

# Woody Encroachment Affects Multiple Dimensions of Ant Diversity in a Neotropical Savanna

Karen Neves (✉ [neves.karen.f@gmail.com](mailto:neves.karen.f@gmail.com))

Universidade Federal de Uberlandia <https://orcid.org/0000-0002-4756-7755>

**Bernardo Santos**

Museum National d'Histoire Naturelle

**Ted Schultz**

Smithsonian Institution

**Dietrich Gotzek**

Smithsonian Institution

**Rodolfo C.R. Abreu**

Universidade Federal Rural do Rio de Janeiro Instituto de Florestas

**Giselda Durigan**

Instituto Florestal

**Heraldo L. Vasconcelos**

Universidade Federal de Uberlandia

---

## Research Article

**Keywords:** alternative stable states, cerrado, fire management, savanna-forest transition, multiplediversity metrics.

**Posted Date:** December 29th, 2021

**DOI:** <https://doi.org/10.21203/rs.3.rs-1103978/v1>

**License:**  This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

---

Woody encroachment affects multiple dimensions of ant diversity in a Neotropical savanna

Neves, K.<sup>1\*</sup>, Santos, B.<sup>2</sup>, Schultz, T.<sup>3</sup>, Gotzek, D.<sup>3</sup>, Abreu, R.C.R.<sup>4,5</sup>, Durigan, G.<sup>6</sup>, Vasconcelos, H.L.<sup>1</sup>.

<sup>1</sup> Instituto de Biologia, Universidade Federal Uberlândia (UFU), Av. Pará 1720, 38405-320, Uberlândia, Minas Gerais, Brazil

<sup>2</sup> Institut de Systématique, Evolution, Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, SU, EPHE, UA, 57 rue Cuvier CP50, 75231, Paris Cedex 05, France

<sup>3</sup> Entomology Department, National Museum of Natural History, Smithsonian Institution, 1000 Madison Drive NW, 20560, Washington, District of Columbia, United States of America

<sup>4</sup> Departamento de Ciências Ambientais (DCA), Instituto de Florestas (IF), Universidade Federal Rural do Rio de Janeiro (UFRRJ), Rod. BR 465, Km 07, Seropédica, 23890-000, Rio de Janeiro, Brazil

<sup>5</sup> Department of Plant and Microbial Biology, North Carolina State University (NCSU), Raleigh, NC, United States

<sup>6</sup> Floresta Estadual de Assis, Instituto de Pesquisas Ambientais, Estrada Assis – Lutécia, km 09, Caixa Postal 104, 19802-300, Assis, São Paulo, Brazil

\*Corresponding author: [neves.karen.f@gmail.com](mailto:neves.karen.f@gmail.com)

Author contribution: HLV and KN conceived the ideas; GB, RCRA and HLV designed methodology; RCRA obtained the LAI data; KN, BS, TS and DG obtained the UCE sequence data; KN and HLV collected, analyzed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

1 **Abstract**

2 Although savanna woody encroachment has become a global phenomenon, few studies have  
3 simultaneously evaluated its effects on multiple dimensions and levels of savanna biodiversity.  
4 We evaluated how the progressive increase in tree cover in a fire-suppressed savanna landscape  
5 affects the taxonomic, functional, and phylogenetic diversity of neotropical ant communities. We  
6 sampled ants along an extensive tree cover gradient, ranging from open savannas to forests  
7 established in former savanna areas due to fire suppression, and found that Leaf Area Index  
8 explained much of the observed variation in ant diversity at both the alpha and beta levels.  
9 However, ant responses to variation in tree cover were largely non-linear as differences in alpha  
10 diversity and in the dissimilarities of the sampled communities were often much more marked at  
11 the savanna/forest transition than at any other part of the gradient. The patterns of functional and  
12 phylogenetic diversity mirrored those of taxonomic diversity, notably at the beta level. At the  
13 alpha level, functional diversity tended to increase, whereas taxonomic and phylogenetic  
14 diversity decreased or was unrelated to tree cover. Our results indicate that savanna ant  
15 communities switch rapidly to an alternative state once savanna turns into forest. Ant  
16 communities in the newly formed forest areas lacked many of the species typical of the open  
17 habitats, suggesting that the maintenance of a fire suppression policy, is likely to result in a  
18 decrease in ant diversity and in the homogenization of the ant fauna at the landscape level.

19

20 Keywords: alternative stable states; cerrado; fire management; savanna-forest transition; multiple  
21 diversity metrics.

## 22 **Introduction**

23           Tropical savannas are one of the most biodiverse and most threatened terrestrial biomes  
24 (Bond and Parr 2010, Murphy et al. 2016). Expansion of agriculture and cattle ranching has  
25 rapidly and substantially reduced the extent of tropical savannas in many parts of the world  
26 (Strassburg et al. 2017). Changes in fire regimes are also a threat to tropical savannas, but as  
27 opposed to tropical forests, this threat comes not only from frequent, severe and/or uncontrolled  
28 fires, but also from fire suppression (Bond and Parr 2010, Rosan et al. 2019). Fire was a key  
29 element in the evolution of tropical savannas and as such many species of its flora have  
30 adaptations to or are dependent on fire (Simon and Pennington 2012). In the absence of fire, the  
31 tree cover gradually increases and, as a result, savannas can be replaced by forests, notably in  
32 high-resource environments (Hoffmann et al. 2012) or in transitional regions where forest  
33 remnants share the landscape with grassland and savanna patches. In higher-rainfall savannas  
34 (also known as mesic savannas), for instance, this process can take place within a matter of only  
35 a few decades (Abreu et al. 2017, Durigan 2020). The biome shift from savanna to forest  
36 involves a major switch in the structure and composition of plant communities – with the  
37 replacement of fire-adapted species by species that are both fire-sensitive and shade-tolerant –,  
38 so that forests and savannas are regarded as alternative stable states mediated by plant-fire  
39 feedbacks (Hoffmann et al. 2012; Dantas et al. 2013).

40           While the patterns and mechanisms involved in the development of the vegetation in fire-  
41 suppressed savanna areas are relatively well documented (e.g., Stevens et al. 2017, Flake et al.  
42 2021), relatively little is known about how animal communities respond to woody encroachment  
43 (but see Woinarski et al. 2008, Leitner et al. 2018). The few existing studies have compared  
44 communities from areas with highly contrasting woody-plant cover (such as those that have been

45 protected from fire for a relatively long time versus those that have been burned, e.g., Andersen  
46 et al. 2006) and therefore it is unclear whether the observed changes in the structure of animal  
47 communities are gradual or rather become more abrupt at certain phases of the woody  
48 encroachment process.

49 Furthermore, there is limited information on the extent to which woody encroachment  
50 affects the functional and phylogenetic structure of savanna communities (but see Parr et al.  
51 2012). Measures of functional and phylogenetic diversity can complement those provided by the  
52 traditional taxonomic diversity metrics given that they take into account the evolutionary history  
53 and the functional traits of the members of a community. Functional diversity is a key  
54 component of biodiversity as it provides a link between species traits (morphological,  
55 physiological, or behavioral) and the role they play in the environment (Swenson 2014).  
56 Phylogenetic diversity, in turn, helps to address whether species in a community are drawn from  
57 the same clades or from distantly related lineages (Webb et al 2002, Cavender-Bares et al 2006).

58 Herein we combine species occurrence data drawn from extensive fieldwork, a species-  
59 level phylogeny built with phylogenomic data, and functional metrics drawn from a  
60 morphological dataset to evaluate the extent to which variation in tree cover in a fire-suppressed  
61 savanna landscape affects the taxonomic, functional, and phylogenetic diversity of Neotropical  
62 ant communities at the alpha and beta levels. More specifically, we tested the hypothesis that  
63 habitat openness is key driver of variation in ant communities (Andersen, 2019). For this, we  
64 sampled ants along an extensive tree cover gradient, ranging from open savannas to recently  
65 formed forest areas, and asked the following questions: (a) What is the relationship between tree  
66 cover and ant diversity? (b) Are changes in ant diversity along the tree cover gradient gradual or  
67 is there evidence of a rapid switch from one community state to another at a particular point of

68 the gradient? (c) To what extent are responses of phylogenetic and functional diversity congruent  
69 with those of taxonomic diversity?

