




# Landscape genetics in a highly threatened environment: how relevant to ants is the physiognomic mosaic of the cerrado savanna?

Marianne Azevedo-Silva<sup>1</sup> · Marina C. Côrtes<sup>2</sup> · Carolina S. Carvalho<sup>3</sup> · Gustavo M. Mori<sup>4</sup> · Anete P. Souza<sup>5</sup> · Paulo S. Oliveira<sup>6</sup> 

Received: 19 December 2022 / Accepted: 18 May 2023  
© The Author(s), under exclusive licence to Springer Nature B.V. 2023

## Abstract

The Brazilian cerrado is one of the world's biodiversity hotspots, comprising a mosaic of vegetation physiognomies. The cerrado presents a high ant diversity, and ant genetic variation can be subjected to the influence of landscape features. Here, we investigate how the composition and configuration of a cerrado reserve (4500 ha) in SE Brazil influence dispersal and gene flow (through measures of genetic distance) in two abundant carpenter ants, *Camponotus renggeri* and *C. rufipes*. Based on landscape genetics, we evaluated the degree of permeability of different land covers on the dispersal of ant queens, males and workers, employing a genetic optimization algorithm framework. We found little genetic structure in *C. renggeri*, regardless of caste. By contrast, we observed the formation of clear genetic clusters in *C. rufipes*, mainly for workers and queens. For workers of both species, we found that genetic distance was not influenced by geographic distance or landscape composition. For queens and males of *C. renggeri*, geographic distance was the most important factor explaining genetic distance. For *C. rufipes* queens and males, however, the best model considered the effect of landscape resistance to gene flow (i.e. the cost imposed by land use and cover types), with males dispersing through human-affected areas such as roads, and queens through forested cerrado areas. Our results showed that cerrado landscape can differentially affect ant dispersal, even for closely related species, reinforcing the importance of using different castes and sexes in landscape genetics of social insects. Our study also highlights that preservation of different vegetation physiognomies of cerrado is relevant for ant dispersal performance.

**Keywords** Anthropogenic disturbance · Gene flow · Hymenoptera · Isolation by environment · Population genetics · Social insects

## Introduction

The cerrado savanna is the second largest biome in Brazil, originally covering nearly 22% of the country's surface area (Oliveira and Marquis 2002). The so-called *cerrados* comprise a mosaic of vegetation physiognomies, mainly determined by soil fertility, water availability and fire incidence. The cerrado domain ranges from (i) open grasslands with scattered shrubs and small trees to (ii) areas known as “cerrado sensu stricto”, characterized by a fair amount of herbaceous plants, with trees and shrubs counting for more than 30% of vegetation cover, and (iii) dense woodlands known as “cerradão” where trees are often 8–12 m tall, with crown cover ranging from 50 to 90% and a very reduced herbaceous layer (Oliveira-Filho and Ratter 2002). As one of the 25 world's biodiversity hotspots (Myers et al. 2000), the *cerrados* are considered

Paulo S. Oliveira  
pso@unicamp.br

- <sup>1</sup> Programa de Pós-Graduação em Ecologia, Universidade Estadual de Campinas, Campinas, SP, Brazil
- <sup>2</sup> Departamento de Biodiversidade, Universidade Estadual Paulista, Rio Claro, SP, Brazil
- <sup>3</sup> Instituto Tecnológico Vale–Desenvolvimento Sustentável, Belém, PA, Brazil
- <sup>4</sup> Instituto de Biociências, Universidade Estadual Paulista, São Vicente, SP, Brazil
- <sup>5</sup> Departamento de Biologia Vegetal, Centro de Biologia Molecular e Engenharia Genética, Universidade Estadual de Campinas, Campinas, SP, Brazil
- <sup>6</sup> Departamento de Biologia Animal, Universidade Estadual de Campinas, Campinas, SP, Brazil

the most diverse tropical savanna in the world (Colli et al. 2020), with a high endemism of plants (Myers et al. 2000). Although invertebrates are poorly investigated compared to vertebrates, the Neotropical cerrado hosts a large amount of the butterfly, bee, and termite species (Myers et al. 2000; Cavalcanti and Joly 2002). Only 8.3% of the cerrado's original territory is under protection—40% to 50% of its domain has been converted into croplands, pastures, and forest plantations—and the lack of basic biological and natural history records makes it difficult to unveil species risk in cerrado areas (Colli et al. 2020).

Compared to other savannas, at large spatial scales, the cerrado presents a high ant species diversity, with 38% more ant species than Australian savannas (150 vs 93 species; see Campos et al. 2011). Different factors contribute to the dominance of ants on cerrado foliage. The proximal causes include (i) many woody plants have hollowed out stems whose galleries are frequently used as nest sites by arboreal ant species, and (ii) a high occurrence of predictable liquid food sources found in extrafloral nectaries and exudate-producing insects (Oliveira and Leitão-Filho 1987; Oliveira and Freitas 2004). Ultimately, the cerrado hosts many arboreal ant species derived from tropical rainforests, given its location between Amazonian and Atlantic rainforests, as well as the historical expansion and retraction events in these areas (see Campos et al. 2011). Moreover, the mosaic of vegetation physiognomies and multilayer structure in cerrado woodlands leads to a high arboreal ant richness through increased spatial heterogeneity (Ribas et al. 2003). Indeed, structural environmental heterogeneity throughout the cerrado domain influences ant diversity. Different studies have reported a high variation in richness, turnover, and composition of ant species across the range of vegetation types in the cerrado (Marques and Del-Claro 2006; Andrade et al. 2007; Pacheco and Vasconcelos 2012; Silva et al. 2017). The amount of grass and herbaceous strata affects ant diversity in open grasslands, whereas tree richness and litter diversity are the main determinants of ant diversity in the physiognomies cerrado sensu stricto and *cerradão* (Vasconcelos et al. 2019; De Queiroz et al. 2020).

Ant diversity has also been negatively affected by cerrado conversion into agriculture, pastures, tree plantations (Neves et al. 2012; Dalle Laste et al. 2019; De Queiroz et al. 2020; Aguiar et al. 2022), urbanization (Pacheco and Vasconcelos 2007), and fragmentation (Brandão et al. 2011). Human-driven changes in land use can also influence how ants interact with other components of the biota. For instance, pastures and tree plantations increase herbivore diversity and abundance in ant-plant protective mutualisms (Neves et al. 2012), whereas habitat fragmentation may decrease seed dispersal by ants at fragment edges (Christianini and Oliveira 2013). Although these studies highlight the relevance of cerrado's physiognomic mosaic for maintenance of ant species

