



Dirt roads and fire breaks produce no edge effects on litter-dwelling arthropods in a tropical dry-forest: a case study

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Abstract

Edge effects threaten organisms and ecological processes in habitat remnants, but they have been poorly studied in non-humid forests such as *cerradão*, a tropical dry forest sometimes derived from fire-suppressed savanna in Brazil. The diverse ecosystem functions performed by arthropods may be disrupted by edge effects, and there is pressing need for more studies on this subject. We sampled fragments of *cerradão* facing either a road or fire breaks, assessing edge effects in: beta diversity and community composition of epigeic (litter-dwelling) arthropod orders, ant species, and ant functional groups; ant species richness and diversity; leaf litter depth; and colony residence time of a predatory ground-dwelling ant, *Odontomachus chelifer* (Ponerinae). None of the variables measured differed between edge and interior of the sites sampled. Dry forests have high micro-climatic variations caused by discontinuities in the canopy cover and, as such, changes in abiotic variables in *cerradão* edges might not be as clear as those observed in tropical rainforests. Our study demonstrates that edge effects may not be so prevalent in *cerradão* facing roads or fire breaks, which possibly increases the chances of survival of a higher fraction of the original arthropod fauna compared to rainforest fragments.

Keywords Ant communities · Arthropod communities · Cerrado · Functional diversity · Habitat fragmentation

Introduction

Habitat fragmentation has multiple impacts on organisms and ecosystem processes (Saunders et al. 1991), many of them resulting from edge effects (Murcia 1995; Ewers and Didham 2006; Tabarelli et al. 2008; Laurance et al. 2011). In human-modified landscapes, forest fragments are usually left surrounded by matrices of low vegetation cover, such as plantations and pastures (Melo et al. 2013). This usually leaves forest edges subject to influxes of energy in the form

of light, heat and wind that penetrate the edges and change local abiotic conditions, which in turn may give rise to a myriad of consequences for organisms and ecosystem processes (Murcia 1995; Ewers and Didham 2006).

Arthropods are ideal organisms for monitoring ecological disturbances due to their crucial roles in several ecosystem functions and the relatively easy sampling methods they require (Kremen et al. 1993). Indeed, several studies show that they respond to habitat fragmentation and can be efficiently employed in environmental assessment (Kremen et al. 1993; Delgado et al. 2013), even at the order level (Bolger et al. 2000; Haskell 2000). Within arthropods, ants stand out due to their numeric dominance and widespread occurrence throughout several ecosystems, and they are also regarded as useful organisms to assess ecological disturbances due to their ease of sampling, functional diversity, and sensitiveness to environmental changes (Crist 2009). Many studies demonstrate that the composition of ant communities shifts in fragmented landscapes due to disturbance-adapted species replacing vulnerable ones in disturbed areas (Carvalho and Vasconcelos 1999; Hoffmann and Andersen 2003; Crist 2009; Brandão et al. 2011; Leal et al. 2012; Delgado et al. 2013). This pattern is commonly observed

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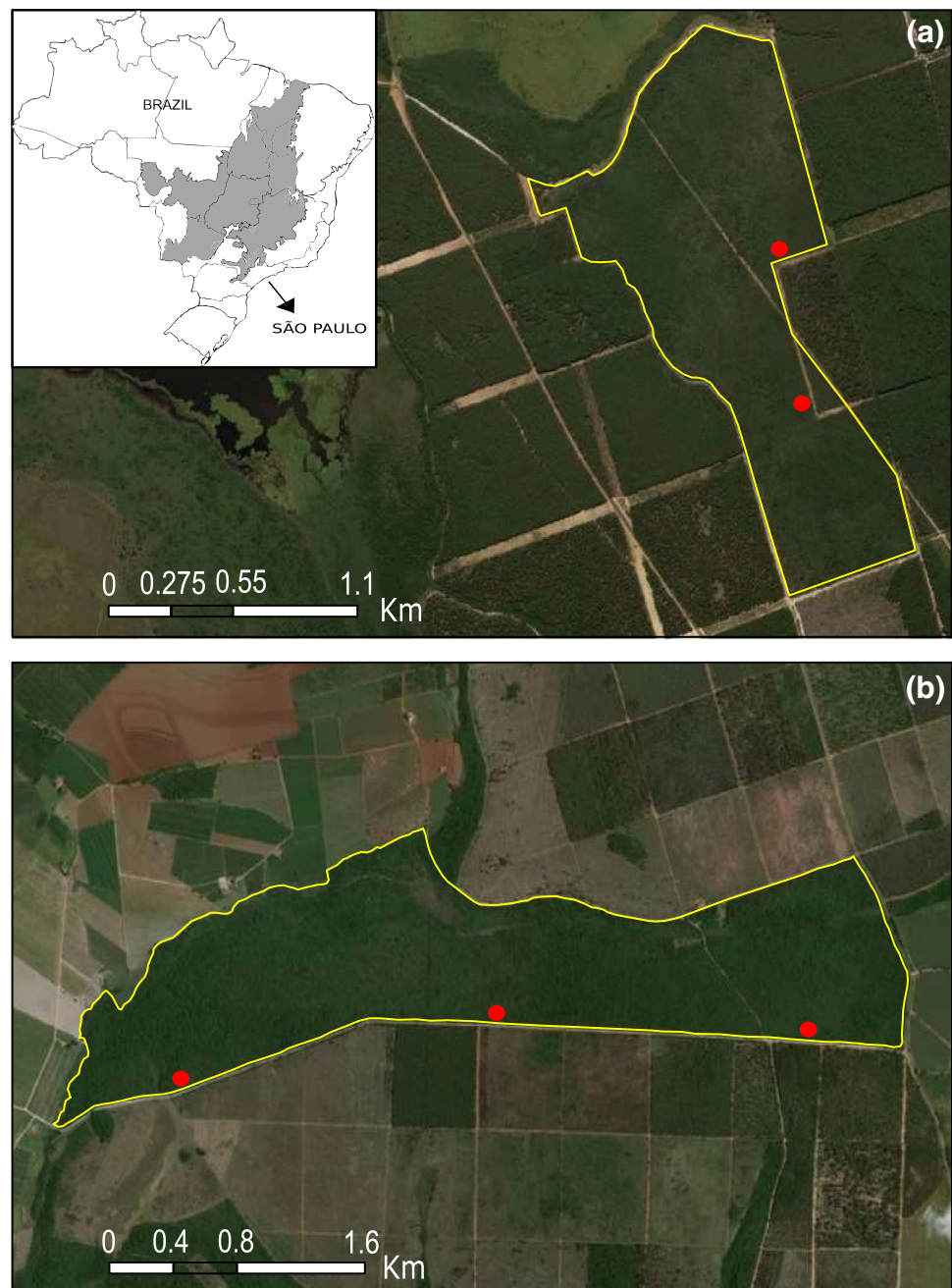
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in studies that classify ants into functional groups. For example, the most used functional group classification of ants shows considerable predictive capacity concerning the response of each group to anthropogenic impacts (Andersen 1995). Generalist groups commonly thrive in disturbed areas and replace other, more specialized groups (Hoffmann and Andersen 2003; Crist 2009; Leal et al. 2012).