70

## 71 **Material and Methods**

### 72 *Study area*

73 The study was performed at Santa Barbara Ecological Station (SBES), a biological  
74 reserve with an area of 2,715 ha located in Águas de Santa Barbara, São Paulo, Brazil (22°48'S,  
75 49°14'W), at an elevation 600 to 680 m a.s.l. Climate in the region is classified as Koppen's  
76 Cwa, characterized by a warm summer and a dry winter (Alvares et al. 2013), annual rainfall  
77 varies from 1,000 to 1,300 mm, and mean temperature of the coldest month is 18°C, while the  
78 hottest month exceeds 22°C of temperature (Meira-Neto et al. 2007).

79 At SBES, a fire suppression policy was in force for several decades, and an analysis of  
80 the vegetation development over a 30-yr period (1985- 2015) shows a steady temporal increase  
81 in tree cover (Abreu et al. 2017). At the time of our study, several of the former grassland and  
82 open savanna areas had turned into dense savanna or even forest (Abreu et al. 2017). In 2015, a  
83 prescribed fire experiment was initiated at SBES (Durigan et al. 2020) and the data analyzed here  
84 represents pre-fire data collected in December 2014 in all plots (each 20 x 50 m) designated for  
85 the fire experiment. These plots encompassed the entire variation in tree cover found in the study  
86 area and included plots established in open savanna (*campo sujo*), dense savanna (*cerrado sensu*  
87 *stricto*), and forest (*cerradão*). The fire history differs slightly among the study plots: 23 of the  
88 30 plots did not burn over the 1985-2015 period, six burned once, and one several times. The last  
89 fire event in any plot took place in 2011.

90

91 ***Tree cover***

92 As a measure of tree cover in each plot at the time of our sampling, we used the Leaf  
93 Area Index (LAI), a satellite-derived metric that is strongly and positively correlated with tree  
94 basal area (Abreu et al. 2017). LAI data for the study plots was obtained in April and May 2015.  
95 Each sampling plot was subdivided into ten subplots of 10 x10m. Each subplot had four  
96 collection points of LAI with hemispherical photographs. Photos were taken before sunrise, after  
97 sunset, or under homogeneous overcast skies. A tripod was used to position the camera (Canon  
98 EF 8-15mm fisheye lens) at a height of 1m, and the top of the camera was oriented relative to the  
99 north. Photos were taken with an underexposure of one f stop (Macfarlane et al. 2014), and the  
100 color images were converted to black and white using Hemisfer 2.12 (Thimonier et al. 2010;  
101 Schleppei et al. 2007) and using maximum blue contrast (Nobis and Hunziker 2005). The images  
102 were then analyzed with Hemisfer 2.12 using an automatic threshold for closed-canopy  
103 vegetation and with a supervised manual threshold under open canopies. The LAI values were  
104 averaged over the 40 subplots to obtain a single value for each plot (for more details see Abreu et  
105 al. 2017).

106

107 ***Ant sampling***

108 We used pitfall traps as the only method to sample ants as the large number of traps  
109 installed (600 in total) and the amazing abundance and diversity of ants at SBES precluded the  
110 use of other sampling methods. A total of 20 pitfall traps were installed in each plot, arranged in  
111 five grids of approximately  $2.5 \times 2.5$  m (keeping a minimum distance of 20 m between any two  
112 grids), with four pitfall traps installed at the corners of each grid. Each trap consisted of a small  
113 plastic cup (250 ml, 8.5 cm high and 7.8 cm in diameter) partially filled with water and

114 detergent. The traps remained in operation for 48 hours. Upon collection, the contents from the  
115 four traps set within the same grid were combined to make a composite sample. In the lab, ant  
116 workers were sorted into morphospecies and a representative specimen from each sample was  
117 dry-mounted for subsequent identification using available taxonomic keys (Fernández 2003,  
118 Bolton et al. 2007, Fernández and Ortiz-Sepúlveda 2019) or by comparison with specimens  
119 previously identified by ant taxonomists deposited at the Zoological Collection of the Federal  
120 University of Uberlândia (UFU), where the specimens collected were also deposited. Specimens  
121 for which a species-level identification was not possible received a morphospecies code.

122

### 123 *Ant phylogeny*

124 To compute the phylogeny-based diversity metrics (as detailed below), we used a  
125 maximum-likelihood tree created using DNA sequences of ultraconserved elements (UCEs) for  
126 one representative specimen of 167 of the 180 species/morphospecies collected (Online  
127 Resource 1: Fig. 1). Laboratory methods for sequence generation followed well-established  
128 protocols for library preparation, targeted capture, and sequencing of UCE data (see Online  
129 Resource 2 for a detailed overview). For the enrichment of UCE loci, we used an ant-customized  
130 bait set (“myBaits UCE Hymenoptera 2.5Kv2A”; ArborBiosciences, MI) that includes 9,898  
131 baits targeting 2,524 UCE loci conserved in Hymenoptera (Branstetter et al. 2017).

132 All sequence data processing and analysis was conducted using the Smithsonian’s High-  
133 Performance Computing cluster (Smithsonian Institution 2021). Sequencing reads were filtered  
134 and trimmed using Illumiprocessor (Faircloth 2013) and assembled using Trinity v. r2013-02-25  
135 (Grabherr et al. 2011). The resulting contigs were then processed following the Phyluce v1.5  
136 pipeline (Faircloth 2016). The UCE loci were extracted to separate FASTA files, and each locus



137 was aligned using MAFFT v. 7.130b (Katoh et al. 2002) and trimmed with GBLOCKS v. 0.91b  
138 (Castresana 2000). The alignment was filtered to include only loci available for at least 50% of  
139 the taxa, resulting in alignment including 2,258 loci. The concatenated dataset was partitioned by  
140 partition schemes defined by PartitionFinder2 (Lanfear et al. 2016), incorporating also the  
141 SWSC-EN algorithm (Tagliacollo and Lanfear 2018). The maximum-likelihood analyses were  
142 run with IQTREE v. 1.6.12 (Nguyen et al. 2015).

143

#### 144 *Ant morphological data and phylogenetic signal*

145 We measured five morphological traits that are commonly used in studies of ant  
146 functional diversity (Weiser and Kaspari 2006, Parr et al. 2017; Martello et al 2018; Online  
147 Resource 1: Table 2). Measurements were made of at least five specimens from each species;  
148 when fewer than five specimens were available, we measured all specimens. Whenever possible,  
149 the measured individuals were from different sampling plots. A detailed account of the  
150 hypothesized functions of each trait can be found in Parr et al. (2017) and Martello et al. (2018)  
151 but, briefly, (1) Weber's length is a measure of body size and is correlated with metabolic  
152 characteristics; (2) eye length is indicative of food searching behavior; (3) inter-ocular distance is  
153 involved in the perception of habitat complexity and the performance of visual predators; (4)  
154 femur length is indicative of locomotory abilities and food searching behavior; (5) mandible  
155 length is indicative of the ant's diet (Table S2). Prior to the analyses we obtained a relative  
156 measure of each trait (except Weber's length) by dividing the value of the particular trait by the  
157 Weber's length of the measured ant individual. All trait measures were then standardized to zero  
158 mean and unit variance.

159 We evaluated the degree of phylogenetic signal for each measured morphological trait  
160 using the Blomberg's K statistic (Blomberg et al. 2003). This metric uses a Brownian motion of  
161 trait evolution to evaluate whether the observed distribution of trait values differs from  
162 expectation under Brownian motion. K-values close to 1 indicate that traits exhibit phylogenetic  
163 signal, indicating that closely related species have more similar traits than expected under the  
164 Brownian motion model; K-values close to 0 indicate an absence of phylogenetic signal,  
165 meaning that closely related species are not more similar in their traits than distantly related  
166 species (Blomberg et al. 2003). The statistical significance of observed K-values was assessed  
167 through randomization tests that produced a null distribution of 999 K-values. We used the R  
168 package "phytools" (Revell 2012) to compute phylogenetic signals and statistical significance.