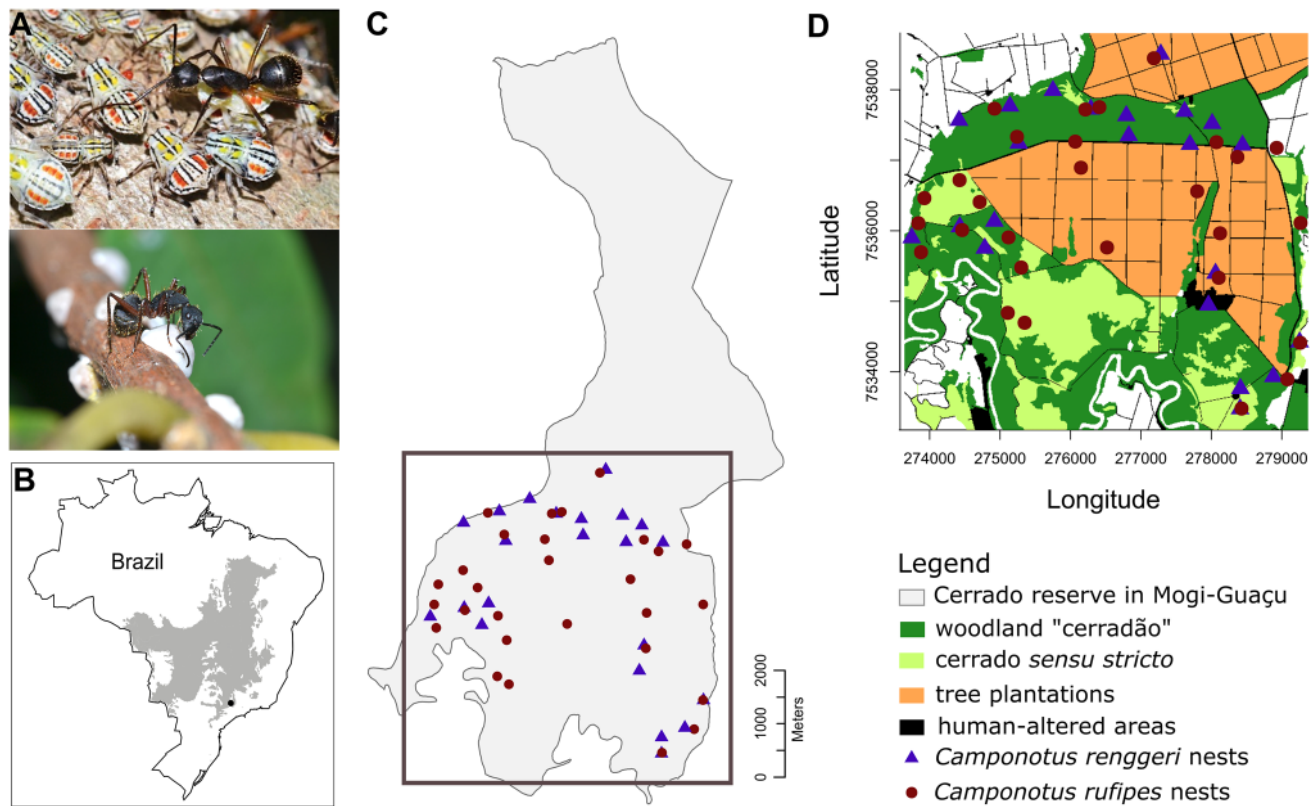
diversity, no ant study in cerrado has yet investigated the most fundamental level of biodiversity, that is, the genetic variation.

The higher the environmental complexity, the more prone populations are to differentially explore the environmental resources (Tews et al. 2004). Thus, environmental heterogeneity influences genetic diversity both by natural selection, with genotypes being favored by different microhabitat conditions, and gene flow (Pamilo 1988; Vellend and Geber 2005). Gene flow plays a central role in structuring genetic variation in heterogeneous environments (Nürnberger 2001). Different methods have been used to measure population gene flow, most of which consist of evaluating the spatial distribution of neutral genetic markers (Nürnberger 2001). In this context, landscape genetics offers a promising approach to detect population genetic patterns and correlate them with environmental heterogeneity, elucidating how much landscape attributes facilitate or prevent movement and, consequently, gene flow of natural populations (Manel et al. 2003; Cushman et al. 2013; Manel and Holderegger 2013).

Here, we investigate how the landscape mosaic of cerrado physiognomies in Southeast Brazil influence dispersal and gene flow in two abundant carpenter ants, *Camponotus renggeri* and *C. rufipes*. Specifically, we investigated (i) the genetic structure and (ii) the influence of cerrado physiognomies (cerrado sensu stricto, “cerradão” woodland) and human altered areas in the gene flow of queens, males and workers of both species. Our study contributes to the understanding of ant genetic patterns in the cerrado, providing evidence for sex biased dispersal, and highlights the importance of considering different species, castes and sexes in conservation biology of social insects, a group commonly neglected in landscape genetic research.

## The study species, natural history, and genetic background

*Camponotus renggeri* and *C. rufipes* (Formicinae) are particularly relevant due to their abundance and ecological interactions on the cerrado ground and on foliage (Fig. 1A). Both species participate in mutualistic interactions with hemipteran trophobionts and plants bearing extrafloral nectaries, exhibiting aggressive behavior towards intruding organisms at their food sources, which often results in increased plant protection and hemipteran survival (Oliveira and Brandão 1991; Oliveira 1997; Del-Claro and Oliveira 2000). *Camponotus renggeri* is more frequently found in “cerradão”, nesting mainly in fallen dead trunks, while *C. rufipes* nests are mostly found in open physiognomies and may present a peculiar nest architecture made of dry straw; colonies of both species may relocate their nests and exhibit facultative polygyny (for more details, see Ronque et al. 2016, 2018). Non-related queens were found in *C. renggeri*



**Fig. 1** Ant species under study and sampling area. **A** *Camponotus renggeri* (upper) and *C. rufipes* (lower) tending honeydew-producing trophobionts (photographs by L. Mota). **B** Geographic distribution of cerrado vegetation (in gray) and location of study area in SE Brazil.

**C** cerrado reserve at Mogi-Guaçu (gray area) showing the distribution of *C. renggeri* and *C. rufipes* nests in the (sampling area indicated by the square), and **D** Sampling area mapped for four land use and cover types, showing the location of *Camponotus* nests

polygynous colonies, with queens mating with a few males, whereas in *C. rufipes* nestmate queens are closely related and present high levels of polyandry (Azevedo-Silva et al. 2020). In addition to contrasting ecological habits and natural history, the two species present distinct patterns of genetic diversity: *C. renggeri* presents a weaker population genetic structure compared to *C. rufipes*, which exhibits the formation of genetic clusters (Ronque et al. 2016). Previous work showed that such patterns of genetic diversity organization are not related to breeding system: although *C. renggeri* and *C. rufipes* present different reproductive strategies, the level of genetic diversity within colonies is indistinguishable (Azevedo-Silva et al. 2020). As such, landscape genetics is a useful approach to evaluate potential determinants of gene flow between the two species.

## Materials and methods

### Data collection

The genetic data used in this study result from our work on *Camponotus renggeri* and *C. rufipes* breeding systems,

based on the analyses of microsatellite molecular markers (Azevedo-Silva et al. 2020). In December 2014 and February 2015, colonies of *C. renggeri* and *C. rufipes* were sampled in a cerrado reserve near Mogi-Guaçu (22° 18' S, 47° 11' W), São Paulo state, Southeast Brazil (Fig. 1B, C). The reserve occupies an area of 4500 ha and presents different physiognomies that vary from cerrado sensu stricto to “cerradão” woodland. cerrado patches are also permeated by areas occupied by *Pinus* and *Eucalyptus* plantations. The reserve is surrounded by an extensive agriculture matrix and has numerous trails and roads (Giudice-Neto et al. 2010). Ant nests were searched for nearly 60 h based on their typical architectures, as previously described by Ronque et al. (2016, 2018). In all, 22 colonies of *C. renggeri* and 35 of *C. rufipes* were collected. Colonies were at least 100 m apart from one another and assessment of genetic differentiation between them a posteriori ensured the distinctiveness of sampled nests (Azevedo-Silva et al. 2020). The geographic coordinates of tagged nests were recorded. Nine to 22 workers per colony of each species were genotyped using different sets of 17 highly polymorphic microsatellite loci developed by Azevedo-Silva et al. (2015). Parental genotypes (queens and males) were

reconstructed based on workers' genotypes using a full likelihood method implemented in the program COLONY v2.0 (Jones and Wang 2010). Further details of data collection are given in Azevedo-Silva et al. (2020).