The Cerrado is a Neotropical savanna-like vegetation which once covered ca. 2 million km², corresponding to nearly 22% of the land area of Brazil (Fig. 1; see also Bueno et al. 2018). Cerrado vegetation is composed by grasslands

and savanna formations occurring in mosaics with different types of forest along environmental and fire disturbance gradients (Bueno et al. 2018 and references therein). Woody encroachment in long-term fire-free savanna may convert woodland savannas to a dry forest known as *cerradão* (Moreira 2000; Abreu et al. 2017). The Cerrado suffers great anthropogenic disturbance. For instance, from 1990 to 2010 land use for production of soybean, a major Brazil crop, increased from 4.6 to 12.4 million ha (Dias et al. 2016). Habitat conversions for agriculture and pasture are the main threats to the Cerrado, and have driven it towards

Fig. 1 Itirapina (a) and Mogi-Guaçu (b) *cerradão* fragments (yellow lines). Red circles show site locations. Inset map shows Brazil and the state of São Paulo, where the fragments are located. Areas shaded in gray color are the original distribution of the Cerrado savanna. Source: Esri; DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community. (Color figure online)



increasingly fragmented landscapes (Carvalho et al. 2009), potentially subjecting the remaining areas to edge effects (Melo et al. 2013). Habitat conversion was accompanied by an increase in road buildings, which also fragment habitats and may produce edge effects (Haskell 2000; Delgado et al. 2013). However, edge effects have so far been more studied in tropical rainforests (Laurance 2004; Tabarelli et al. 2008; Laurance et al. 2011), which are expected to be more vulnerable to fragmentation-induced disturbance than biomes with lower structural complexity of the vegetation, such as savannas and dry forests (Murphy and Lugo 1986; Mendonça et al. 2015; Moreno et al. 2014; Arruda and Eisenlohr 2016). Indeed, a search in Web of Science using the terms “edge effects” and “dry forest” returns only 27 results, while a search for “edge effects” and “rainforest” returns 94 results (as of 21st September 2017) (Online Resource 3).

Since habitat fragmentation disrupts the ecosystem processes in which arthropods participate (Didham et al. 1996), a proper understanding of how arthropods—and especially ants (Christianini et al. 2014)—can be affected in disturbed ecosystems is crucial for the maintenance of ecosystem functions (Didham et al. 1996) and of viable ecological communities (Crist 2009). Here, we provide a first assessment of edge effects in cerradão (tropical dry forest, see [Study areas](#)) involving several arthropod orders and ant functional groups. We investigated whether epigaeic arthropod communities (i.e., living and/or foraging above ground) are subject to edge effects in cerradão sites in southeast Brazil. We analyzed changes to arthropod orders, ant species, and ant functional groups. We also examined possible edge effects on leaf litter depth, since changes in this layer are known to affect ground-dwelling arthropod communities (Haskell 2000; Delgado et al. 2013). Finally, in order to substantiate previous findings by Christianini and Oliveira (2013), who found that colonies of the predatory ant *Odontomachus chelifer* (Ponerinae) survived less at the edge than at the interior of one cerradão fragment, we followed colonies of this species at the same sites in which we sampled the arthropod communities. Since *O. chelifer* is an important seed disperser of many plant species and may influence plant population regeneration (Oliveira et al. 2017 and references therein), edge effects on its colony survival may have long-term impact on plant populations (Christianini and Oliveira 2013; Christianini et al. 2014).

Materials and methods

Study areas

Given that the Cerrado is a highly variable biome with diverse physiognomies, we chose to focus on fragments of *cerradão*, which is a forest physiognomy of Cerrado

consisting of 50–90% canopy cover with a discontinuous grass layer and trees 8–12 m tall (Oliveira-Filho and Ratter 2002). Cerradão growing on dystrophic soils is often derived from savanna vegetation in long-term absence of fire and the woody component is floristically indistinguishable from typical savannas, although physiognomically similar to a dry forest (Abreu et al. 2017; Bueno et al. 2018). Fragments were located in the state of São Paulo, southeast Brazil. Local climate is characterized by two well-defined seasons: a cold and dry season from April to September (hereafter “dry season”) and a hot and wet season from October to March (hereafter “rainy season”). We conducted samplings in different seasons because we expected that climate variation typical of Cerrado (Oliveira-Filho and Ratter 2002) might lead to different edge effects on the arthropod communities (e.g. Barbosa and Marquet 2002).