169

#### 170 ***Diversity metrics***

171 A dataset was built using information about the number of occurrences of each species in  
172 each plot (number of grids in which the species was recorded, for a maximum of five grids in  
173 each plot), the functional traits of each species, and the phylogenetic relationship between  
174 species. To estimate the taxonomic, functional, and phylogenetic alpha diversity of ant  
175 communities in each plot and the dissimilarity (beta diversity) between communities in different  
176 plots, we used the Rao's quadratic entropy index (Rao 1982, Pavoine et al. 2005). The Rao index  
177 is known to reflect community assembly processes well (Mouchet et al. 2010) and allows  
178 comparing the alpha and beta components of taxonomic, functional, and phylogenetic diversity  
179 within the same mathematical framework (De Bello et al. 2010). All diversity metrics were  
180 calculated using the "Rao" function and applying Jost's correction as recommended by De Bello  
181 et al. (2010). We estimated the pairwise functional and phylogenetic Euclidean distances

182 between species using the functions “*daisy*” and “*cophenetic.dist*”. The functions are  
183 implemented by “cluster” and “picante” packages, respectively (Maechler et al. 2019, Paradis  
184 and Schliep 2018).

185 The standardized effect size (SES) of the functional and phylogenetic, alpha and beta  
186 diversity metrics were also calculated. Standardized metrics are less sensitive to species richness  
187 differences and, in addition, allow the test of hypotheses regarding the functional and  
188 phylogenetic structure of the communities (Webb 2000). Negative values of SES ( $< -1.96$ ) are  
189 indicative of a clumped structure (i.e., greater importance of environmental filtering in  
190 determining the traits or lineages that are found in a given community), whereas positive values  
191 ( $> 1.96$ ) are indicative of a dispersed, functional or phylogenetic structure (i.e., greater  
192 importance of interspecific competition and niche partitioning) (Gotelli and Rohde 2002). We  
193 generated null communities by randomizing (999 randomizations) the community data matrix  
194 using the ‘independent swap’ algorithm. This algorithm maintains the row and column totals of  
195 the original matrix, meaning that the species richness and total number of ant records in each plot  
196 are not altered (Gotelli 2000). The null models were built using the “picante” package (Kembel  
197 et al. 2010). Then, we determined the difference between the observed diversity value and the  
198 mean of the null values and divided this difference by the standard deviation of the null values.  
199 All analyses were performed using the R environment (R Core Team 2021).

200

### 201 ***Statistical analyses***

202 We evaluated the relationship between tree cover and alpha diversity (taxonomic,  
203 functional or phylogenetic) using both linear and non-linear (quadratic and generalized additive -

204 GAM) regression models and selected the most appropriated model using the Akaike  
205 Information Criterion.

206 We performed Multiple Regression on Distance Matrices (MRDM) to assess the  
207 influence of geographic distance and tree cover on the taxonomic, functional, or phylogenetic  
208 dissimilarities between ant communities from different plots. The MRDM was based on  
209 Spearman correlation between the distance (dissimilarity) matrices, in order to test for a  
210 monotonic but not necessarily linear relationship between the matrices (Goslee and Urban 2007).  
211 We used the Euclidean distance to build the matrix of dissimilarity in tree cover (using the LAI  
212 of each plot) and the geographic distance matrix (using the coordinates of each plot). Statistical  
213 significance of the predictor variables was assessed through permutation tests (1000  
214 permutations). To assess the unique and shared influences of geographic distance and  
215 dissimilarity in tree cover on the dissimilarity (taxonomic, functional, or phylogenetic) of the  
216 sampled communities we partitioned the total variance explained by each model into percentages  
217 explained by each predictor variable alone or in combination (Borcard et al. 1992).

218 To illustrate differences in taxonomic, functional, or phylogenetic composition of the  
219 sampled communities, we built non-metric multidimensional (nMDS) ordination plots based on  
220 the matrices of pairwise dissimilarities generated by the “*Rao*” function. We evaluated if  
221 communities in plots classified as forest (i.e., with a LAI > 2, cf. Abreu et al. 2017) at the time of  
222 our study differed from those in dense (LAI < 2 and > 0.5) or open savanna (LAI < 0.5; Fig. 1d)  
223 using a Multivariate Analysis of Variance (MANOVA) and the ordination scores generated by  
224 our two-dimensional ordination analysis as the response variable (Peck 2011).

225 Moran’s I correlogram (Dray et al. 2011), based on six distance classes, were built to  
226 assess the presence of spatial autocorrelation in model residuals (Online Resource 1: Fig. 2).

227 Analyses were performed in R version 3.6.1 using the ‘vegan’, ‘ecodist’, and ‘mgcv’ packages  
228 (R core team 2021, Oksanen et al. 2020, Goslee and Urban 2007, Wood 2017).

229

## 230 **Results**

231 In total, we had 2,158 specimen records of 180 ant species from 51 genera (Online  
232 Resource 1: Table 1) The most diverse genus was *Pheidole* with 35 species, followed by  
233 *Camponotus* (16 species) and *Solenopsis* (9 species). The most common ant species were  
234 *Pheidole oxyops*, *Pheidole fracticeps*, *Solenopsis* sp. 01, *Ectatomma permagnum* and  
235 *Pachycondyla striata*. Together they accounted for 20.01% of all ant specimen records.

236 All five morphological traits exhibited Blomberg’s K values of less than one, indicating a  
237 significant albeit weak phylogenetic signal (Online Resource 1: Table 2).

238

### 239 ***Tree cover and alpha diversity***

240 We found significant variation in the taxonomic, functional, and phylogenetic alpha  
241 diversity of ant communities along the tree cover gradient (Fig. 1, Online Resource 1: Table 3).  
242 Taxonomic alpha diversity (TD) presented a non-linear relationship with LAI, peaking at LAI  
243 values around one and showing a more abrupt decline at values  $> 2$  (Fig. 1a). Phylogenetic alpha  
244 diversity (PD) was strongly correlated with TD ( $r = 0.814$ ,  $p < 0.001$ ) and, accordingly, showed a  
245 negative relationship with LAI (Fig. 1e). However, this relationship was no longer significant  
246 when we controlled for the effect of taxonomic diversity using a null model approach (ses.PD;  
247 Fig. 1f; Online Resource 1:Table 3). Looking at all the 30 ant communities sampled along the  
248 tree cover gradient we found that mean ses.PD did not differ significantly from zero (one sample  
249 t-test,  $t = 1.20$ ,  $p = 0.12$ ).

250 Functional alpha diversity (FD) was not correlated to either TD ( $r = -0.265$ ,  $p = 0.14$ ) or  
251 PD ( $r = -0.115$ ,  $p = 0.53$ ). Both FD and ses.FD showed a positive, non-linear relationship with  
252 LAI (Fig. 1b and c). There was a trend toward more positive than negative ses.FD values,  
253 notably in plots with a greater tree cover ( $LAI > 2$ ; Fig. 1c), but the mean ses.FD was not  
254 significantly different from zero (one sample t-test,  $t = 1.58$ ,  $p = 0.063$ ).

255 Overall, we did not detect any sign of spatial autocorrelation in the residuals of the  
256 models that evaluated the influence of LAI on ant alpha diversity (Online Resource 1: Fig. 2).

257

### 258 ***Tree cover and beta diversity***

259 Our multiple regression analyses indicate that geographic distance accounted for only a  
260 small and nearly negligible part of the observed dissimilarities in the taxonomic composition of  
261 the ant communities. Rather, much of the observed dissimilarity in the taxonomic composition of  
262 the sampled communities was explained by the dissimilarity in tree cover (LAI) among the  
263 survey plots (Fig. 2, Online Resource 1: Fig. 3).

