.469	0.459	0.178 (0.99)	0.094 (0.71)	−0.008 (0.19)	−0.002 (0.19)
Savanna specialists	Null	0.297		0.065 (0.33)	−0.005 (0.21)	−0.008 (0.21)	0.061 (0.31)
Forest-associated	AR + RDQ + RWQ	0.340	0.382	0.170 (0.64)	0.196 (0.81)	0.186 (0.82)	−0.005 (0.21)

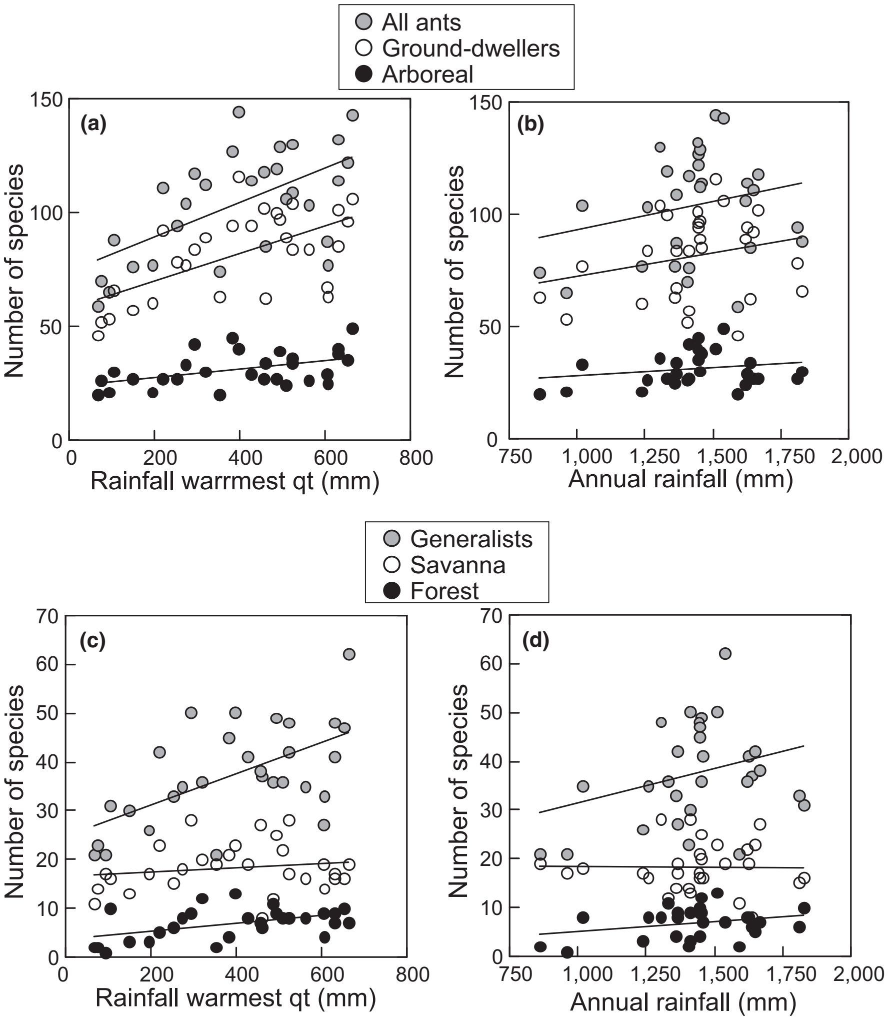

FIGURE 3 Scatterplot of the relationship between rainfall and ant species richness. (a) Rainfall during the warmest quarter and overall species richness, species richness on ground, and in trees. (b) Annual rainfall and overall species richness, species richness on ground, and in trees. (c) Rainfall during the warmest quarter and species richness of habitat generalists, savanna specialists and forest-associated. (d) Annual rainfall and species richness of habitat generalists, savanna specialists and forest-associated. Lines represent simple regression lines

1,000 m gained in elevation (Szewczyk & McCain, 2016), here the difference in mean annual temperatures between our lowest (206 m asl) and highest (1,135 m asl) elevation sites was only 3.5°C.

For most ant functional groups, longitude had a much smaller influence on species richness than did latitude, even though the longitudinal extent of our sampling was almost as large as that of latitude. Notably, however, longitude was nearly as important as latitude for forest-associated ants, which increased in richness from east to west. This unique pattern for forest-associated species can be related to the influence of the Amazon forest (to the west) on the Cerrado species pool (Valdujo et al., 2013). For example, we recorded the notorious bullet ant (*Paraponera clavata*) only at sites within 250 km of the Amazon forest. The highest diversity of forest-associated species occurred at sites relatively close to the Amazon; for example, the *Araguaina* (ARA) site is located within 30 km from the Amazon forest, and has five times as many forest-associated species than do other sites at similar latitudes (Fig. 2).