One of the fragments (hereafter “Itirapina”) is located in the natural reserve “Estação Experimental de Itirapina” (22°12’S, 47°51’W) (Fig. 1a). Local mean annual temperature is 21.9 °C, with mean maximum and minimum temperatures reaching 24.9 °C (January) and 17.8 °C (June), respectively. Mean annual rainfall is 1459 mm, with highest and lowest precipitation rates in February (275 mm) and July (24 mm), respectively. The study area is a 61-year-old man-made 177 ha fragment of cerradão cut by fire breaks (ca. 20 m wide) dominated by herbs and grasses, and surrounded by pastures and *Pinus* and *Eucalyptus* plantations. Local vegetation is described in Giannotti (1998). Edges sampled in this fragment face fire breaks which cut the fragment (Fig. 1). Edge effects on abiotic variables and ant-seed interactions have already been detected at the same edges in this fragment (Christianini and Oliveira 2013, see below).

The other fragment (hereafter “Mogi-Guaçu”) is located in the natural reserve “Reserva Biológica de Mogi-Guaçu” (22°18’S, 47°11’W) (Fig. 1b). Local mean annual temperature is 20.6 °C, with maximum and minimum temperatures ranging from 23.5 °C (February) to 16.3 °C (July), respectively. Mean annual rainfall is 1352 mm, with highest and lowest precipitation rates in January (235.5 mm) and August (30.4 mm), respectively. The study area is a 50-year-old man-made 343.42 ha fragment surrounded by roads, farms and *Pinus* and *Eucalyptus* plantations. Local vegetation is described in Mantovani and Martins (1993). Edges sampled in this site face a ca. 20 m wide unpaved road that cuts the fragment (Fig. 1). Although edge effects are expected to be more intense in habitat fragments exposed to extensively cleared areas such as farmland, roads may also produce edge effects (Haskell 2000; Delgado et al. 2013; Withworth et al. 2015; Vieira-Neto et al. 2016).

Sampling design

Arthropods were sampled with pitfall traps consisting of plastic cups (5 cm in diameter \times 6 cm in depth) filled with 70% ethanol, detergent drops, and salt. There is scarce reliable quantitative data that could allow a more refined approach to the study of edge effects in cerradão. We therefore based our sampling distances on the work of Christianini and Oliveira (2013), who detected edge effects on microclimatic variables, seed removal, seedling establishment and *O. chelifera* colony survival in the Itirapina fragment. Samplings were made in sites consisting of two parallel transects, one in the fragment edge (< 15 m from the fragment edge) and another in the fragment interior (> 45 m from the fragment edge; following Christianini and Oliveira 2013). Dodonov et al. (2013, 2016) measured depth of edge influence in savanna and cerradão fragments and found that edge effects on microclimate, vegetation structure and litter characteristics generally occur between 10 and 40 m from the edge, and thus our sampling distances seem to be adequate for comparing different habitats (an edge and an interior one). In each transect we set eight pitfalls 37 ± 10 m (mean \pm SD) apart from one another, left open for 24 h. Two sites were established in Itirapina and three in Mogi-Guaçu. Sites were 1300 ± 282 m (mean \pm SD) apart from one another and were thus considered independent from each other (e. g. Uehara-Prado et al. 2009). Our sampling design thus considers a sample size of $N = 5$ sites, which did not influence hypothesis testing for edge effects in our analyses (see “Data analyses”). Samplings took place in the rainy (January) and dry (July) seasons of 2016. A total of $N = 160$ traps were set (80 pitfalls per season). Trapped arthropods were taken to the laboratory for sorting and identification. Arthropods were identified to the order level and ants to the species or morphospecies level.

Litter depth measurements were taken with a graded metal tube at eight sampling points in the same sites used for pitfall sampling. At each point we took three measures (1 m apart from one another) in four directions perpendicular to one another, totaling 12 measurements for each point. The mean of these 12 measurements was used in the analyses. These measurements were made twice, once in the rainy (January) and once in the dry (July) season of 2016 (e. g. Sizer et al. 2000). Thus, out of a total of 1920 measurements taken, $N = 160$ sampling units were used in the analyses.

During the rainy season (December) of 2015, we tagged *O. chelifera* colonies in the same sites used for pitfall and litter depth sampling. In each site we tagged 12 nests, thus making a total of $N = 60$. After 1 year, colonies were checked for activity. The nest entrance was poked with a stick, and if no ant activity was detected in the nest or within 30 cm around it, the colony was considered inactive.

Ant functional groups

We used a classification of ant functional groups based on the work of Leal et al. (2012). This classification assigns ant genera to the following functional groups: (1) cryptic predators—small and minute species specialized on preying arthropods; (2) cryptic omnivores—small and minute generalist species; (3) epigaeic predators—medium and large specialist predators of arthropods; (4) epigaeic omnivores—medium and large generalist or scavenger species; (5) arboreal dominants—highly aggressive species which nest in trees; (6) arboreal subordinates—other ant species which also nest in trees; (7) opportunists—generalist and poorly competitive species; (8) army ants—nomadic species which recruit in huge numbers; (9) leaf-cutting Attini—*Atta* and *Acromyrmex* genera, highly specialized and polymorphic ants which cultivate fungus using cut leaves; (10) non leaf-cutting Attini—monomorphic ant species with small colonies which also cultivate fungus, but do not cut leaves for doing so.

Data analyses

Ants and termites were excluded from the arthropod community analyses because diversity analyses using total or mean abundances in social groups are problematic (Gotelli et al. 2011). We hereafter exclude ants and termites from what we call “arthropod community”, and refer to the ant community classified at the species level using the terms “ant community” or “ant species”, and to ants classified in functional group level using the terms “functional community” or “functional groups”.

All analyses described below were performed treating all sites independently and thus achieving a sample size of $N = 5$ sites (e. g. Uehara-Prado et al. 2009). Since this could possibly confound between-fragment variability with edge–interior differences, we also performed analyses incorporating between-fragment variability by either running separate analyses for each fragment (in diversity analyses), or by incorporating fragment as a permutation constraint (in multivariate analyses) or random effect (in linear models). No change in results was observed in any analysis.