264 The ordination analyses reinforced the view that variation in tree cover is a strong  
265 determinant of variation in taxonomic beta diversity. Notably, we found strong differences in the  
266 taxonomic composition between ant communities in plots with a LAI greater or lower than 2;  
267 i.e., between the forest and the dense or open savanna plots (Manova, followed by Hotelling's T-  
268 squared all-pairs comparison,  $p < 0.001$ ; Fig. 3). Species such as *Acromyrmex subterraneus*,  
269 *Carebara brevipilosa*, *Gnamptogenys striata*, *Hypoponera sp. 14*, *Neoponera marginata*,  
270 *Nylanderia sp. 05*, and *Pheidole fimbriata* were found only or mostly in the forest plots, whereas  
271 species such as *Apterostigma sp. 01*, *Camponotus renggeri*, *Cephalotes pusillus*, *Dinoponera*  
272 *australis*, *Dorymyrmex goeldii*, *Ectatomma opaciventris*, *Linepithema cerradenses*,

273 *Mycetophylax lectus*, *Pheidole jelskii* and *Solenopsis loretana* only or predominantly in the  
274 savanna plots (Online Resource 1: Fig. 4). Only a few species, such as *Forelius albiventris*,  
275 *Gnamptogenys sp. 05*, *Pogonomyrmex naegelli* and *Pheidole schwarzaieri*, were more  
276 characteristic of the most open savanna plots (LAI < 0.5; Online Resource 1: Fig. 4)

277 Patterns of functional and phylogenetic beta diversity were correlated with those of  
278 taxonomic beta diversity (standardized Mantel statistic: FD = 0.653; ses.FD = 0.649; PD = 0.762  
279 ; ses.PD = 0.693,  $P < 0.001$  in all Mantel tests with TD). Therefore, as also found for taxonomic  
280 beta diversity, both the functional and phylogenetic dissimilarities of the sampled communities  
281 increased as the dissimilarity in tree cover increased (Online Resource 1: Fig. 3), even though the  
282 standardized effect size of these metrics indicate that in general beta FD and PD values were not  
283 different from random expectation (Online Resource 1: Fig. 3).

284 Differences in the functional and phylogenetic composition of ant communities were  
285 particularly marked between the forest and savanna plots, with differences in ordination scores  
286 between these two groups being significant in all the analyses (Manova, followed by Hotelling's  
287 T-squared all-pairs comparison,  $p < 0.025$  in all pairwise comparisons, Fig. 3). Differences  
288 between open and dense savanna plots were only significant in the analyses of phylogenetic  
289 composition (PD Hotelling's T-squared = 10.9,  $p = 0.02$ : ses.PD, Hotelling's T-squared = 14.5,  $p$   
290 < 0.008, Fig. 3).

291

## 292 **Discussion**

293 Our study is the first to evaluate how variation in tree cover within a savanna-dominated  
294 landscape (the Cerrado) affects the taxonomic, functional, and phylogenetic diversity of ground-  
295 dwelling ants at the alpha and beta levels. We sampled ants along a relatively large tree cover

296 gradient and found that variation in tree cover (and thus in habitat openness) explained much of  
297 the variation in ant diversity. Furthermore, we found that variation in ant diversity was not  
298 uniform along the tree cover gradient. Rather, there is evidence of thresholds, at which major  
299 changes occur. At the alpha level, for instance, we found relatively little variation in taxonomic  
300 diversity (TD) along the first half of the tree cover gradient (i.e., from open to dense savanna),  
301 but at plots that became forest as result of the fire suppression policy at our study site (plots with  
302 a LAI > 2), alpha TD declined sharply.

303         In addition, there were marked differences in the taxonomic composition (beta diversity)  
304 between the forest and savanna communities, with several species occurring exclusively or  
305 predominantly in one side of the gradient, whereas those that were found throughout the tree  
306 cover gradient often showed major shifts in abundance at the savanna-forest transition. That  
307 woody encroachment resulting from fire suppression can affect the species richness and  
308 composition of savanna ant communities has been demonstrated previously (Andersen et al.  
309 2006, Maravalhas and Vasconcelos 2014, Abreu et al. 2017). However, as shown here, changes  
310 are largely non-linear, with savanna ant communities switching rapidly to an alternative state  
311 once savanna turns into forest. In this sense, patterns of taxonomic ant diversity in tropical  
312 savannas subject to woody encroachment appear to be in sharp contrast with those found in  
313 studies of secondary succession in tropical forests, during which ant diversity changes gradually  
314 as the forest grows older (Bihn et al. 2010, Rocha-Ortega et al. 2018).

315         Patterns of functional and phylogenetic beta diversity largely mirrored those of  
316 taxonomic beta diversity. The major changes in the functional and phylogenetic composition of  
317 ant communities often occurred at the savanna-forest transition, indicating that the observed  
318 turnover of species at this transition resulted in concomitant changes in the traits and lineages of



319 the species composing the local communities. Studies in Australia also report marked turnover of  
320 ant species at the savanna/forest transition (Andersen et al. 2012, Andersen 2019), suggesting  
321 that the non-linear response of the ant fauna to variation in tree cover that we detected here  
322 occurs more widely in tropical savannas.

323         Functional and phylogenetic diversity showed contrasting responses to variations in tree  
324 cover at the alpha level, and this may well reflect the fact that all morphological/functional traits  
325 we measured showed a weak phylogenetic signal (Cadotte et al. 2013). In general, savanna plots  
326 presented greater alpha PD than did the forest plots, indicating that the diversity of ant lineages  
327 was greater in the former than in the latter. In contrast, alpha FD tended to increase as the tree  
328 cover increased. Nevertheless, the relationship between PD and tree cover (but not that between  
329 FD and tree cover) disappeared when the difference in species richness between the sampled  
330 communities was taken into account using a null model approach (ses.PD). This indicates that  
331 the relationship between PD and tree cover was largely mediated by the variation in TD along  
332 the gradient. This was expected given the strong correlation between TD and PD. The correlation  
333 between TD and other diversity metrics (FD and PD) has been reported previously. For instance,  
334 the dependency of these diversity metrics on TD was detected in studies comparing ant  
335 communities in contrasting habitats (Blaimer et al. 2015, Agavekar et al. 2019, Dröse et al. 2019)  
336 and along elevational gradients (Silvestre et al. 2021).

337         In none of the ant communities we sampled did we find greater or lower than expected  
338 PD (given the TD of the community), suggesting that these communities have a random  
339 phylogenetic structure. Similarly, all the communities sampled presented non-significant ses.FD  
340 values. However, communities in the more closed habitats tended to present more positive  
341 ses.FD values than those in the more open habitats, suggesting that the relative importance of

342 interspecific competition and niche partitioning in structuring these communities potentially  
343 increases as tree cover increases. Studies of tropical forest succession also found significant  
344 variation in the FD of ant communities (Bihn et al. 2010, Rocha-Ortega et al. 2018), and there is  
345 evidence that such variation appears to be associated with the greater occurrence of  
346 morphologically unique, predatory species in the more advanced successional stages (Rocha-  
347 Ortega et al. 2018, Santoandré et al. 2019). Similarly, here we found that predatory species of the  
348 genera *Hypoponera*, *Odontomachus*, and *Pachycondyla* were largely associated with the more  
349 closed forest plots.

350

## 351 **Conclusions**

352 Overall, our results give support to the idea that habitat openness is a key driver of  
353 variation in ant communities, and that ant responses to disturbance are strongly linked to their  
354 responses to habitat openness (Andersen 2019). In addition, we found strong support to the idea  
355 that fire mediates alternative states of ant communities in tropical savannas (Andersen et al.  
356 2012). Thirty years of a fire suppression policy at our study area resulted in a substantial increase  
357 in tree cover, with former grassland and savanna areas becoming forest in several cases (Abreu et  
358 al. 2017). Where this occurred, the ant community changed abruptly, as the newly formed forest  
359 areas favored the development of a shade-adapted fauna at the expense of the fauna more  
360 characteristic of the savanna habitat. Forests and savannas coexist in many tropical landscapes,  
361 and such habitat heterogeneity is key to explaining the high local diversity of many taxonomic  
362 groups (e.g. da Mata and Tidon 2013, Ribeiro et al. 2020, Costa et al. 2020), including ants  
363 (Pacheco and Vasconcelos, 2012). Therefore, the adoption of a fire suppression policy, as is  
364 currently the case in many protected areas of the Cerrado, is likely to result in the local loss of

365 many open habitat specialists, and consequently in a decrease in ant diversity and in the  
366 homogenization of the ant fauna at the landscape level. Ecosystem management in such  
367 landscapes should aim at maintaining the high heterogeneity of habitats which characterizes the  
368 alternative states within the Cerrado biome.

369 **Acknowledgments**

370 We thank R. Pacheco and J. Vieira for helping with the ant sorting and taxonomic  
371 identification. E. Koch and J. Maravalhas for helping with the field work, W. Hoffman for  
372 helping design and set up the fire experiment and collect the LAI data, and A. Andersen for  
373 commenting on a previous version of the manuscript. KN was supported by a Peter Buck  
374 Predoctoral Fellowship at the Smithsonian Institution's National Museum of Natural History and  
375 a PhD scholarship from CAPES. The laboratory and the computer work were conducted in and  
376 with the support of the LAB facilities of the National Museum of Natural History and the  
377 Smithsonian Institution OCIO team.