In the current work we use all previously collected data of *C. renggeri* (Azevedo-Silva et al. 2020). However, a subset of *C. rufipes* data was selected to assure that the same landscape extension was used for both species, and to optimize computational demands performance (Fig. 1C). Seven nests of our original survey of *C. rufipes* (Azevedo-Silva et al. 2020) were then excluded because they were located away from the area selected for landscape genetics analyses in the current study. Thus, our dataset included a total of 389 workers, 51 queens and 72 males (from 22 nests) of *C. renggeri*, and 537 workers, 48 queens and 105 males (from 28 nests) of *C. rufipes*.

### Population genetic analyses

To estimate pairwise genetic distances between workers (from different nests), and between individual queens and males (within and between nests), we calculated the proportion of shared alleles (Dps) using the package *adegenet* v2.1.10 (Jombart 2008) in the software R v4.2.2 (R Core Team 2022). This method is considered appropriate for inferring genetic distance at both the individual (i.e. queens and males) and population levels (i.e. workers in nests; see Murphy et al. 2016). Estimates were transformed into a dissimilarity index by making 1-Dps (used in landscape genetic analysis—see below). To compare the performance of 1-Dps with other metrics, we conducted correlation tests between 1-Dps and other genetic distance estimates (Kosman, Bray–Curtis, Euclidean, Loiselle, and Ritland) for workers, queens and males using the R package *corrplot* v0.92 (Wei and Simko 2021; Fig. S1). Pearson correlation tests revealed that 1-Dps was significantly correlated ( $p < 0.05$ ) to other estimates of genetic differentiation for workers and reproductives of both species (correlation coefficients are shown in Fig. S1). We thus maintained 1-Dps as the metric of genetic differentiation in landscape genetics analyses.

Because we aimed to evaluate the genetic structure (i.e. the number of distinct clusters and membership of individuals to the genetic clusters) for each ant species, we used Discriminant Analysis of Principal Components (DAPC; Jombart et al. 2010) implemented in the R package *adegenet* v2.1.10 (Jombart 2008). We used nests as a priori groups and determined the optimal number of PCs based on a-score. This method is employed to deal with the trade-off between power of discrimination and over-fitting of using multiple PCs (i.e. the proportion of successful

reassignment corrected for the number of retained PCs; see Jombart et al. 2010).

### Landscape genetics analyses

Ecological and evolutionary processes, including within-species genetic variation over space and time, are largely influenced by environmental features that may be assessed with geographic information system (GIS) tools (Kozak et al. 2008). Thus, to quantify the influence of landscape features on *Camponotus renggeri* and *C. rufipes* genetic structure, we mapped the study area using high resolution images in the software ArcGIS 10.3.1 (ESRI, Redlands, CA, USA) at a scale of 1:5000 and with World Geodetic System 84 (WGS84) datum. We classified the study area into four land use and cover categories (see Fig. 1D): (i) woodland areas of cerrado with trees forming a closed canopy (“cerradão”); (ii) scrub of trees and shrubs with scarce vegetation cover (cerrado sensu stricto); (iii) areas with tree plantations (*Pinus*, *Eucalyptus*); and (iv) human-altered areas (housing, trails, paved and unpaved roads).

We adopted a link-based landscape genetic analysis (sensu Wagner and Fortin 2013), whose focus relies on relating genetic distance between individuals (or demes) with environmental distance (Wagner and Fortin 2013). Consequently, the link-based analysis can be used to evaluate how gene flow is likely to occur between patches according to spatial features interposing them (Wagner and Fortin 2013). The landscape can be represented by a resistance surface, that is, a spatial layer whose value at each grid cell designates the cost to movement or gene flow (Spear et al. 2010); the higher the value, the higher the landscape resistance to flow. We evaluated the degree of permeability of the different land use and covers on dispersal of workers and reproductives of *Camponotus renggeri* and *C. rufipes*. Because we have no previous information about the cost imposed by different environmental conditions on *Camponotus* spp. dispersal, we used a genetic optimization algorithm framework implemented in the R package ResistanceGA v4.0-14 (Peterman 2018) that conducts the surface parametrization iteratively. This method is widely used in landscape genetics because it requires no a priori assumption about resistance surface values (Peterman 2018). Therefore, we were able to determine the resistance surface values that optimize the statistical relationship between 1-Dps pairwise genetic distances (response) and cost-distances (predictor) for the two *Camponotus* species. We used random-walk commute time to estimate the effective distances. Statistical relationships were assessed through linear mixed effects models, with maximum likelihood population effects parameterization (MPLE; Clarke et al. 2002), which accounts for the non-independence of pairwise genetic data. We also contrasted



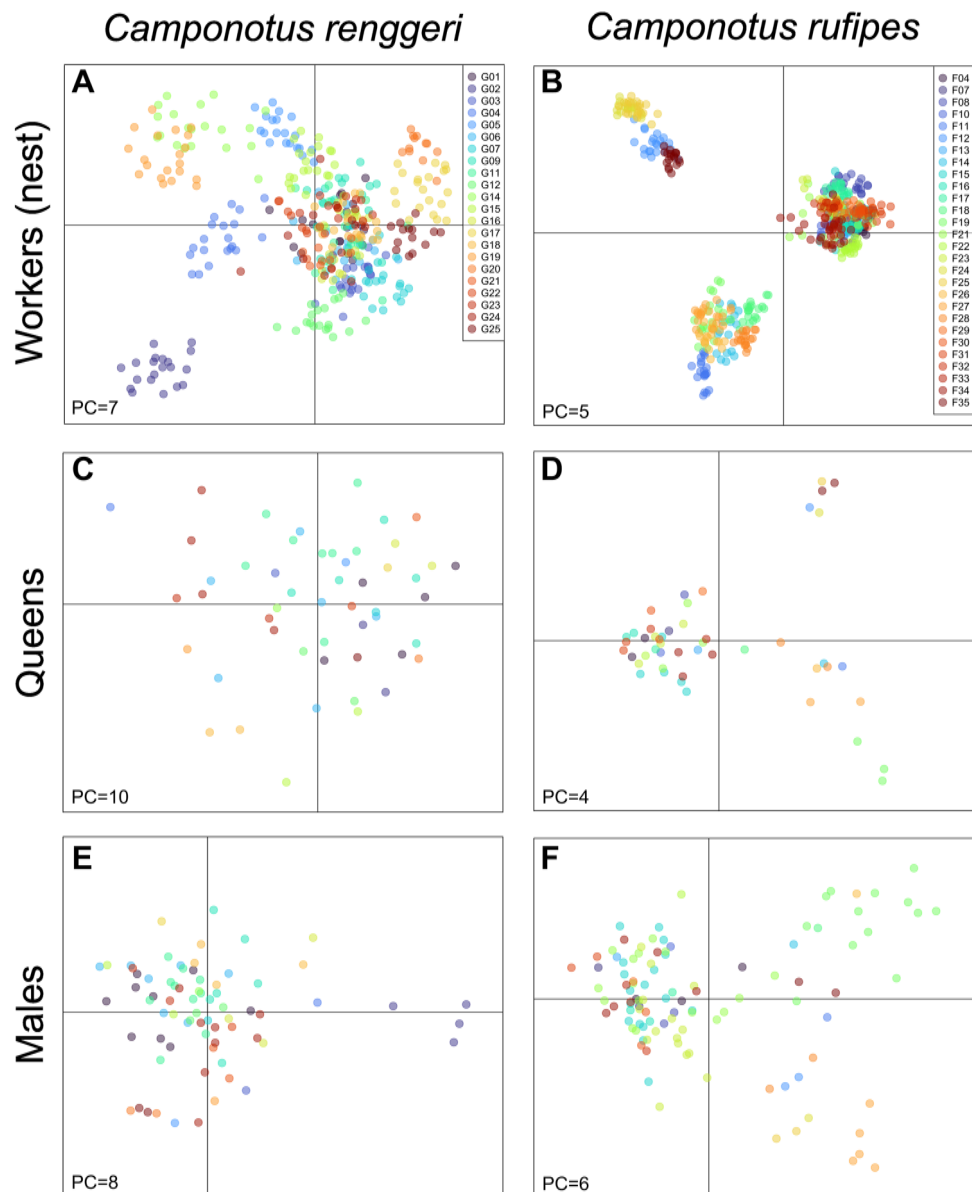
the land use models with an isolation by distance model (IBD) that only considers the geographic distance as predictor, and a null model to represent the absence of geographic distance and landscape effects on genetic structure. MLPE model performance was examined through the Akaike Information Criterion, corrected for small sample sizes (AICc). Models were ranked according to the difference between each model and best model ( $\Delta\text{AICc}$ ). Models with  $\Delta\text{AICc} < 2$  were considered the most plausible among candidates (Zuur et al. 2009). Marginal  $R^2$  ( $R^2_m$ , proportion of variance explained by the fixed factor) and conditional  $R^2$  ( $R^2_c$ , proportion of variance explained by both fixed and random factors) were also estimated for each model. Because ResistanceGA is based on a stochastic optimization routine, it is important to evaluate if