Beta diversity and community composition

We constructed NMDS ordinations with 1000 restarts for visual inspection of the arthropod, ant and functional communities. We then used permutation tests to compare beta diversity between edge and interior sites. In this context, beta diversity is considered as the variability in community composition in a given area, and it is measured as the average distance of group members to the group centroid in a multivariate space (Anderson et al. 2006). We used

this beta diversity measure since we expected that different arthropod orders/ant species/ant functional groups would respond in different ways to habitat edges. This could cause communities in edge sites to have more variable composition than communities in interior sites (e.g. Didham et al. 1998), an effect that would not be detected in multivariate analyses testing for differences in centroid location, such as permANOVA (see below). Calculating beta diversity in this way thus serves two purposes (Anderson et al. 2006): (1) assessing beta diversity of communities; (2) checking multivariate homogeneity of variances before running a permANOVA. We then performed permANOVAs with 999 permutations in order to test for edge effects on the sampled communities. In all these three analyses, the arthropod community was analyzed by pooling the mean abundance from all traps within sites, while ant and functional communities were analyzed with relative abundances, that is, the count of incidences of each species in samples within a site. Rainy and dry seasons were treated separately for all these three analyses, and all of them were performed with the Morisita-Horn dissimilarity index, which gives more value to abundant species, and as such as (Jost et al. 2011; Chao et al. 2014): (1) resistant to under-sampling; (2) a good index to understand functional differences between ecosystems, given that ecological processes are often more influenced by the most abundant species.

Ant diversity

We used Hill numbers to compare ant species richness and diversity between edge and interior sites. Hill numbers integrate species richness and abundance into a class of measures differing only by an exponent q . These measures have several statistical advantages over other diversity indexes (Chao et al. 2014). We constructed rarefaction curves using species richness ($q=0$), and calculated the inverse of Simpson concentration ($q=2$) (Chao et al. 2014). We chose the Simpson diversity measure as it is, just as the Morisita-Horn index, more influenced by the most abundant species (Jost et al. 2011). Diversity indexes were calculated with 1000 bootstrap replications of relative abundances. Separate curves/indexes were calculated for each season sampled. All curves were extrapolated to twice the number of sampling units in each site, so as to detect if our sampling effort was sufficient to detect most ant species and if our results would have changed with additional samplings.

Litter depth

We tested for differences in litter depth between edge and interior sites using a GLMM with a quasi-Poisson family and log link function, with sites as a random factor to

account for the paired transects. Parameter estimates were performed with maximum likelihood.

Colony residence time of *O. chelifera*

Colony residence time of *O. chelifera* was analyzed using a GLMM with Binomial family and logit link function. The response variable, colony activity (active/inactive), was modeled in response to the predictor variable edge effect, with sites as a random effect. Parameter estimates were performed with Laplace approximation and maximum likelihood. The dispersion parameter defined in the model was checked and considered acceptable for the estimation of p values.

All analyses were performed using the R language version 3.2.3 (R Core Team 2015). Diversity indexes and rarefaction curves were calculated with the iNEXT package (Hsieh et al. 2016); NMDS, permANOVA and beta diversity analyses were performed with the vegan package (Oksanen et al. 2016); and GLMMs were performed with the MASS package (Venables and Ripley 2002).

Results

We sampled a total of 1206 and 1186 arthropods from 10 to 11 orders in the rainy and dry seasons, respectively (Online Resource 1). Ant abundance was represented by 3019 and 2409 individuals in the rainy and dry seasons, respectively, which corresponded to 59 and 45 ant species and 9 and 7 functional groups (Online Resource 2).

NMDS ordinations did not show a clear separation between cerradão edge and interior sites for any group sampled (Fig. 2). No differences in beta diversity (Table 1) or change in community composition (Table 2) were detected for any group between edge and interior sites.

Extrapolation of the rarefaction curves (Fig. 3) shows that more ant species would have been sampled with additional sampling effort, yet ant species richness would not reach a clear asymptote for any site, nor would our results have changed, even with twice the sample size we employed. Overlap of the 95% confidence intervals of curves indicates that ant species richness did not differ significantly between edge and interior sites of cerradão, regardless of season (Fig. 3). Neither ant richness nor Simpson diversity differed between edge and interior sites for any season sampled, as indicated by the overlap of all 95% confidence intervals (Table 3).

There were no detectable differences in leaf litter depth between edge and interior sites in any season, as indicated by the GLMM results (Table 4).

Of the 24 *O. chelifera* nests tagged in Itirapina, 10 were inactive after 1 year: four (40%) in the edge and six (60%)

Fig. 2 NMDS ordinations of arthropod communities in cerradão sites in São Paulo, southeast Brazil. “Ed” and “In” indicate edge and interior transects, respectively, and letters A through E indicate sites. Clustering was verified statistically through permANOVA (see Table 2). Circles: edge sites; triangles: interior sites. Stress values: arthropod community, rainy season = 0.05; Arthropod community, dry season = 0.09; ant community, rainy season = 0.04; ant community, dry season = 0.07; functional community, rainy season = 0.07; functional community, dry season = 0.09

