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PROGRAMA DE PÓS-GRADUAÇÃO EM
BIODIVERSIDADE**

ERIKA DOS SANTOS SOUZA

**SHORT- AND LONG-TERM EFFECTS OF FIRE AND FIRE-INDUCED
VEGETATION COVER ON FOUR LIZARD SPECIES IN AMAZONIAN SAVANNAS**

SANTARÉM - PA

2020

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**SHORT- AND LONG-TERM EFFECTS OF FIRE AND FIRE-INDUCED
VEGETATION COVER ON FOUR LIZARD SPECIES IN AMAZONIAN SAVANNAS**

Dissertação apresentada ao Programa de Pós-Graduação em Biodiversidade para obtenção do título de mestre em Biodiversidade pela Universidade Federal do Oeste do Pará, área de concentração Biodiversidade.

Orientador: Dr. Ricardo Kawashita-Ribeiro.

Coorientador: Dr. Rafael de Fraga

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A banca examinadora foi composta pelos examinadores professores doutores listados abaixo. Os pareceres assinados seguem em sequência.

RICARDO ALEXANDRE KAWASHITA RIBEIRO

Orientador

ERIKA DOS SANTOS SOUZA

Discente

À minha família, e ao meu amor.

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Mas é preciso ter força
É preciso ter raça
É preciso ter gana sempre
Quem traz no corpo a marca
Maria, Maria
Mistura a dor e a alegria

Trecho da música *Maria, Maria* de Milton Nascimento.

RESUMO

A sucessão ecológica em savanas tropicais é limitada pelo fogo sazonal previsível, mas irregular, que pode causar variação temporal na qualidade de habitats para a fauna. Embora o fogo possa causar efeitos desprezíveis ou positivos em animais que ocupam savanas, a maioria dos estudos em curto prazo é baseada em um único período de amostragem, e estudos em longo prazo são raros. Nesse estudo, amostramos quatro espécies de lagartos em savanas da Amazônia para testar os efeitos do fogo e da cobertura vegetal mediada pelo fogo sobre densidades de lagartos em duas escalas temporais. Em curto prazo, usamos três períodos de amostragem para testar os efeitos do fogo e da cobertura vegetal sobre densidades de lagartos estimadas nos períodos entre os 1–5 anos subsequentes. Em longo prazo, testamos os efeitos acumulados do fogo e das mudanças na cobertura vegetal ao longo de 21 anos sobre diferenças a variação temporal nas densidades de lagartos. Em curto prazo, encontramos alguns efeitos significativos do fogo e da cobertura vegetal sobre as densidades de lagartos, geralmente consistentes com os modos de forrageio e termorregulação das espécies estudadas. No entanto, os resultados variaram amplamente entre as espécies e os anos de amostragem, sugerindo que as relações ecológicas mediadas pelo fogo dependem de variáveis desconhecidas e altamente dinâmicas ao longo do tempo. Em longo prazo, os efeitos mais significativos do fogo e da cobertura vegetal mostraram que variação na qualidade de habitats pode afetar a distribuição espacial de lagartos, o que não implica necessariamente em mudanças temporais. O fogo é uma característica natural de savanas, e parece ter pouco impacto sobre as espécies residentes de lagartos que são adaptadas aos processos de queimadas sazonais e naturais nesses ambientes.

PALAVRAS-CHAVE: Alter do Chão, Oeste do Pará, Conservação, Termorregulação e Sucessão Ecológica.

ABSTRACT

Ecological succession in tropical savannas is limited by seasonally predictable, but irregular fire, which consequently causes temporal variation in habitat quality for the fauna. Although fire may cause negligible or positive effects on animals occupying savannas, most short-term studies are based on a single temporal sampling snapshot, and long-term studies are rare. In this study, we sampled four lizard species in Amazonian savannas to test the effects of fire and fire-mediated vegetation cover on lizard densities at two temporal scales. In the short term, we use three sampling snapshots to test the effects of fire and vegetation cover on estimated lizard densities over the subsequent 1–5 years. In the long term, we test the cumulative effects of fire and changes in vegetation cover over 21 years on current lizard density differences. In the short term, we found some significant effects of fire and vegetation cover on lizard densities, usually consistent with foraging and thermoregulation modes. However, results varied widely among species and years, suggesting that fire-mediated ecological relationships depend on unknown, highly dynamic variables over time. In the long-term, the most significant effects of fire and vegetation cover show that variation in habitat quality may change density spatial structure, which does not necessarily imply temporal changes in lizard densities. Fire is a natural feature of savannas, and appears to have little impact on resident species of lizards that are adapted to seasonal and natural burning processes in these environments.

KEYWORDS: Alter do Chão, West of Pará, Conservation, Thermoregulation and Ecological succession.

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INTRODUÇÃO GERAL

Efeitos do fogo e da cobertura vegetal afetada pelo fogo sobre quatro espécies de lagartos em savanas Amazônicas

O que é a pesquisa?

Savanas são ecossistemas abertos, ensolarados, dominados por gramíneas, arbustos e árvores dispersas. Mesmo que o clima úmido da Amazônia possa oferecer condições propícias para o crescimento de florestas, savanas têm suas características estruturais mantidas por eventos sazonais e irregulares de fogo. Embora o fogo possa destruir ecossistemas naturais e converter compostos orgânicos em produtos minerais, a maioria dos organismos que vivem nesses ambientes é altamente resistente às condições geradas pelas queimadas, e a paisagem tende a se recuperar rapidamente.