378

379 **Declarations**

380 ***Funding***

381 This study was supported by grants from the Brazilian Council of Research and Scientific  
382 Development (CNPq grants 302588/2015-9, 304628/2020-4 to HLV, and 309709/2020-2 to  
383 GD), and the U.S. National Science Foundation (NSF grant 1654829 to TRS, DEB-1354943 to  
384 W. Hoffmann, and DEB-1654829 and CAREER DEB-1943623 to Christian Rabeling).

385 ***Conflicts of interest/Competing interests***

386 The authors declare that they have no conflict of interest.

387 ***Ethics approval***

388 Not applicable

389 ***Consent to participate***

390 Not applicable

391 ***Consent for publication***

392 Not applicable

393 **Availability of data and material**

394 After acceptance for publication, the DNA sequence data will be deposited in a proper  
395 repository.

396 **Code availability**

397 Not applicable

398

399 **Literature Cited**

400 Abreu RCR Hoffmann WA, Vasconcelos HL, Pilon NA, Rossatto DR, Durigan G (2017) The  
401 biodiversity cost of carbon sequestration in tropical savanna. *Science Advances*. 3:e1701284.  
402 <https://doi.org/10.1126/sciadv.1701284>

403

404 Agavekar G, Agashe D, and Economo EP (2019) Dimensions of ant diversity on a small tropical  
405 island. *Insect Conservation and Diversity*. 12:161-171. <https://doi.org/10.1111/icad.12326>

406

407 Alvares CA, Stape JL, Sentelhas PC, Gonçalves JLM and Sparovek G (2013) Köppen's climate  
408 classification map for Brazil. *Meteorologische Zeitschrift*. 22:711–728.

409 <https://doi.org/10.1127/0941-2948/2013/0507>

410

411 Andersen AN, Hertog T and Woinarski JC (2006) Long-term fire exclusion and ant community  
412 structure in an Australian tropical savanna: congruence with vegetation succession. *Journal of*  
413 *Biogeography*. 33: 823–832. <https://doi.org/10.1111/j.1365-2699.2006.01463.x>

414

415 Andersen AN, Woinarski JC, and Parr CL (2012) Savanna burning for biodiversity: fire  
416 management for faunal conservation in Australian tropical savannas. *Austral Ecology*. 37:658–  
417 667. <https://doi.org/10.1111/j.1442-9993.2011.02334.x>

418

419 Andersen AN (2019) Responses of ant communities to disturbance: five principles for  
420 understanding the disturbance dynamics of a globally dominant faunal group. *Journal of Animal*  
421 *Ecology*. 88:350–362. <https://doi.org/10.1111/1365-2656.12907>

422

423 Bihn JH, Gebauer G and Brandl R (2010) Loss of functional diversity of ant assemblages in  
424 secondary tropical forests. *Ecology*. 91: 782-792. <https://doi.org/10.1890/08-1276.1>

425

426 Blaimer BB, Brady SG, Schultz TR, Fisher BL (2015) Functional and phylogenetic approaches  
427 reveal the evolution of diversity in a hyper diverse biota. *Ecography* 38:901–912.

428 <https://doi.org/10.1111/ecog.01370>

429

430 Blomberg SP, Garland TJR, and Ives AR (2003) Testing for phylogenetic signal in comparative  
431 data behavioral traits are more labile. *Evolution*. 57: 717-745. <https://doi.org/10.1111/j.0014->

432 [3820.2003.tb00285.x](https://doi.org/10.1111/j.0014-3820.2003.tb00285.x)

433

434 Bolton B, Alpert G, Ward PS, Naskrecki P (2007) Bolton's catalogue of ants of the world.

435 (Harvard University Press, 2007). <https://doi.org/10.5860/choice.44-6566>

436

437 Bond WJ and Parr CL (2010) Beyond the forest edge: ecology, diversity and conservation of the  
438 grassy biomes. *Biological Conservation*. 143: 2395-2404.

439 <https://doi.org/10.1016/j.biocon.2009.12.012>

440

441 Borcard D, Legendre P and Drapeau P (1992) Partialling out the spatial component of ecological  
442 variation. *Ecology*. 73:1045-1055. <https://doi.org/10.2307/1940179>

443

444 Branstetter MG, Longino JT, Ward PS and Faircloth BC (2017) Enriching the ant tree of life:  
445 enhanced UCE bait set for genome-scale phylogenetics of ants and other Hymenoptera. *Methods*  
446 *Ecology and Evolution*. 8: 768-776. <https://doi.org/10.1111/2041-210X.12742>  
447

448 Cadotte M, Albert CH and Walker SC (2013) The ecology of differences: assessing community  
449 assembly with trait and evolutionary distances. *Ecology Letters*, 16:1234-1244.  
450 <https://doi.org/10.1111/ele.12161>  
451

452 Castresana J (2000) Selection of conserved blocks from multiple alignments for their use in  
453 phylogenetic analysis. *Molecular Biology and Evolution*. 17:540-52.  
454 <https://doi.org/10.1093/oxfordjournals.molbev.a026334>  
455

456 Cavender-Bares J, Keen A and Miles B (2006) Phylogenetic structure of Floridian plant  
457 communities depends on taxonomic and spatial scale. *Ecology*. 87:109-122.  
458 [https://doi.org/10.1890/0012-9658\(2006\)87\[109:PSOFPC\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[109:PSOFPC]2.0.CO;2)  
459

460 Costa BM, Pantoja DL, Sousa HC, de Queiroz TA and Colli GR (2020) Long-term, fire-induced  
461 changes in habitat structure and microclimate affect Cerrado lizard communities. *Biodiversity*  
462 *and conservation*. 29:1659-1681. <https://doi.org/10.1007/s10531-019-01892-8>  
463

464 Da Mata RA and Tidon R (2013) The relative roles of habitat heterogeneity and disturbance in  
465 drosophilid assemblages (Diptera, Drosophilidae) in the Cerrado. *Insect Conservation and*  
466 *Diversity*. 6:663-670. <https://doi.org/10.1111/icad.12020>



467

468 Dantas VL, Batalha MA and Pauasas JG (2013) Fire drives functional thresholds on the savanna-  
469 forest transition. *Ecology* 94: 2454-2463. <https://doi.org/10.1890/12-1629.1>

470

471 De Bello F, Lavergne S, Meynard CN, Leps J and Thuiller W (2010) The partitioning of  
472 diversity: showing Theseus a way out of the labyrinth. *Journal of Vegetation Science* 21:992-  
473 1000. <https://doi.org/10.1111/j.1654-1103.2010.01195.x>

474

475 Dray, S (2011) A new perspective about Moran's coefficient: spatial autocorrelation as a linear  
476 regression problem. *Geographical Analysis*. 43:127-141. [https://doi.org/10.1111/j.1538-  
477 4632.2011.00811.x](https://doi.org/10.1111/j.1538-4632.2011.00811.x)

478

479 Dröse W, Podgaiski LR, Dias CF and Mendonça MS (2019) Local and regional drivers of ant  
480 communities in forest-grassland ecotones in South Brazil: a taxonomic and phylogenetic  
481 approach. *Plos one* 14:1–20. <https://doi.org/10.1371/journal.pone.0215310>

482

483 Durigan G (2020) Zero-fire: Not possible nor desirable in the Cerrado of Brazil. *Flora*. 268:  
484 151612. <https://doi.org/10.1016/j.flora.2020.151612>

485

486 Faircloth BC, MacCormack JE, Crawford NG, Harvey MG, Brumfield RT, Glenn TC (2012)  
487 Ultraconserved elements anchor thousands of genetic markers spanning multiple evolutionary  
488 timescales. *Systematic Biology*. 61:717-726. <https://doi.org/10.1093/sysbio/sys004>

489

490 Faircloth BC (2013) Illumiprocessor: a trimmomatic wrapper for parallel adapter and quality  
491 trimming. <http://dx.doi.org/10.6079/J9ILL>.