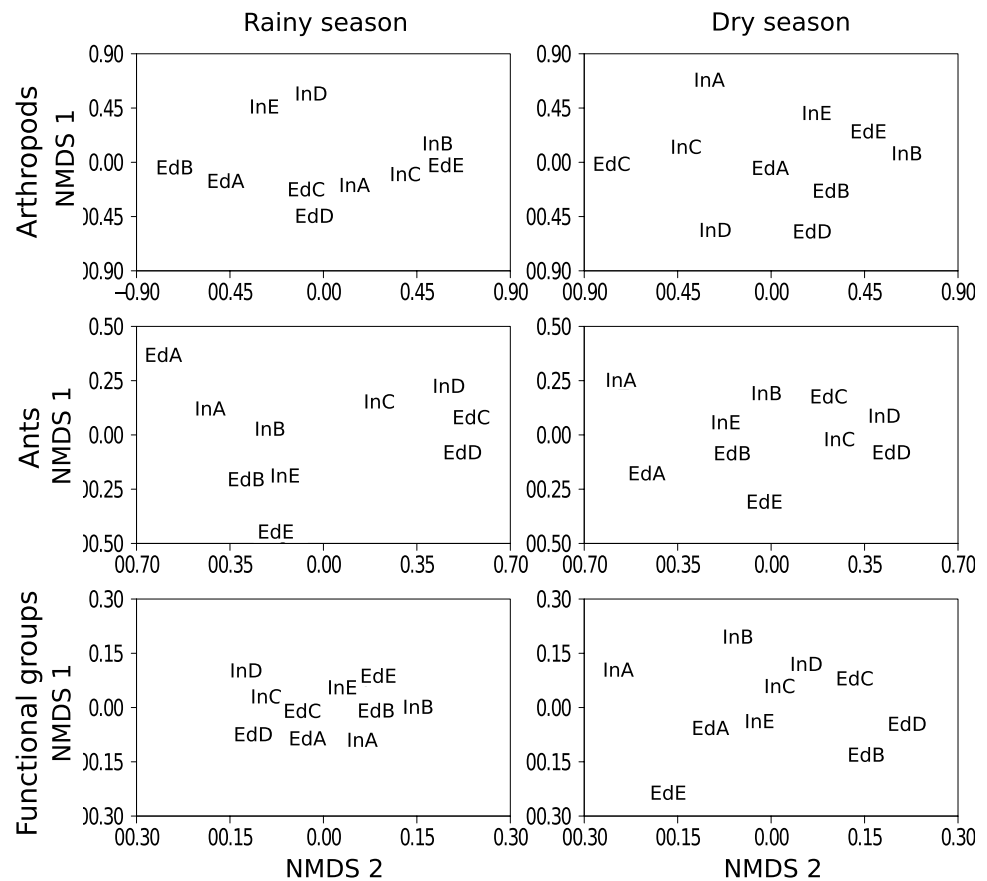


Table 1 Beta diversity (measured as average distance of group members to group centroid in multivariate space) of arthropods, ants, and functional communities at fragment edge and interior of cerradão in the rainy and dry seasons

Community	Season	Edge/interior	Beta diversity	Pairwise permuted p-value
Arthropods	Rainy	Edge	0.068	0.58
		Interior	0.088	–
Arthropods	Dry	Edge	0.138	0.229
		Interior	0.078	–
Ants	Rainy	Edge	0.218	0.492
		Interior	0.251	–
Ants	Dry	Edge	0.176	0.588
		Interior	0.195	–
Functional groups	Rainy	Edge	0.042	0.495
		Interior	0.036	–
Functional groups	Dry	Edge	0.053	0.376
		Interior	0.073	–

in the interior. In Mogi-Guaçu, nine out of 36 tagged nests were inactive after 1 year: three (33%) in the edge and six (66%) in the interior. GLMM results showed that nest persistence in this species did not differ between edge and interior sites (Table 5).

Discussion

Our study adds to the still incipient knowledge on edge effects in Cerradão by demonstrating that epigeic arthropod and ant communities, leaf litter depth, and colony residence time of an epigeic predatory ant do not differ between the edge and interior of some cerradão sites. Current knowledge on edge effects is heavily based upon studies in tropical rainforests (Laurance 2004; Laurance et al. 2011), and their dynamics may differ from habitat remnants of less complex vegetation, such as dry forests and savannas (Murphy and Lugo 1986; Moreno et al. 2014; Mendonça et al. 2015; Arruda and Eisenlohr 2016).

Anthropogenic disturbances often simplify vegetation structure (Didham and Lawton 1999; Laurance et al. 2011), bringing about harsh abiotic factors (Didham and Lawton 1999; Crist 2009; Laurance et al. 2011; Christianini and Oliveira 2013) that may impact community composition

Table 2 permANOVA results of edge effects on the arthropods, ants, and functional communities in cerradão, for the rainy and dry seasons

Community	Season	Predictor variable	DF	F	R ²	Pr (>F)
Arthropods	Rainy	Edge effect	1	-0.076	-0.009	0.808
		Residuals	8	-	1.009	-
		Total	9	-	1	-
Arthropods	Dry	Edge effect	1	0.447	0.052	0.418
		Residuals	8	-	0.947	-
		Total	9	-	1	-
Ants	Rainy	Edge effect	1	0.190	0.023	0.853
		Residuals	8	-	0.976	-
		Total	9	-	1	-
Ants	Dry	Edge effect	1	0.858	0.096	0.484
		Residuals	8	-	0.903	-
		Total	9	-	1	-
Functional groups	Rainy	Edge effect	1	0.673	0.077	0.576
		Residuals	8	-	0.922	-
		Total	9	-	1	-
Functional groups	Dry	Edge effect	1	2.542	0.241	0.184
		Residuals	8	-	0.758	-
		Total	9	-	1	-

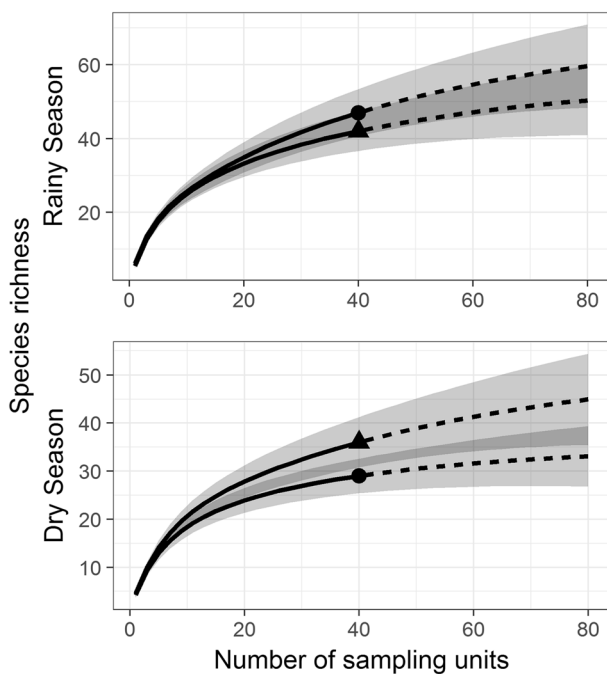


Fig. 3 Rarefaction curves constructed for the ant community sampled in cerradão sites in São Paulo, southeast Brazil. Vertical axis shows species richness calculated using Hill numbers ($q=0$). Triangles/circles indicate the point where the sample size of edge/interior was reached ($N=40$ per season). Dashed lines are the extrapolation of curves up to twice the number of sampling units of edge/interior. Overlap of confidence intervals (darker shaded areas) indicates that ant species richness in fragment edge and interior of cerradão sites does not differ significantly. Curves marked with a triangle: interior sites; curves marked with a circle: edge sites