parameters converge by rerunning the algorithm (Peterman 2018). Therefore, to assess the consistency of the results for each caste and sex, we performed five independent runs of ResistanceGA, with resolution of 25 m. Mean and standard deviation were calculated for the five independent runs for all model statistics.

## Results

For *Camponotus renggeri*, the optimal number of PCs retained in DAPC analyses were 7, 10, and 8 for workers, queens and males, respectively (Fig. S2). We thus found little genetic structure for *C. renggeri* workers and reproductives in DAPC analyses (Fig. 2A, C, E), although some

**Fig. 2** Genetic structure of workers, queens, and males of *Camponotus renggeri* and *C. rufipes* based on Discriminant Analysis of Principal Components (DAPC). The optimal number of PCs based on a-score is shown for each DAPC. For all DAPCs, the color code of each ant nest is shown in the upper-right legends in graphs A and B, and their numerical IDs follow the original codes in Azevedo-Silva et al. (2020)



genetic clusters can be observed for *C. renggeri* workers. For *C. renggeri* queens and males, genotypes were less differentiated and the genetic variation was more homogeneously distributed throughout the studied area (see also heatmaps of pairwise genetic distance in Fig. S3A, C, E). Contrastingly, in *C. rufipes*, DAPC analyses retained the optimal number of PCs equal to 5 for workers, 4 for queens, and 6 for males (Fig. S2). Even using nests as a priori groups, we found a clear formation of three genetic groups when considering *C. rufipes* worker genotypes (Fig. 2B). A similar pattern was found for queens (Fig. 2D), but was not clearly observed for males (Fig. 2F). These results revealed some individuals to be more genetically differentiated than others for *C. rufipes*, with clear formation of genetic clusters (see also heatmaps of pairwise genetic distance in Fig. S3B, D, F).

Landscape genetics analyses compared three competing models (land use, isolation by distance, and null model) to explain the genetic differentiation for species' castes and sexes (Table 1). The top ranked model sheds light on which tested predictor best explains gene flow and ant dispersal. Landscape genetic analysis of the worker caste for *C. renggeri* and *C. rufipes* revealed that the null model was better ranked than the IBD and land use models, indicating that neither geographic distance nor landscape composition have effect on ant dispersal in the cerrado (Table 1).

For *C. renggeri* queens and males, the model including geographic distance was the best one, although  $R^2m$  for both models were close to zero, indicating that geographic distance explains little of the variation (Table 1). Contrastingly, for *C. rufipes* queens and males, the land use models were top ranked, indicating that landscape composition and configuration are important predictors of genetic differentiation in the reproductive caste of *C. rufipes* (Table 1).

These results revealed that land use is affecting the dispersal of *C. rufipes* queens and males. Therefore, we evaluated the optimized resistance surface values only for this species. Low resistance values indicate high probability of gene flow (i.e., dispersal) across land use or cover type. The optimized resistance surface for *C. rufipes* males based on the best land use and cover model indicated that the most permeable land use type is the human-affected category, with resistance value of 1 (urbanized area and trails, paved and unpaved roads; Table 2). On the other hand, for *C. rufipes* queens, "cerradão" woodland presented the lowest resistance value (equal to 1; Table 2), suggesting this land cover is the most suitable for dispersal by *C. rufipes* queens. The findings were consistent across all five runs of ResistanceGA (Table 2), suggesting that this number of runs was enough to unveil dispersal patterns in each caste and sex of

**Table 1** Model selection for linear mixed effects models of landscape (i.e. the optimized resistance surface including all land uses) and geography on pairwise genetic distances of castes and sexes of *Camponotus renggeri* and *C. rufipes*. Mean  $\pm$  standard deviation are shown for the five runs of ResistanceGA for all castes and sexes (workers, queens and males) of *C. renggeri* and *C. rufipes*

Species	Caste	Model	$k$	$AICc$	$\Delta AICc$	$R^2m$	$R^2c$
<i>Camponotus renggeri</i>	Workers	<b>Null</b>	<b>1</b>	<b><math>-758.75 \pm 0</math></b>	<b><math>0 \pm 0</math></b>	<b><math>0 \pm 0</math></b>	<b><math>0.52 \pm 0</math></b>
		Geographic distance	2	$-756.32 \pm 0$	$2.42 \pm 0$	$0 \pm 0$	$0.52 \pm 0$
		Land cover	5	$-748.61 \pm 0.042$	$10.14 \pm 0.042$	$0.06 \pm 0.002$	$0.54 \pm 0.001$
	Queens	Null	1	$-3372.68 \pm 0$	$8.69 \pm 0$	$0 \pm 0$	$0.26 \pm 0$
		<b>Geographic distance</b>	<b>2</b>	<b><math>-3381.37 \pm 0</math></b>	<b><math>0 \pm 0</math></b>	<b><math>0.01 \pm 0</math></b>	<b><math>0.27 \pm 0</math></b>
		Land cover	5	$-3370.19 \pm 0.321$	$11.18 \pm 0.321$	$0.04 \pm 0.003$	$0.32 \pm 0.004$
	Males	Null	1	$-4662.53 \pm 0$	$36.31 \pm 0$	$0 \pm 0$	$0.18 \pm 0$
		<b>Geographic distance</b>	<b>2</b>	<b><math>-4698.85 \pm 0</math></b>	<b><math>0 \pm 0</math></b>	<b><math>0.01 \pm 0</math></b>	<b><math>0.19 \pm 0</math></b>
		Land cover	5	$-4685.61 \pm 0.108$	$13.24 \pm 0.108$	$0.05 \pm 0.002$	$0.23 \pm 0.002$
<i>Camponotus rufipes</i>	Workers	<b>Null</b>	<b>1</b>	<b><math>-630.8 \pm 0</math></b>	<b><math>0 \pm 0</math></b>	<b><math>0 \pm 0</math></b>	<b><math>0.27 \pm 0</math></b>
		Geographic distance	2	$-628.58 \pm 0$	$2.22 \pm 0$	$0 \pm 0$	$0.27 \pm 0$
		Land cover	5	$-628.12 \pm 0.039$	$2.67 \pm 0.039$	$0.13 \pm 0$	$0.31 \pm 0$
	Queens	Null	1	$-1744.28 \pm 0$	$168.12 \pm 0.022$	$0 \pm 0$	$0.23 \pm 0$
		Geographic distance	2	$-1819.69 \pm 0$	$92.7 \pm 0.022$	$0.07 \pm 0$	$0.29 \pm 0$
		<b>Land cover</b>	<b>5</b>	<b><math>-1912.39 \pm 0.022</math></b>	<b><math>0 \pm 0</math></b>	<b><math>0.34 \pm 0</math></b>	<b><math>0.53 \pm 0.001</math></b>
	Males	Null	1	$-9203.86 \pm 0$	$424.2 \pm 0.655$	$0 \pm 0$	$0.15 \pm 0$
		Geographic distance	2	$-9421.28 \pm 0$	$206.78 \pm 0.655$	$0.04 \pm 0$	$0.19 \pm 0$
		<b>Land cover</b>	<b>5</b>	<b><math>-9628.06 \pm 0.655</math></b>	<b><math>0 \pm 0</math></b>	<b><math>0.15 \pm 0.001</math></b>	<b><math>0.28 \pm 0.001</math></b>