492

493 Faircloth BC (2016) PHYLUCE is a software package for the analysis of conserved genomic  
494 loci. *Bioinformatics*. 32: 786-788. <https://doi.org/10.1093/bioinformatics/btv646>

495

496 Fernández F (2003) *Introducción a las hormigas de la región Neotropical*. Instituto de  
497 Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá.

498

499 Fernández F, Ortiz-Sepúlveda CM (2019). Subfamily Formicidae. In: Fernandez F, Guerrero RJ,  
500 Delsinne T. *Hormigas de Colombia*. Universidad Nacional de Colombia. Bogotá. pp 721-741.

501

502 Flake SW, Abreu RCR, Durigan G and Hoffmann WA (2021) Savannas are not old fields:  
503 Functional trajectories of forest expansion in a fire-suppressed Brazilian savanna are driven by  
504 habitat generalists. *Functional Ecology*. 35:1797-1809. <https://doi.org/10.1111/1365-2435.13818>

505

506 Goslee SC and Urban DL (2007) The ecodist package for dissimilarity-based analysis of  
507 ecological data. *Journal of Statistical Software*. 22:1-19. <https://doi.org/10.18637/jss.v022.i07>

508

509 Gotelli NJ (2000) Null model analysis of species co-occurrence patterns. *Ecology*. 81: 2606-  
510 2621. [https://doi.org/10.1890/0012-9658\(2000\)081\[2606:NMAOSC\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[2606:NMAOSC]2.0.CO;2)

511

512 Gotelli NJ and Rohde K (2002) Co-occurrence of ectoparasites of marine fishes: a null model  
513 analysis. *Ecology Letters*. 5:86-94. <https://doi.org/10.1046/j.1461-0248.2002.00288.x>  
514

515 Grabherr MG, Haas BJ, Yassour M, Levin JZ, Thompson DA, Amit I, Adiconis X, Fan L,  
516 Raychowdhury R, Zeng Q, Chen Z, Mauceli E, Hacohen N, Gnirke A, Rhind N, de Palma F,  
517 Birren BW, Nusbaum C, Lindblad-Toh K and Friedman N (2011) Trinity: reconstructing a full-  
518 length transcriptome without a genome from RNA-Seq data. *Nature Biotechnology*. 29: 644-652.  
519 <https://doi.org/10.1038/nbt.1883>  
520

521 Hoffmann WA, Geiger EL, Gotsch SG, Rossatto DR, Silva LCR, Lau OL, Haridasan M, and  
522 Franco AC (2012) Ecological thresholds at the savanna–forest boundary: how plant traits,  
523 resources and fire govern the distribution of tropical biomes. *Ecology Letters*. 5:759–  
524 768. <https://doi.org/10.1111/j.1461-0248.2012.01789.x>.  
525

526 Katoh K, Misawa K, Kuma K and Miyata T (2002) MAFFT: a novel method for rapid multiple  
527 sequence alignment based on fast Fourier transform. *Nucleic Acids Research*. 30:3059-66.  
528 <https://doi.org/10.1093/nar/gkf436>  
529

530 Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, Blomberg SP and  
531 Webb CO (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*.  
532 26:1463-1464. <https://doi.org/10.1093/bioinformatics/btq166>  
533

534 Lanfear R, Frandsen PB, Wright AM, Senfeld T and Calcott B (2016) PartitionFinder2: New  
535 methods for selecting partitioned models of evolution for molecular and morphological  
536 phylogenetic analyses. *Molecular Biology and Evolution*. 34:772-773.  
537 <https://doi.org/10.1093/molbev/msw260>  
538

539 Leitner M, Davies AB, Parr CL, Eggleton P and Robertson MK (2018) Woody encroachment  
540 slows decomposition and termite activity in an African savanna. *Global Change Biology* 24:  
541 2597-2606. <https://doi.org/10.1111/gcb.14118>  
542

543 Macfarlane C, Ryu Y, Ogden GN and Sonnentag O (2014) Digital canopy photography: exposed  
544 and in the raw. *Agricultural and Forest Meteorology*. 197:244-253.  
545 <https://doi.org/10.1016/j.agrformet.2014.05.014>  
546

547 Maechler M, Rousseeuw P, Struyf A, Hubert M and Hornik K (2019) cluster: Cluster Analysis  
548 Basics and Extensions. R package version 2.1.0.  
549

550 Maravalhas J and Vasconcelos HL (2014) Revisiting the pyrodiversity–biodiversity hypothesis:  
551 long-term fire regimes and the structure of ant communities in a Neotropical savanna hotspot.  
552 *Journal of Applied Ecology*. 51: 1661-1668. <https://doi.org/10.1111/1365-2664.12338>  
553

554 Martello F, de Bello F, Morini MSC, Silva RR, Souza-Campana DR, Ribeiro MC and Carmona  
555 CP (2018) Homogenization and impoverishment of taxonomic and functional diversity of ants  
556 in Eucalyptus plantations. *Scientific reports* 8:3266. <https://doi.org/10.1038/s41598-018-20823-1>

557

558 Meira-Neto JA, Martins FR and Valente GE (2007) Composição florística e espectro biológico  
559 na Estação Ecológica de Santa Bárbara, Estado de São Paulo, Brasil. *Revista Árvore* 31:907–  
560 922. <https://doi.org/10.1590/S0100-67622007000500015>

561

562 Mouchet MA, Villéger S, Mason NWH and Mouillot D (2010) Functional diversity measures: an  
563 overview of their redundancy and their ability to discriminate community assembly rules.  
564 *Functional Ecology*. 24:867-876. <https://doi.org/10.1111/j.1365-2435.2010.01695.x>

565

566 Murphy BP, Andersen AN and Parr CL (2016) The underestimated biodiversity of tropical  
567 grassy biomes. *Philosophical Transactions of The Royal Society B*. 371: 20150319.  
568 <https://doi.org/10.1098/rstb.2015.0319>

569

570 Nguyen LT, Schmidt HA, Haeseler A and Minh BQ (2015) IQ-TREE: A fast and effective  
571 stochastic algorithm for estimating maximum likelihood phylogenies. *Molecular Biology and*  
572 *Evolution*. 32:268-274. <https://doi.org/10.1093/molbev/msu300>

573

574 Nobis M and Hunziker U (2005) Automatic thresholding for hemispherical canopy-photographs  
575 based on edge detection. *Agricultural and Forest Meteorology*. 128:243-250.  
576 <https://doi.org/10.1016/j.agrformet.2004.10.002>

577

578 Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara  
579 RB, Simpson GL, Solymos P, Henry M, Stevens H, Szoecs E and Wagner H (2020) *vegan*:

580 Community Ecology Package. R package. Version 2.5-7.

581

582 Pacheco RPN and Vasconcelos HL (2012) Habitat diversity enhances ant diversity in a naturally  
583 heterogeneous Brazilian landscape. *Biodiversity and Conservation*. 21:797-809.

584 <https://doi.org/10.1007/s10531-011-0221-y>

585

586 Paradis E and Schliep K (2018) ape 5.0: an environment for modern phylogenetics and  
587 evolutionary analyses in R. *Bioinformatics*. 35: 526-528.

588 <https://doi.org/10.1093/bioinformatics/bty633>

589

590 Parr CL, Dunn RR, Sanders NJ, Weiser MD, Photakis M, Bishop TR, Fitzpatrick MC, Arnan X,  
591 Baccaro F, Brandão CRF, Chick L, Donoso DA, Fayle TM, Gómez C, Grossman B, Munyai TC,  
592 Pacheco R, Retana J, Robinson A, Sagata K, Silva RR, Tista M, Vasconcelos HL, Yates M and  
593 Gibb H. 2017. GlobalAnts: a new database on the geography of ant traits (Hymenoptera:  
594 Formicidae). *Insect Conservation and Diversity* 10: 5-20. <https://doi.org/10.1111/icad.12211>

595

596 Parr CL, Gray E, and Bond WJ (2012) Cascading biodiversity and functional consequences of a  
597 global change-induced biome switch. *Diversity and Distributions*. 18: 493-503.

598 <https://doi.org/10.1111/j.1472-4642.2012.00882.x>

599

600 Pavoine S, Ollier S and Pontier D (2005) Measuring diversity from dissimilarities with Rao's  
601 quadratic entropy: are any dissimilarities suitable? *Theoretical Population Biology*. 67: 231-9.