(Carvalho and Vasconcelos 1999; Hoffmann and Andersen 2003; Crist 2009; Brandão et al. 2011; Leal et al. 2012; Delgado et al. 2013) and leaf litter characteristics (Didham and Lawton 1999; Haskell 2000; Delgado et al. 2013; Dodonov et al. 2016) in fragment edges. Even small-scale clearings such as relatively narrow (up to 10 m wide) roads may lead to edge effects on invertebrate fauna in temperate (Haskell 2000) and tropical (Delgado et al. 2013; Withworth et al. 2015) biomes, including the Cerrado (Vieira-Neto et al. 2016).

Changes in beetle (Martello et al. 2016) and ant communities (Brandão et al. 2011) have already been recorded in Cerrado fragment edges, yet these changes depended on type of matrix (Martello et al. 2016) and fragment (Brandão et al. 2011). No change, however, was detected in small-mammal assemblage richness, diversity and composition (Napoli and Caceres 2012). Other studies in dry forests found no (Moreno et al. 2014) or weak (Hastwell and Morris 2013) edge effects on leaf litter decomposition. Dry forests have high micro-climatic variations caused by discontinuities in the canopy cover (Murphy and Lugo 1986) and, as such, changes in abiotic variables in these dry ecosystems might not be as straightforward as those observed in tropical rainforests (Didham and Lawton 1999; Carvalho et al. 2009; Laurance et al. 2011; Mendonça et al. 2015). Edge effects in abiotic variables have already been reported in cerrado savanna and cerradão (Christianini and Oliveira 2013; Dodonov et al. 2013; Mendonça et al. 2015) but these changes may be weak (Mendonça et al. 2015) or absent (Dodonov et al. 2013) in some fragments. Indeed, a review of 21 studies on tropical dry biomes showed that 4 (19%) of them

Table 3 Ant community diversity estimates using Hill numbers ($q=0; 2$)

Season	Site	Diversity measure	Observed	Estimator	Estimated SE	95% CI
Rainy	Edge	Species richness	42	55.731	10.157	45.762–92.124
		Simpson diversity	20.292	21.74	1.594	20.292–24.864
	Interior	Species richness	47	68.998	13.578	54.224–113.989
		Simpson diversity	19.255	20.323	1.402	19.255–23.072
Dry	Edge	Species richness	36	52.477	12.423	40.424–97.365
		Simpson diversity	13.858	14.582	1.198	13.858–16.931
	Interior	Species richness	29	34.972	5.939	30.176–59.334
		Simpson diversity	13.184	13.878	1.113	13.184–16.06

Overlap of all confidence intervals demonstrates that diversity measures did not differ between edge and interior of cerradão sites

Table 4 Results of the quasi-Poisson GLMM for litter depth for both seasons sampled

Rainy season				
Random factor				SD
Transect (block)				1.105
Response variable	Value	SE	t	Pr (> t)
Intercept	1.088	0.200	5.425	<0.001
Edge effect	0.036	0.137	0.263	0.793
Dry season				
Random factor				SD
Transect (block)				0.731
Response variable	Value	SE	t	Pr (> t)
Intercept	1.345	0.134	10.010	<0.001
Edge effect	–0.029	0.082	–0.349	0.727

Table 5 Results of the Binomial GLMM for *O. chelifera* colony residence time in cerradão

Random factor				
Transect (block)				SD
Transect (block)				0.989
Response variable	Value	SE	t	Pr (> t)
Intercept	1.224	0.474	2.580	0.001
Edge effect	–0.784	0.575	–1.370	0.175

detected no edge effects on any variable whatsoever, while this was true for 2 out of 46 (4%) studies in tropical rainforests (Online Resource 3). It is also possible that changes induced by edge effects have been relaxed as our fragments were created decades ago, since remnant vegetation may grow and seal the edges with time (see Laurance et al. 2011 for tropical rainforest), but no temporal evaluations of edge effects in tropical dry forests are available. Moreover, Dodonov et al. (2013, 2016) found edge effects on many savanna and cerradão fragments that have been fragmented for more than 50 years, and thus we do not believe that edge age may

account for our results. What the published data suggest is that, although edge effects have already been detected in dry biomes, they are probably less prominent in these biomes when compared to humid ones.

Contrary to what we expected, *O. chelifera* colonies did not survive less at fragment edges in comparison to the interior. This result contrasts with that of Christianini and Oliveira (2013), who followed *O. chelifera* colony residence time in the Itirapina fragment during one year and found that 92% of colonies were still active in the fragment interior, as opposed to only 33% in the edge. Edge effects in dry

forests probably depend on at least one factor that is rarely taken into consideration in most studies on edge effects: temporal variability (Murcia 1995; Barbosa and Marquet 2002). Climatic factors may play a role in ant colony activity (Raimundo et al. 2009) and survival, which may vary significantly across years (Gordon and Kulig 1998; Sanders and Gordon 2004), and may be related to large-scale climatic events (Sanders and Gordon 2004). In fact, data from a local climatological station (IF/Suzano Papel e Celulose) show that in 2005 and 2006 (study by Christianini and Oliveira 2013) temperature and rainfall at the Itirapina reserve were, respectively, 12–23% and 18–26% lower than in 2015 and 2016 (L.F.P. Salles, unpublished data; current study). This unaccounted-for climatic variation might explain contrasting outcomes of edge effects on colony survival in *O. chelifera* across years in the Itirapina fragment.