The best model among candidates is highlighted in bold. Commute Distance algorithm was used for optimizing resistance values

For data of each ResistanceGA run, please see Table S1

$K$  number of estimated parameters in each model;  $AICc$  Akaike Information Criteria corrected for small samples;  $\Delta AICc$  difference between Akaike Information Criteria corrected for small samples between each model and the best model;  $R^2m$  marginal r-square;  $R^2c$  conditional r-square

**Table 2** Landscape resistance values estimated in each of the five independent runs of ResistanceGA for *Camponotus rufipes* queens and males

Caste	Run	Estimate	SE	t	Woodland ("cerradão")	Open cer- rado vegeta- tion	Tree plantations	Human- affected areas
Queens	1	0.0822	0.0059	13.9628	1	862.3801	789.6606	2499.089
	2	0.0824	0.0059	13.9661	1	848.4017	800.9681	2455.811
	3	0.0825	0.0059	13.9650	1	907.2689	856.9074	2494.792
	4	0.0824	0.0059	13.9656	1	876.5276	819.1913	2487.733
	5	0.0826	0.0059	13.9704	1	860.9106	824.5047	2496.762
Males	1	0.0452	0.0021	21.2136	85.30296	147,636.8	124,093.7	1
	2	0.0454	0.0021	21.2421	42.14621	103,509.9	86,194.81	1
	3	0.0450	0.0021	21.2023	8.581545	16,542.63	14,466.53	1
	4	0.0455	0.0021	21.2335	37.25611	83,907.4	67,125.51	1
	5	0.0451	0.0021	21.2094	5.716394	12,453.38	10,763.48	1

Estimate, standard error (SE), and t-value (t) for each model is also shown. Low resistance values indicate high probability of gene flow (i.e., dispersal) across land use or cover type

*Camponotus renggeri* and *C. rufipes*. Detailed model performance for each run of ResistanceGA for ant castes and species can be found in Table S1.

## Discussion

By comparing the effect of landscape composition and configuration of cerrado on gene flow of the two carpenter ant species, we found that genetic diversity is little structured in *Camponotus renggeri*. Although we detected the formation of some genetic groups for workers of *C. renggeri*, no clear formation of genetic clusters was observed for queens and males. In this species, geographic distance is the main, albeit weak, factor influencing the dispersal of the reproductive caste. Contrastingly, we observed the formation of genetic clusters in *C. rufipes*, mainly for workers and queens. In this species, gene flow was influenced by land use and cover, with queens dispersing through the “cerradão” woodland, whereas males are more prone to disperse through human-modified areas. For both species, worker dispersal was not influenced by geographic distance or land cover.

The absence of effects of landscape composition and geographic distance on worker genetic distance is not surprising, given that workers are not the truly dispersing caste (reproductive alates are; Hölldobler and Wilson 1990). Nest relocation (i.e. the changing in nest location) promoted by workers is found throughout ant phylogeny (McGlynn 2012) and has been reported for *C. renggeri* and *C. rufipes* (Ronque et al. 2016, 2018). In general, small-scale nest movement and relocation is not considered dispersal. However, frequent nest relocation over extended time periods may lead to long distance dispersal, and therefore has the potential to influence genetic distribution (Hakala et al. 2019). This process does not seem to influence genetic dissimilarity between nests in *C. renggeri* and *C. rufipes*, probably due

to the high extension of our sampling site and the small foraging areas reported for these ants in the same cerrado area (up to 4 m<sup>2</sup> for *C. renggeri* and 9.8 m<sup>2</sup> for *C. rufipes*; Ronque et al. 2018). Thus, nearby factors should be more important as mediators of forager movement and nest relocation than large-scale landscape and geographic distance. Workers typically search for resources in the vicinity of the nest (Peeters and Ito 2015). Conversely, nest relocation may occur in response to nearby resource availability, competition for food, physical damages to the nest, microclimate changes, environmental disturbance, site quality, seasonality, and predation evasion (Smallwood and Culver 1979; Smallwood 1982; Hölldobler and Wilson 1990; Leal and Oliveira 1995; Dornhaus et al. 2004; Heller et al. 2006; McGlynn 2012; Hakala et al. 2019).

We recorded patterns of genetic variation similar to the ones previously reported by Ronque et al. (2016), that is, weak genetic structure for *C. renggeri* and a strong genetic subdivision for *C. rufipes*. Azevedo-Silva et al. (2020) further showed that *C. renggeri* and *C. rufipes* presented indistinguishable amount of genetic diversity within the colony. However, as shown in the current study, this similarity is not maintained at the population level. The genetic structure among the nests of *C. rufipes* is consistent with the occurrence of closely related queens in polygynous colonies (Azevedo-Silva et al. 2020). Interestingly, here we showed that these discrepancies likely originated from differences in dispersal strategies between species. It is known that genetic structure and gene flow in ants are mainly influenced by the dispersal of reproductive individuals (queens and males), and limitations in this process may lead to spatial genetic differentiation (Suarez et al. 2010; Pamilo et al. 2016). Indeed, intrinsic and extrinsic factors may influence gene flow in ants, such as mode of dispersal, nutrition of reproductives, colony structure, competition, and predation (Shigesada and Kawasaki 1997).

In most ant species, dispersal is mediated by flight, the shortest phase of the ant life cycle during which reproductives mate, disperse, locate a nest site, and face mortality risks (Hölldobler and Wilson 1990). Intrinsically, queen dispersal is influenced by a trade-off between *founding* and *flight* ability, mediated by abdomen investment (Helms and Kaspari 2014; Helms 2018). Although, the flight muscles in the thorax are used as resources in the founding phase (Hölldobler and Wilson 1990), it is also known that queens with heavier abdomens present higher energy reserves for offspring production (Helms and Kaspari 2014; Helms 2018). In turn, such heavier abdomens negatively impact their flight, their ability to mate, to disperse through long-distances, to avoid predators, and to find suitable nest sites (Helms and Kaspari 2014; Helms 2018). Additionally, in some ant species, queen movement may depend on workers through a process known as assisted dispersal, in which workers carry their female sexual sisters over several meters to promote outbreeding with unrelated males (e.g. Vidal and Heinze 2022). Extrinsically, long-distance dispersal is regarded as a product of other ecological pressures, such as habitat quality, which impacts dispersal by influencing the amount and quality of virgin queens and males produced by the colony (e.g. Cremer and Heinze 2003; Clobert et al. 2009; Lowe and McPeck 2014). Considering intrinsic and extrinsic factors is therefore crucial to unveil effective dispersal in ants.