602 <https://doi.org/10.1016/j.tpb.2005.01.004>

603

604 Peck JE (2011) Fast, easy, and publication-quality ecological analyses with PC-ORD. The  
605 Bulletin of the Ecological Society of America. 92: 298-301. [https://doi.org/10.1890/0012-9623-](https://doi.org/10.1890/0012-9623-92.3.298)  
606 92.3.298

607

608 R Core Team (2021). R: A language and environment for statistical computing. R Foundation for  
609 Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

610

611 Rao CR (1982) Diversity and dissimilarity coefficients: a unified approach. Theoretical  
612 population biology. 21:24-43. [https://doi.org/10.1016/0040-5809\(82\)90004-1](https://doi.org/10.1016/0040-5809(82)90004-1)

613

614 Revell LJ (2012) phytools: an R package for phylogenetic comparative biology (and other  
615 things). Methods in Ecology and Evolution. 3: 217-223. [https://doi.org/10.1111/j.2041-](https://doi.org/10.1111/j.2041-210X.2011.00169.x)  
616 210X.2011.00169.x

617

618 Ribeiro R, Ricklefs RE, and Marinho J (2020) Partitioning beta diversity to unravel mechanisms  
619 underlying the distributions of nonvolant small mammals in Brazil's Cerrado. Journal of  
620 Mammalogy. 101:1438-1450. <https://doi.org/10.1093/jmammal/gyaa085>

621

622 Rocha-Ortega M, Arnan X, Ribeiro-Neto JD, Leal IR, Favila ME and Martínez-Ramos M (2018)  
623 Taxonomic and functional ant diversity along a secondary successional gradient in a tropical  
624 forest. Biotropica. 50: 290-301. <https://doi.org/10.1111/btp.12511>

625

626 Rosan TM, Aragão LEOC, Oliveras I, Phillips OL, Malhi Y, Gloor E. and Wagner FH (2019)  
627 Extensive 21st-Century woody encroachment in South America's savanna. *Geophysical*  
628 *Research Letters*. 46:6594-6603. <https://doi.org/10.1029/2019GL082327>  
629  
630 Santoandré S, Filloy J, Zurita GA and Bellocq MI (2019) Ant taxonomic and functional diversity  
631 show differential response to plantation age in two contrasting biomes. *Forest Ecology and*  
632 *Management*. 437:304-313. <https://doi.org/10.1016/j.foreco.2019.01.021>  
633  
634 Schleppi P, Conedera M, Sediyy I and Thimonier A (2007) Correctiong non-linearity and slope  
635 effects in the estimation of the leaf area index of forests from hemispherical photographs.  
636 *Agricultural and Forest Meteorology*. 144:236-242.  
637 <https://doi.org/10.1016/j.agrformet.2007.02.004>  
638  
639 Silvestre M, Carmona CP, Azcárate FM and Seoane J (2021) Diverging facets of grassland ant  
640 diversity along a Mediterranean elevational gradient. *Ecological Entomology*.  
641 <https://doi.org/10.1111/een.13077>  
642  
643 Simon MF and Pennington T (2012) Evidence for fire adaptation to fire regimes in the tropical  
644 savannas of the Brazilian Cerrado. *International Journal of Plant Sciences*. 173:711-723.  
645 <https://doi.org/10.1086/665973>  
646  
647 Smithsonian Institution. 2021. High Performance Computing Cluster.  
648 <https://doi.org/10.25572/SIHPC>



649

650 Stevens N, Lehmann CER, Murphy BP and Durigan G (2017) Savanna woody encroachment is  
651 widespread across three continents. *Global Change Biology*. 23:235-244.

652 <https://doi.org/10.1111/gcb.13409>

653

654 Strassburg B, Brooks T, Feltran-Barbieri R, Iribarrem A, Crouzeilles R, Loyola R, Latawiec AE,  
655 Oliveira-Filho FJB, Scaramuzza CAM, Scarano FR, Soares-Filho B and Balmford A (2017)  
656 Moment of truth for the Cerrado hotspot. *Nature Ecology and Evolution*. 1:0099.

657 <https://doi.org/10.1038/s41559-017-0099>

658

659 Swenson NG and Weiser, MD (2014) On the packing and filling of functional space in eastern  
660 North American tree assemblages. *Ecography*. 37:1056–1062.

661 <https://doi.org/10.1111/ecog.00763>

662

663 Tagliacollo VA and Lanfear R (2018) Estimating improved partitioning schemes for  
664 Ultraconserved Elements. *Molecular Biology and Evolution*. 35:1798–1811.

665 <https://doi.org/10.1093/molbev/msy069>

666

667 Thimonier A, Sedivy I and Schleppei P (2010) Estimating leaf area index in different types of  
668 mature forest stands in Switzerland: a comparison of methods. *European Journal of Forest  
669 Research*. 129:543-562. <https://doi.org/10.1007/s10342-009-0353-8>

670

671 Webb CO (2000) Exploring the phylogenetic structure of ecological communities : an example

672 for rain forest trees. *American Naturalist*.156:145–155. <https://doi.org/10.1086/303378>

673

674 Webb CO, Ackerly DD, McPeck MA and Donoghue MJ (2002) Phylogenies and community  
675 ecology. *Annual Review of Ecology and Systematics*. 33:475–505.

676 <https://doi.org/10.1146/annurev.ecolsys.33.010802.150448>

677

678 Weiser MD and Kaspari M (2006) Ecological morphospace of New Worlds ants. *Ecological*  
679 *Entomology*. 31:131-142. <https://doi.org/10.1111/j.0307-6946.2006.00759.x>

680

681 Woinarski J, Risler L and Kean JCZ (2008) Response of vegetation and vertebrate fauna to 23  
682 years of fire exclusion in a tropical Eucalyptus open forest, Northern Territory, Australia. *Austral*  
683 *Ecology*. 29:156-176. <https://doi.org/10.1111/j.1442-9993.2004.01333.x>

684

685 Wood SN (2017) *Generalized Additive Models: An Introduction with R, Second Edition (2nd*  
686 *ed.)*. Chapman and Hall/CRC.

687 **Figure legends**

688 Figure 1. The relationship between tree cover (Leaf Area Index, LAI) and ant alpha diversity. (a)  
689 Taxonomic diversity, (b) observed functional diversity, (c) standardized effect size of functional  
690 diversity, (e) observed phylogenetic diversity, (f) standardized effect size of phylogenetic  
691 diversity. (d) Differences in LAI between plots classified as open savanna, dense savanna or  
692 forest at the time of the ant sampling.

693

694 Figure 2. Results of the variation partitioning analysis showing the amount of variation in the  
695 taxonomic, functional or phylogenetic dissimilarity of ant communities explained uniquely by  
696 differences in tree cover (LAI), by the spatial distance between sampling plots, or by these two  
697 factors combined.

698

699 Figure 3. nMDS ordination plot of the ant communities in relation to their (a) taxonomic, (b, c)  
700 functional, or (d, e) phylogenetic dissimilarities (beta diversity). The symbol size is proportional  
701 to the Leaf Area Index (LAI) of the sampling plot.