Our study demonstrates that litter-dwelling arthropod communities and leaf litter depth do not suffer edge effects at some cerradão sites at the spatial scales investigated, and suggests that the response of *O. chelifera* colony survival to edges may vary across years. Since our study deals with two cerradão fragments, our sampling design does not allow us to verify the generality of edge effects in Cerradão as a whole, but our work, along with previous research (Christianini and Oliveira 2013; Dodonov et al. 2013, 2016), sheds light onto the poor understood effects of fragmentation on tropical dry forests. Our work also adds to the knowledge on the conservation status of small tropical dry forest fragments, which are representative of most remnants of Cerrado left in the southern portion of the biome (see Cavalcanti and Joly 2002). Our study suggests that the limited impact of edge effects in cerradão detected here may increase the chance that small fragments in these formations may still maintain a significant fraction of their original epigeic arthropod diversity in fragmented landscapes. However, fire management may be needed if the conservation of species typical from savanna is a goal in conservation management (see Abreu et al. 2017). Given the great role that arthropods play in ecosystem functions (Kremen et al. 1993), small fragments may still hold significant conservation value. We believe that research on edge effects in Cerrado and dry forests must take into account their mechanistic causes and temporal dynamics (Murcia 1995) to better evaluate how pervasive they are in these threatened ecosystems.

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Compliance with ethical standards

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

Research involving human participants and/or animals This work did not involve human subjects or experiments on animals. All invertebrate samplings were made under the approval of due regulatory agencies of Brazil.

Informed consent Informed consent statement does not apply to this work since it did not involve human subjects.

References

- Abreu RCR, Hoffmann WA, Vasconcelos HL, Pilon NA, Rossato DR, Durigan G (2017) The biodiversity cost of carbon sequestration in tropical savanna. *Sci Adv* 3:e1701284
- Andersen AN (1995) A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. *J Biogeogr* 22:15–29
- Anderson MJ, Ellingsen KE, McArdle BH (2006) Multivariate dispersion as a measure of beta diversity. *Ecol Lett* 9:683–693
- Arruda DM, Eisenlohr PV (2016) Analyzing the edge effects in a Brazilian seasonally dry tropical forest. *Braz J Biol* 76:169–175
- Barbosa O, Marquet PA (2002) Effects of forest fragmentation on the beetle assemblage at the relict forest of Fray Jorge, Chile. *Oecologia* 132:296–306
- Bolger DT, Suarez AV, Crooks KR et al (2000) Arthropods in urban habitat fragments in southern California: area, age, and edge effects. *Ecol Appl* 10:1230–1248
- Brandão CRF, Silva RR, Feitosa RM (2011) Cerrado ground-dwelling ants (Hymenoptera: Formicidae) as indicators of edge effects. *Zoologia* 28:379–387
- Bueno LM, Dexter KG, Pennington RT, Pontara V, Neves DM, Ratter JA, Oliveira-Filho (2018) The environmental triangle of the Cerrado domain: ecological factors driving shifts in tree species composition between forests and savannas. *J Ecol*. <https://doi.org/10.1111/1365-2745.12969>
- Carvalho KS, Vasconcelos HL (1999) Forest fragmentation in central Amazonia and its effects on litter-dwellings ants. *Biol Conserv* 91:151–157
- Carvalho FMV, De Marco P, Ferreira LG (2009) The Cerrado intopieces: habitat fragmentation as a function of landscape use in the savannas of central Brazil. *Biol Conserv* 142:1392–1403
- Cavalcanti RB, Joly CA (2002) Biodiversity and conservation priorities in the cerrado region. In: Oliveira PS, Marquis RJ (eds) *The cerrados of Brazil: ecology and natural history of a neotropical savanna*. Columbia Press University, New York, pp 351–367
- Chao A, Gotelli NJ, Hsieh TC et al (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecol Monogr* 84:45–67
- Christianini AV, Oliveira PS (2013) Edge effects decrease ant-derived benefits to seedlings in a neotropical savanna. *Arthropod Plant Interact* 7:191–199