We found that geographic distance weakly influences the dispersal of *C. renggeri* queens and males, suggesting that intrinsic and extrinsic factors beyond landscape composition may prevent reproductives to disperse farther. For instance, in the studied area *C. renggeri* presents fewer nest types compared to *C. rufipes*, using mainly dead trunks for nesting (Ronque et al. 2016). This could limit *C. renggeri* queens, which would restrict their dispersal distances to suitable sites with available trunks for nesting. Contrastingly, we found no evidence of dispersal limitation by geographic distance for *C. rufipes*, suggesting that this species is more capable of long-distance dispersal. In this scenario, landscape connectivity and habitat quality are crucial for dispersal success (Hanski 1999; Fahrig 2001). For *C. rufipes* males, we found that the landscape with the lowest resistance value was the human-affected category (urbanized area and trails, paved and unpaved roads). Indeed, roads may be used as corridors for movement and dispersal increasing gene flow over long distances for some animal species (Balkenhol and Waits 2009).

Male ants are generally associated with reproduction and allocate their resources only to mating and dispersal, making them the sex that disperses the most (Hakala et al. 2019). Male dispersal can be particularly important for *C. rufipes*. Since queens in this species present strong genetic structure, males play an important role shaping its gene flow, as

shown for other ant species (e.g. Berman et al. 2016). The importance of males in bringing new alleles to colonies of *C. rufipes* has previously been suggested by Azevedo-Silva et al. (2020), and the results from the current study reinforce this idea.

For *C. rufipes* queens, we found that areas of “cerradão” woodland presented the lowest resistance value, suggesting that queens tend to disperse through forested areas. Indeed, studies on landscape genetics with ants have reported that these social insects are especially affected by landscape use. For instance, in two distinct environments (Costa Rica and Panamá), Pérez-Espona et al. (2012) and Soares et al. (2014) showed the inability of *Eciton burchellii* (Ecitoninae) ants to disperse in deforested areas. Additionally, climatic conditions were also found to influence ant dispersal in *Atta cephalotes* (Muñoz-Valencia et al. 2022), affecting reproductive flights in many tropical ants (Donoso et al. 2022). Thus, open vegetation physiognomies in the cerrado landscape (natural and/or human-altered) may represent a barrier for queens of *C. rufipes*.

Our results showed that landscape composition can differentially affect gene flow in *C. renggeri* and *C. rufipes*, reinforcing the fact that environmental traits away from the nest vicinity influence dispersal (Hanski 1999; Fahrig 2001). This can be particularly relevant for population and community dynamics since dispersal alters population viscosity and allows colonization of new habitats (Van Valen 1971; Suarez et al. 2010; Pamilo et al. 2016). Previous studies have reported the impact of changes in vegetation structure on ant species diversity in cerrado (e.g. Dalle Laste et al. 2019; De Queiroz et al. 2020). Our findings with *C. rufipes* suggest that suppression of areas covered with cerrado vegetation would likely decrease gene flow and, consequently, increase genetic differentiation of populations of this carpenter ant. Such changes could potentially impact the ant-based ecological services and negatively affect other components of the flora and fauna, such as the plants with which ants maintain mutualistic interactions (Oliveira and Freitas 2004; Oliveira et al. 2017).

The current study deals with one of the biggest gaps in ant biology, namely dispersal behavior, which is crucial for ant conservation, especially in ecosystems facing strong human impacts such as the cerrado savanna (Cavalcanti and Joly 2002; Colli et al. 2020). We highlight the usefulness of landscape genetics to evaluate dispersal performance in ants, mainly reproductive individuals, an admittedly difficult process to document in the field (Hakala et al. 2019). Our work is a step further in the understanding of landscape effects on ant dispersal in the Neotropics. We show that outcomes from vegetation heterogeneity on ant dispersal performance may vary even between closely related species, highlighting the importance of a species-specific approach, especially if results are to be used in programs of environmental



management (Storfer et al. 2010). Moreover, the effects of landscape on genetic distance in alates were not detected in the workers caste. Although worker genotypes resulted from queen and male genotypes (both in *C. renggeri* and *C. rufipes*), reproduction between unrelated queens and males may cause genotype admixture in workers (Azevedo-Silva et al. 2020). These results highlight the relevance of using different castes when studying ant dispersal, given that workers and reproductives can respond differently to landscape composition. Finally, our study adds to the current knowledge on landscape genetics of invertebrates in the tropics, enhancing that the conservation of the Brazilian cerrado savanna is crucial for the continuity of microevolutionary processes, gene flow in particular, which help to maintain viable ant populations.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10592-023-01537-y>.

**Acknowledgements** We are grateful to Elisabeth Evesham and Rodrigo Cogni for discussions and comments on the manuscript.

**Author contributions** MA-S, GMM, CSC, MCC, APS, and PSO conceived the ideas and designed methodology; MA-S and GMM collected the data; MA-S, GMM, CSC, and MCC analysed the data; MA-S and PSO led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

**Funding** This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES; Finance Code 001). MAS was funded by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq; 131908/2014–6), the Programa Santander de Mobilidade Internacional and the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP, 2017/18291–2). GMM, CSC, and MCC (2018/19011–6) were financially supported by FAPESP (2013/08086–1, 2014/22821–9 and 2014/01029–5). APS was supported by CAPES (Computational Biology Program). PSO was supported by research grants from the CNPq (306115/2013–1, 302219/2017–0, 303730/2021–8) and FAPESP (BIOTA Program, 2014/23141–1, 2017/16645–1, 2022/06529–2).

**Data availability** The main genetic data, GPS coordinates of nest sites and the mapped cerrado reserve are available as Supplementary Information files.