Figure 1

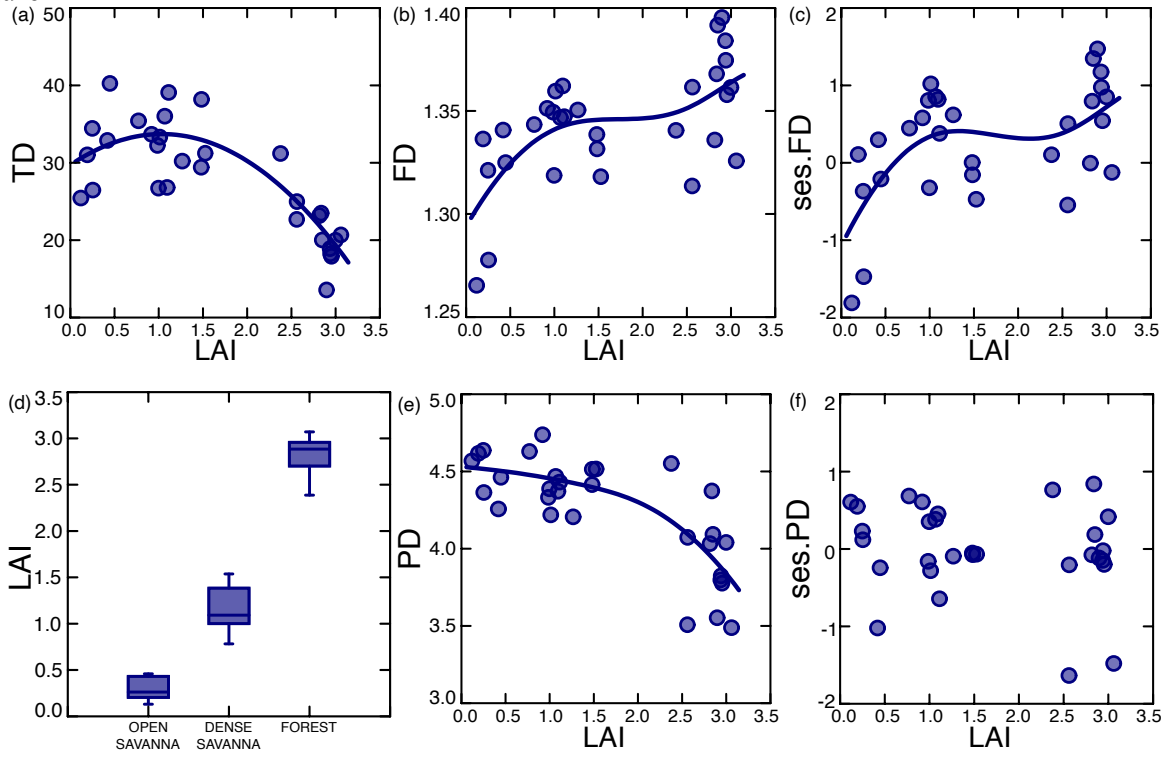


Figure 2

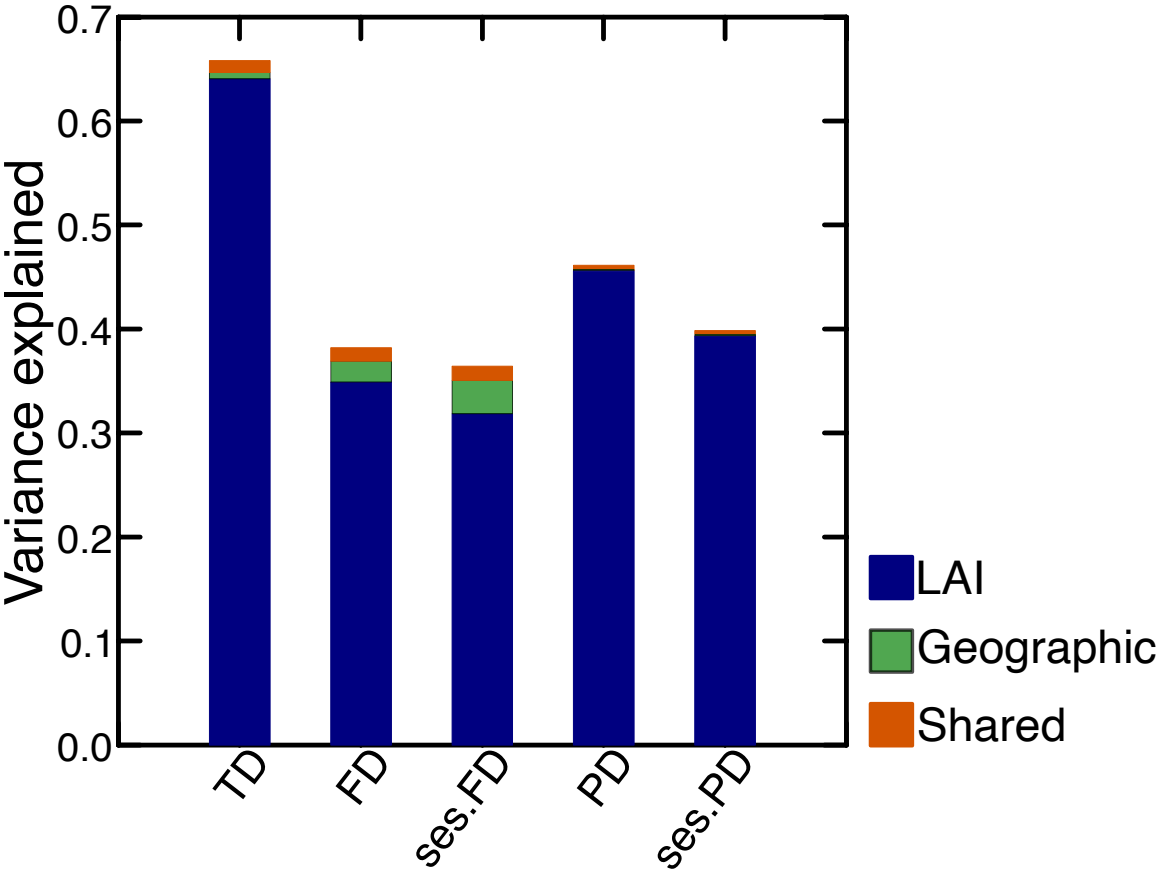
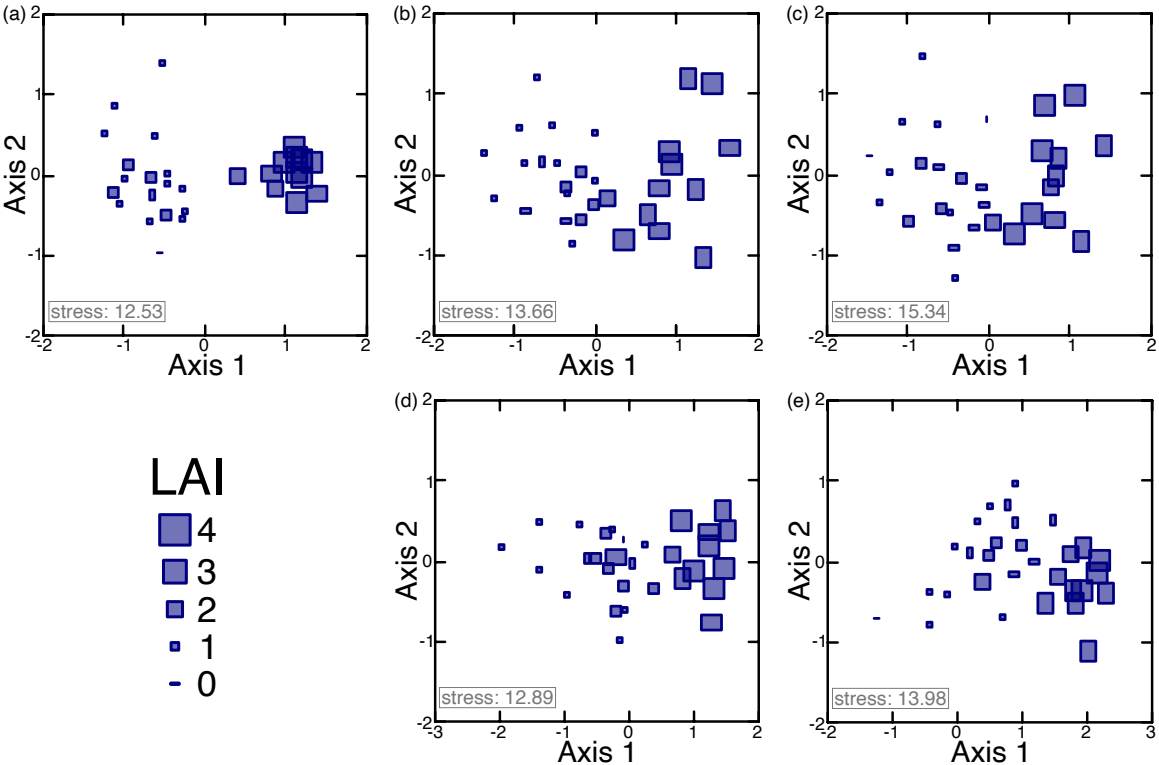


Figure 3



## Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [OnlineResource1TreeCoverAntdiversity.pdf](#)
- [OnlineResource2TreeCoverAntdiversity.pdf](#)