- Christianini AV, Oliveira PS, Bruna EM, Vasconcelos HL (2014) Fauna in decline: meek shall inherit. *Science* 345:1129–1129
- Crist TO (2009) Biodiversity, species interactions, and functional roles of ants (Hymenoptera: Formicidae) in fragmented landscapes: a review. *Myrmecol News* 12:3–13
- Delgado JD, Arroyo NL, Arévalo JR, Fernández-Palacios JM (2013) Road edge effects on litter invertebrate communities of subtropical forests. *J Nat Hist* 47:203–236
- Dias LCP, Pimenta FM, Santos AB et al (2016) Patterns of land use, extensification, and intensification of Brazilian agriculture. *Glob Chang Biol* 22:2887–2903
- Didham RK, Lawton JH (1999) Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. *Biotropica* 31:17–30
- Didham RK, Ghazoul J, Stork NE, Davis AJ (1996) Insects in fragmented forests: a functional approach. *Trends Ecol Evol* 11:255–260
- Didham RK, Hammond PM, Lawton JH et al (1998) Beetle species responses to tropical forest fragmentation. *Ecol Monogr* 68:295–323
- Dodonov P, Harper KA, Silva-Matos DM (2013) The role of edge contrast and forest structure in edge influence: vegetation and microclimate at edges in the Brazilian Cerrado. *Plant Ecol* 214:1345–1359
- Dodonov P, Braga AL, Harper KA, Silva Matos DM (2016) Edge influence on plant litter biomass in forest and savanna in the Brazilian Cerrado. *Austral Ecol*. <https://doi.org/10.1111/aec.12420>
- Ewers RM, Didham RK (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biol Rev* 81:117–142
- Giannotti E (1998) Composição florística e estrutura fitossociológica da vegetação de Cerrado e de transição entre Cerrado e mata ciliar da Estação Experimental de Itirapina (SP). Dissertation, Universidade Estadual de Campinas
- Gordon DM, Kulig A (1998) The effect of neighbours on the mortality of harvester ant colonies. *J Anim Ecol* 67:141–148
- Gotelli NJ, Ellison AM, Dunn RR, Sanders NJ (2011) Counting ants (Hymenoptera: Formicidae): biodiversity sampling and statistical analysis for myrmecologists. *Myrmecol News* 15:13–19
- Haskell DG (2000) Effects of forest roads on macroinvertebrate soil fauna of the southern Appalachian Mountains. *Conserv Biol* 14:57–63
- Hastwell GT, Morris EC (2013) Structural features of fragmented woodland communities affect leaf litter decomposition rates. *Basic Appl Ecol* 14:298–308
- Hoffmann BD, Andersen AN (2003) Responses of ants to disturbances in Australia, with particular reference to functional groups. *Austral Ecol* 28:444–464
- Hsieh TC, Ma KH, Chao A (2016) iNEXT: iNterpolation and EXTrapolation for species diversity. R package version 2.0.8. <http://chao.stat.nthu.edu.tw/blog/software-download>
- Jost L, Chao A, Chazdon RL (2011) Compositional similarity and (beta) diversity. In: Magurran AE, McGill BJ (eds) *Biological diversity: frontiers in measurement and assessment*. Oxford University Press, New York, pp 66–84
- Kremen C, Colwell RK, Erwin TL et al (1993) Terrestrial arthropod assemblages: their use in conservation planning. *Conserv Biol* 7:796–808
- Laurance WF (2004) Forest-climate interactions in fragmented tropical landscapes. *Philos Trans R Soc B* 359:345–352
- Laurance WF, Camargo JLC, Luizão RCC et al (2011) The fate of Amazonian forest fragments: a 32-year investigation. *Biol Conserv* 144:56–67
- Leal IR, Filgueiras BKC, Gomes JP et al (2012) Effects of habitat fragmentation on ant richness and functional composition in Brazilian Atlantic forest. *Biodivers Conserv* 21:1687–1701
- Mantovani W, Martins FR (1993) Florística do Cerrado na reserva biológica de Mogi-Guaçu, SP. *Acta Bot Bras* 7:33–60
- Martello F, Andriolli F, de Souza TB et al (2016) Edge and land use effects on dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) in Brazilian Cerrado vegetation. *J Insect Conserv* 20:957–970
- Melo FPL, Arroyo-Rodríguez V, Fahrig L et al (2013) On the hope for biodiversity-friendly tropical landscapes. *Trends Ecol Evol* 28:462–468
- Mendonça AH, Russo C, Melo ACG, Durigan G (2015) Edge effects in savanna fragments: a case study in the Cerrado. *Plant Ecol Divers* 8:493–503
- Moreira AG (2000) Effects of fire protection on savanna structure in Central Brazil. *J Biogeogr* 27:1021–1029
- Moreno ML, Bernaschini ML, Pérez-Harguindeguy N, Valladares G (2014) Area and edge effects on leaf-litter decomposition in a fragmented subtropical dry forest. *Acta Oecol* 60:26–29
- Murcia C (1995) Edge effects in fragmented forests: implications for conservation. *Trends Ecol Evol* 10:58–62
- Murphy PG, Lugo AE (1986) Ecology of tropical dry forest. *Annu Rev Ecol Syst* 17:67–88
- Napoli RP, Caceres NC (2012) Absence of edge effect on small mammals in woodland-savannah remnants in Brazil. *Community Ecol* 13:11–20
- Oksanen J, Guillaume Blanchet F, Friendly M et al (2016) *Vegan: Community Ecology Package*. R package version 2.4-0. <https://CRAN.R-project.org/package=vegan>
- 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: Oliveira PS, Koptur S (eds) *Ant-plant interactions: impacts of humans on terrestrial ecosystems*. Cambridge University Press, Cambridge, pp 133–156
- 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
- R Core Team (2015) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org/>
- Raimundo RLG, Freitas AVL, Oliveira PS (2009) Seasonal patterns in activity rhythm and foraging ecology in the neotropical forest-dwelling ant, *Odontomachus chelifer* (Formicidae: Ponerinae). *Ann Entomol Soc Am* 102:1151–1157
- Sanders NJ, Gordon DM (2004) The interactive effects of climate, life history, and interspecific neighbours on mortality in a population of seed harvester ants. *Ecol Entomol* 29:632–637
- Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation: a review. *Conserv Biol* 5:18–32
- Sizer NC, Tanner EVJ, Ferraz IDK (2000) Edge effects on litterfall mass and nutrient concentrations in forest fragments in central Amazonia. *J Trop Ecol* 16:853–863
- Tabarelli M, Lopes AV, Peres CA (2008) Edge-effects drive tropical forest fragments towards an early-successional system. *Biotropica* 40:657–661
- Uehara-Prado M, de Oliveira Fernandes J, de Moura Bello A et al (2009) Selecting terrestrial arthropods as indicators of small-scale disturbance: a first approach in the Brazilian Atlantic Forest. *Biol Conserv* 142:1220–1228

- Venables WN, Ripley BD (2002) Modern Applied Statistics with S, 4th edn. Springer, New York
- Vieira-Neto EHM, Vasconcelos HL, Bruna EM (2016) Roads increase population growth rates of the native leaf-cutter ant *Atta laevigata* in Neotropical savannahs. *J Appl Ecol.* <https://doi.org/10.1111/1365-2664.12651>
- Whitworth A, Beirne C, Rowe J et al (2015) The response of faunal biodiversity to an unmarked road in the Western Amazon. *Biodivers Conserv* 24:1657–1670. <https://doi.org/10.1007/s10531-015-0883-y>