## Declarations

**Competing interests** The authors have no conflict of interest.

## References

- Aguiar JJM, Anjos DV, Carvalho RL et al (2022) Plant richness drives ant diversity in Eucalyptus -dominated landscape on Brazilian savanna. *Austral Ecol* 47:17–25. <https://doi.org/10.1111/aec.13060>
- Andrade T, Marques GDV, Del-Claro K (2007) Diversity of ground dwelling ants in cerrado: an analysis of temporal variations and distinctive physiognomies of vegetation (Hymenoptera: Formicidae). *Sociobiology* 50:1–14
- Azevedo-Silva M, Mori GM, Souza AP, Oliveira PS (2015) Microsatellites for two Neotropical dominant ant species, *Camponotus renggeri* and *C. rufipes* (Hymenoptera: Formicidae). *Conserv Genet Resour* 7:459–462. <https://doi.org/10.1007/s12686-014-0395-1>
- Azevedo-Silva M, Mori GM, Carvalho CS et al (2020) Breeding systems and genetic diversity in tropical carpenter ant colonies: different strategies for similar outcomes in Brazilian cerrado savanna. *Zool J Linn Soc* 190:1020–1035. <https://doi.org/10.1093/zoolinnean/zlaa035>
- Balkenhol N, Waits LP (2009) Molecular road ecology: exploring the potential of genetics for investigating transportation impacts on wildlife. *Mol Ecol* 18:4151–4164. <https://doi.org/10.1111/j.1365-294X.2009.04322.x>
- Berman M, Austin CM, Burridge CP, Miller AD (2016) Social structure and landscape genetics of the endemic New Caledonian ant *Leptomyrmex pallens* Emery, 1883 (Hymenoptera: Formicidae: Dolichoderinae), in the context of fire-induced rainforest fragmentation. *Conserv Genet* 17:931–947. <https://doi.org/10.1007/s10592-016-0833-6>
- Brandão CRF, Silva RR, Feitosa RM (2011) cerrado ground-dwelling ants (Hymenoptera: Formicidae) as indicators of edge effects. *Zoologia (curitiba)* 28:379–387. <https://doi.org/10.1590/S1984-46702011000300012>
- Campos RI, Vasconcelos HL, Andersen AN et al (2011) Multi-scale ant diversity in savanna woodlands: an intercontinental comparison. *Austral Ecol* 36:983–992. <https://doi.org/10.1111/j.1442-9993.2011.02255.x>
- Cavalcanti RB, Joly CA (2002) Biodiversity and conservation priorities in the cerrado region. In: Marquis RJ (ed) *The cerrados of Brazil: ecology and natural history of a neotropical Savanna*. Columbia University Press, New York, pp 351–368
- Christianini AV, Oliveira PS (2013) Edge effects decrease ant-derived benefits to seedlings in a Neotropical savanna. *Arthropod–plant Interact* 7:191–199. <https://doi.org/10.1007/s11829-012-9229-9>
- Clarke RT, Rothery P, Raybould AF (2002) Confidence limits for regression relationships between distance matrices: estimating gene flow with distance. *JABES* 7:361. <https://doi.org/10.1198/108571102320>
- Clobert J, Galliard JFLE, Cote J, Meylan S, Massot M (2009) Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecol Lett* 12:197–209. <https://doi.org/10.1111/j.1461-0248.2008.01267.x>
- Colli GR, Vieira CR, Dianese JC (2020) Biodiversity and conservation of the cerrado: recent advances and old challenges. *Biodivers Conserv* 29:1465–1475. <https://doi.org/10.1007/s10531-020-01967-x>
- Cremer S, Heinze J (2003) Stress grows wings: environmental induction of winged dispersal males in *Cardiocondyla* ants. *Curr Biol* 13:219–223. [https://doi.org/10.1016/S0960-9822\(03\)00012-5](https://doi.org/10.1016/S0960-9822(03)00012-5)
- Cushman SA, Shirk AJ, Landguth EL (2013) Landscape genetics and limiting factors. *Conserv Genet* 14:263–274. <https://doi.org/10.1007/s10592-012-0396-0>
- Dalle Laste KC, Durigan G, Andersen AN (2019) Biodiversity responses to land-use and restoration in a global biodiversity hotspot: ant communities in Brazilian cerrado. *Austral Ecol* 44:313–326. <https://doi.org/10.1111/aec.12676>
- de Queiroz ACM, Rabello AM, Braga DL et al (2020) cerrado vegetation types determine how land use impacts ant biodiversity. *Biodivers Conserv* 29:2017–2034. <https://doi.org/10.1007/s10531-017-1379-8>
- Del-Claro K, Oliveira PS (2000) Conditional outcomes in a neotropical treehopper-ant association: temporal and species-specific variation in ant protection and homopteran fecundity. *Oecologia* 124:156–165
- Donoso DA, Basset Y, Shik JZ et al (2022) Male ant reproductive investment in a seasonal wet tropical forest: consequences of

- future climate change. *PLoS ONE* 17:e0266222. <https://doi.org/10.1371/journal.pone.0266222>
- Dornhaus A, Franks NR, Hawkins RM, Shere HNS (2004) Ants move to improve: colonies of *Leptothorax albigipennis* emigrate whenever they find a superior nest site. *Anim Behav* 67:959–963. <https://doi.org/10.1016/j.anbehav.2003.09.004>
- Fahrig L (2001) How much habitat is enough? *Biol Conserv* 100:65–74. [https://doi.org/10.1016/S0006-3207\(00\)00208-1](https://doi.org/10.1016/S0006-3207(00)00208-1)
- Giudice-Net J, Pinto MM, Rossi L (2010) Plano de manejo integrado das unidades de conservação: reserva biológica e estação ecológica de Mogi Guaçu-sp. Instituto de Botânica, São Paulo
- Hakala SM, Perttu S, Helanterä H (2019) Evolution of dispersal in ants (Hymenoptera: Formicidae): a review on the dispersal strategies of sessile superorganisms. *Myrmecol News* 29:35–55
- Hanski I (1999) Metapopulation ecology. Oxford University Press, Oxford
- Heller NE, Sanders NJ, Gordon DM (2006) Linking temporal and spatial scales in the study of an Argentine ant invasion. *Biol Invasions* 8:501–507. <https://doi.org/10.1007/s10530-005-6411-3>
- Helms JA (2018) The flight ecology of ants (Hymenoptera: Formicidae). *Myrmecol News* 26:19–30
- Helms JA, Kaspari M (2014) Found or Fly: Nutrient loading of dispersing ant queens decreases metrics of flight ability (Hymenoptera: Formicidae). *Myrmecol News* 19:85–91
- Hölldobler B, Wilson EO (1990) The ants. Harvard University Press, Cambridge
- Jombart T (2008) ADEGENET: a R package for the multivariate analysis of genetic markers. *Bioinformatics* 24:1403–1405. <https://doi.org/10.1093/bioinformatics/btn129>
- Jombart T, Devillard S, Balloux F (2010) Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. *BMC Genet* 11:94. <https://doi.org/10.1186/1471-2156-11-94>
- Jones OR, Wang J (2010) COLONY: a program for parentage and sibship inference from multilocus genotype data. *Mol Ecol Resour* 10:551–555. <https://doi.org/10.1111/j.1755-0998.2009.02787.x>
- Kozak KH, Graham CH, Wiens JJ (2008) Integrating GIS-based environmental data into evolutionary biology. *Trends Ecol Evol* 23:141–148. <https://doi.org/10.1016/j.tree.2008.02.001>
- Leal IR, Oliveira PS (1995) Behavioral ecology of the neotropical termite-hunting ant *Pachycondyla* (= *Termitopone*): colony founding, group-raiding and migratory patterns. *Behav Ecol Sociobiol* 37:373–383. <https://doi.org/10.1007/BF00170584>
- Lowe WH, McPeck MA (2014) Is dispersal neutral? *Trends Ecol Evol* 29:444–450. <https://doi.org/10.1016/j.tree.2014.05.009>
- Manel S, Holderegger R (2013) Ten years of landscape genetics. *Trends Ecol Evol* 28:614–621. <https://doi.org/10.1016/j.tree.2013.05.012>
- Manel S, Schwartz MK, Luikart G, Taberlet P (2003) Landscape genetics: combining landscape ecology and population genetics. *Trends Ecol Evol* 18:189–197. [https://doi.org/10.1016/S0169-5347\(03\)00008-9](https://doi.org/10.1016/S0169-5347(03)00008-9)
- Marques GDV, Del-Claro K (2006) The ant fauna in a cerrado area: the influence of vegetation structure and seasonality (Hymenoptera: Formicidae). *Sociobiology* 47:1–18
- McGlynn TP (2012) The ecology of nest movement in social insects. *Annu Rev Entomol* 57:291–308. <https://doi.org/10.1146/annurev-ento-120710-100708>
- Muñoz-Valencia V, Vélez-Martínez GA, Montoya-Lerma J, Díaz F (2022) Role of the Andean uplift as an asymmetrical barrier to gene flow in the neotropical leaf-cutting ant *Atta cephalotes*. *Biotropica* 54:191–204. <https://doi.org/10.1111/btp.13050>
- Murphy M, Dyer R, Cushman S (2016) Graph theory and network models in landscape genetics. In: Balkenhol N, Cushman S, Storfer A, Waits L (eds) *Landscape genetics: concepts*. Wiley, Hoboken, pp 165–182
- Myers N, Mittermeier RA, Mittermeier CG et al (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853–858. <https://doi.org/10.1038/35002501>
- Neves FS, Braga RF, Araújo LS et al (2012) Differential effects of land use on ant and herbivore insect communities associated with *Caryocar brasiliense* (Caryocaraceae). *Rev Biol Trop* 60:1065–1073
- Nürnberg B (2001) Ecological genetics. In: Levin SA (ed) *Encyclopedia of biodiversity*. Elsevier, New York, pp 245–258
- Oliveira PS (1997) The ecological function of extrafloral nectaries: herbivore deterrence by visiting ants and reproductive output in *Caryocar brasiliense* (Caryocaraceae). *Funct Ecol* 11:323–330. <https://doi.org/10.1046/j.1365-2435.1997.00087.x>
- Oliveira PS, Marquis RJ (eds) (2002) The cerrados of Brazil: ecology and natural history of a neotropical savanna. Columbia University Press, New York
- Oliveira PS, Brandão CRF (1991) The ant community associated with extrafloral nectaries in Brazilian cerrados. In: Cutler DF, Huxley CR (eds) *Ant–plant interactions*. Oxford University Press, Oxford, pp 198–212
- Oliveira PS, Freitas AVL (2004) Ant–plant–herbivore interactions in the neotropical cerrado savanna. *Naturwissenschaften* 91:557–570. <https://doi.org/10.1007/s00114-004-0585-x>
- Oliveira PS, Leitão-Filho HF (1987) Extrafloral nectaries: their taxonomic distribution and abundance in the woody flora of cerrado vegetation in southeast Brazil. *Biotropica* 19:140. <https://doi.org/10.2307/2388736>
- Oliveira-Filho AT, Ratter JA (2002) Vegetation physiognomies and woody flora of the cerrado biome. In: Oliveira PS, Marquis RJ (eds) *The cerrados of Brazil: ecology and natural history of a neotropical savanna*. Columbia University Press, New York, pp 91–120
- Oliveira PS, Christianini AV, Bieber AGD, Pizo MA (2017) Anthropogenic disturbances affect the interactions between ants and fleshy fruits in two Neotropical biodiversity hotspots. In: Koptur S (ed) *Ant–plant interactions: impacts of humans on terrestrial ecosystems*. Cambridge University Press, Cambridge, pp 133–156
- Pacheco R, Vasconcelos HL (2007) Invertebrate conservation in urban areas: ants in the Brazilian cerrado. *Landsc Urban Plan* 81:193–199. <https://doi.org/10.1016/j.landurbplan.2006.11.004>
- Pacheco R, Vasconcelos HL (2012) Habitat diversity enhances ant diversity in a naturally heterogeneous Brazilian landscape. *Biodivers Conserv* 21:797–809. <https://doi.org/10.1007/s10531-011-0221-y>
- Pamilo P (1988) Genetic variation in heterogeneous environments. *Ann Zool Fenn* 25:99–106
- Pamilo P, Seppä P, Helanterä H (2016) Population genetics of wood ants. In: Stockan JA, Robinson EJJ (eds) *Wood ant ecology and conservation*. Cambridge University Press, New York, pp 51–80
- Peeters C, Ito F (2015) Wingless and dwarf workers underlie the ecological success of ants (Hymenoptera: Formicidae). *Myrmecol News* 21:117–130
- Pérez-España S, McLeod JE, Franks NR (2012) Landscape genetics of a top neotropical predator. *Mol Ecol* 21:5969–5985. <https://doi.org/10.1111/mec.12088>
- Peterman WE (2018) ResistanceGA: An R package for the optimization of resistance surfaces using genetic algorithms. *Methods Ecol Evol* 9:1638–1647. <https://doi.org/10.1111/2041-210X.12984>
- R Core Team (2022) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Ribas CR, Schoederer JH, Pic M, Soares SM (2003) Tree heterogeneity, resource availability, and larger scale processes regulating arboreal ant species richness. *Austral Ecol* 28:305–314. <https://doi.org/10.1046/j.1442-9993.2003.01290.x>