Our second aim was to examine the importance of climatic variables as correlates of ant species richness in Neotropical savannas. According to Jenkins et al. (2011) our knowledge about the drivers of ant diversity in warm and dry regions is scanty. Previous studies indicate that temperature is a main driver of ant species richness at a global scale (Dunn et al., 2009; Jenkins et al., 2011; Kaspari et al., 2004) as well as at the regional scale in high-latitude regions (Gotelli & Ellison, 2002). In contrast, we found temperature to be a poor correlate of ant species richness. However, we found a strong association between rainfall and species richness. Together, these results lend additional support to the view that temperature best explains gradients of faunal species richness at high latitudes, whereas water variables are the most important drivers in warm climate regions (Hawkins et al., 2003).

Of the three rainfall variables evaluated here as drivers of ant species richness, rainfall during the warmest quarter had the highest relative importance in most regression models. As noted earlier, in the Cerrado there is a strong latitudinal gradient in rainfall during the warmest quarter but not in total annual rainfall. This is because at latitudes higher than about 15°S, the warmest quarter is largely coincident with the austral summer (January to March), whereas at lower latitudes the warmest quarter starts earlier, between August and September (https://pt.climate-data.org/). As the Cerrado rainy season typically starts in November, this means that sites at lower latitude receive less rain during the warmest quarter than do higher latitude sites, even with the same total annual rainfall. The amount of rain falling during the warmest months is strongly correlated ($r = .793$, $p < .001$) with net primary productivity at our study sites, and when we re-analysed our data using NPP instead of rainfall during the warmest quarter, NPP was the most important predictor of species richness. This suggests that the observed latitudinal gradient in ant species richness is driven by variation in plant productivity.

Our final aim was to evaluate the extent to which geographic and climatic drivers of ant diversity vary with ant nesting/foraging stratum and habitat affinity. We predicted that forest-associated species would be especially sensitive to decreasing rainfall. This was indeed the case, with the richness of forest-associated species and habitat generalists increasing with rainfall, whereas that of savanna specialists did not. The richness of forest-associated species showed a positive linear relationship with latitude, whereas intriguingly the richness of specialist savanna species showed a mid-latitudinal peak. Such a mid-latitudinal peak in diversity possibly represents a mid-domain effect (Colwell & Lees, 2000; Colwell, Rahbek, & Gotelli, 2004), caused by increasing overlap of species ranges towards the centre of the Cerrado biome.

We also predicted that the diversity of arboreal ants is especially sensitive to decreasing rainfall, given that all tree-nesting species belong to forest genera. However, we found that the importance of rainfall as a correlate of species richness was actually lower for the arboreal fauna than for most other ant functional groups. This suggests that local rather than geographical factors are more important drivers of arboreal ant diversity. Indeed, several studies have shown that the species richness of arboreal ants is strongly influenced by local variations in tree size, diversity and density (Koch, Camarota, & Vasconcelos, 2016; Powell et al., 2011; Ribas et al., 2003).

5 | CONCLUSION

We have shown that the Cerrado ant fauna follows a reversed latitudinal diversity gradient, driven by latitudinal patterns in rainfall and therefore in plant productivity. The association with rainfall was especially strong for forest-associated species, and this is consistent with the diversity of leaf litter ants being higher in the southern (higher rainfall) than northern sections of Brazilian Atlantic Forest (Silva & Brandão, 2014). Such sensitivity to rainfall is in stark contrast to the maintenance of high ant diversity with increasing aridity in the Australian savanna, whose fauna is dominated by arid-adapted rather than forest elements (Andersen et al., 2015). A similar cross-continental contrast is shown in reptiles. As for ants, the highest diversity of Cerrado snakes and lizards occurs in the (higher rainfall) south rather than north (Costa et al., 2007). However, lizard diversity in Australia shows no systematic relationship with rainfall, and has a peak in the arid end of the gradient (Powney, Grenyer, Orme, Owens, & Meiri, 2010), due to extreme diversification in arid Australia of all five Australian lizard families (Morton & James, 1988; Pianka, 1986). These cross-continental contrasts presumably reflect differences in physiological performance, such as desiccation tolerance, among species from the different faunas. However, relevant comparative data are not available.

The biogeographic origins of African savanna ant faunas have received little research attention, but they are dominated by widely distributed genera such as *Pheidole*, *Monomorium* and *Tetramorium*, without a high diversity of either arid-adapted or forest elements (Schoeman & Foord, 2012; Slingsby, 2017). The limited data available indicate that diversity declines markedly with decreasing rainfall (Parr et al., 2004), which is consistent with a lack of dominance by arid-adapted taxa. Our findings highlight the importance of historical processes as drivers of intercontinental contrasts in macroecological patterns, and help explain why global analyses of climatic drivers of species diversity, such as those for ants (Dunn et al., 2009), generally have low predictive power.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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