- Ronque MUV, Azevedo-Silva M, Mori GM et al (2016) Three ways to distinguish species: using behavioural, ecological, and molecular data to tell apart two closely related ants, *Camponotus renggeri* and *Camponotus rufipes* (Hymenoptera: Formicidae). *Zool J Linn Soc* 176:170–181. <https://doi.org/10.1111/zoj.12303>
- Ronque MUV, Fourcassie V, Oliveira PS (2018) Ecology and field biology of two dominant *Camponotus* ants (Hymenoptera: Formicidae) in the Brazilian savannah. *J Nat Hist* 52:237–252. <https://doi.org/10.1080/00222933.2017.1420833>
- Shigesada N, Kawasaki K (1997) Biological invasions: theory and practice, 1st edn. Oxford University Press, New York
- Silva EF, Corá JE, Harada AY, Sampaio IBM (2017) Association of the occurrence of ant species (Hymenoptera: Formicidae) with soil attributes, vegetation, and climate in the Brazilian savanna northeastern region. *Sociobiology* 64:442–450. <https://doi.org/10.13102/sociobiology.v64i4.1209>
- Smallwood J (1982) Nest relocations in ants. *Insectes Soc* 29:138–147. <https://doi.org/10.1007/BF02228747>
- Smallwood J, Culver DC (1979) Colony movements of some North American ants. *J Anim Ecol* 48:373–382
- Soare TW, Kumar A, Naish KA, O'Donnell S (2014) Genetic evidence for landscape effects on dispersal in the army ant *Eciton burchellii*. *Mol Ecol* 23:96–109. <https://doi.org/10.1111/mec.12573>
- Spear SF, Balkenhol N, Fortin M-J et al (2010) Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. *Mol Ecol* 19:3576–3591. <https://doi.org/10.1111/j.1365-294X.2010.04657.x>
- Storfer A, Murphy MA, Spear SF et al (2010) Landscape genetics: where are we now? *Mol Ecol* 19:3496–3514. <https://doi.org/10.1111/j.1365-294X.2010.04691.x>
- Suarez AV, McGlynn TP, Tsutsui ND (2010) Biogeographic and taxonomic patterns of introduced ants. In: Lach L, Parr C, Abbott K (eds) *Ant ecology*. Oxford University Press, New York, pp 233–244
- Tews J, Brose U, Grimm V et al (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures: animal species diversity driven by habitat heterogeneity. *J Biogeogr* 31:79–92. <https://doi.org/10.1046/j.0305-0270.2003.00994.x>
- Van Valen L (1971) Group selection and the evolution of dispersal. *Evolution* 25:591–598. <https://doi.org/10.2307/2406942>
- Vasconcelos HL, Maravalhas JB, Neves KC et al (2019) Congruent spatial patterns of ant and tree diversity in Neotropical savannas. *Biodivers Conserv* 28:1075–1089. <https://doi.org/10.1007/s10531-019-01708-9>
- Vellend M, Geber MA (2005) Connections between species diversity and genetic diversity: species diversity and genetic diversity. *Ecol Lett* 8:767–781. <https://doi.org/10.1111/j.1461-0248.2005.00775.x>
- Vidal M, Heinze J (2022) Assisted dispersal and reproductive success in ant species with matchmaking. *Ecol Evol* 12:e9236
- Wagner HH, Fortin M-J (2013) A conceptual framework for the spatial analysis of landscape genetic data. *Conserv Genet* 14:253–261. <https://doi.org/10.1007/s10592-012-0391-5>
- Wei T, Simko V (2021) R package “corrplot”: visualization of a Correlation Matrix. (Version 0.92), <https://github.com/taiyun/corrplot>
- Zuur AF, Ieno EN, Walker N et al (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.