Nesse estudo nós testamos os efeitos do fogo e da cobertura vegetal sobre estimativas de densidade de quatro espécies de lagartos em duas escalas temporais distintas. Em curto prazo, testamos a hipótese de que as densidades de lagartos são espacialmente estruturadas em resposta à proporção de áreas queimadas ao longo de 1–5 anos. Nós amostramos lagartos em intervalos de tempo longos o suficiente para que a cobertura vegetal fosse regenerada desde a última temporada de fogo. Embora eventos individuais de fogo possam ter pouco efeito sobre os lagartos, o regime cumulativo de incêndio em longo prazo pode afetar as densidades de lagartos por historicamente reduzir a qualidade de habitats. Por isso também investigamos se as mudanças nos habitats induzidas pelo fogo ao longo de 21 anos preveem mudanças nas densidades de lagartos ao longo desse período. Lagartos são excelentes para testar os efeitos do fogo sobre a biodiversidade, porque os únicos refúgios contra o fogo em savanas Amazônicas são buracos no solo, troncos caídos, arbustos que não foram queimados, e cupinzeiros.

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Como a pesquisa foi realizada?

Nós amostramos quatro espécies de lagartos (*Cnemidophorus lemniscatus*, *Kentropyx striata*, *Norops auratus* e *Ameiva ameiva*) em 26 a 39 parcelas de 3,75 ha (250 x 150 m) distribuídas em manchas de savana próximas à vila de Alter do Chão, Santarém, Pará. Nós caminhamos lentamente ao longo de cada parcela, durante o dia, lado-a-lado (duas pessoas 5 m distantes em cada sessão de procura de lagartos), remexendo os arbustos e capins para estimular o movimento de lagartos. Utilizamos análises estatísticas e gráficos que serviram para mostrar que de forma geral, o fogo não afeta as densidades de lagartos nas savanas estudadas, tanto em curto quanto em logo prazo. No entanto, nossas análises também demonstraram que algumas espécies podem ser eventualmente afetadas pelo fogo, principalmente porque dependem da vegetação para termorregular (ou seja, procurar áreas sombreadas para reduzir a temperatura do corpo durante as horas mais quentes do dia).

Qual a importância da pesquisa?

Nosso trabalho mostra a importância da retroalimentação do fogo para a manutenção da biodiversidade de savanas. O fogo é parte natural de processos ecológicos em savanas, e os organismos que vivem nesses ambientes são altamente adaptados ao fogo sazonal. Então, nós precisamos enxergar as savanas como ecossistemas importantes que abrigam biodiversidade única, e muito diferente das florestas adjacentes. Por exemplo, os lagartos das savanas de Alter do Chão não vivem em áreas de floresta ou estão limitados a bordas e clareiras. Isso nos sugere que o reflorestamento de savanas para reduzir os impactos das mudanças climáticas globais não é uma boa solução, porque poderia causar a perda de conjuntos únicos de espécies, os quais formam ecossistemas altamente complementares às florestas de um ponto de vista biológico, e que são regionalmente raros. Resumindo, várias espécies são restritas a essas áreas abertas. Portanto ações de conservação não deveriam ser enfocadas em controlar o fogo natural em savanas, mas sim o fogo causado por humanos que acabam tomando proporções gigantescas e severas sobre a biodiversidade dentro desses ecossistemas, e aumentar os esforços em preservar as florestas que circundam savanas, as quais funcionam como barreiras naturais que evitam que o fogo se alastre.

Autores

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ÚNICO CAPÍTULO

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1 **Short- and long-term effects of fire and fire-induced vegetation cover on four**
2 **lizard species in Amazonian savannas**

3

4 **ABSTRACT**

5 Ecological succession in tropical savannas is limited by seasonally predictable,
6 but irregular fire, which consequently causes temporal variation in the habitat quality
7 for the fauna. Although fire may cause negligible or positive effects on animals
8 occupying savannas, most short-term studies are based on a single temporal sampling
9 snapshot, and long-term studies are rare. In this study, we sampled four lizard species
10 in Amazonian savannas to test the effects of fire and fire-mediated vegetation cover
11 on lizard densities at two temporal scales. In the short term, we use three sampling
12 snapshots to test the effects of fire and vegetation cover on estimated lizard densities
13 over the subsequent 1–5 years. In the long term, we test the cumulative effects of fire
14 and changes in vegetation cover over 21 years on current lizard density differences.
15 In the short term, we found some significant effects of fire and vegetation cover on
16 lizard densities, usually consistent with foraging and thermoregulation modes.
17 However, results varied widely among species and years, suggesting that fire-
18 mediated ecological relationships depend on unknown, highly dynamic variables over
19 time. In the long-term, the most significant effects of fire and vegetation cover show
20 that variation in habitat quality may change density spatial structure, which does not
21 necessarily imply temporal changes in lizard densities. Fire is a natural resource of
22 savannas and appears to have little impact on the sampled and resident lizards of that
23 ecosystem.

24 **KEYWORDS:** Alter do Chão, West of Pará, Conservation, Thermoregulation and
25 Ecological succession.

26 **INTRODUCTION**

27 Savannas are open ecosystems, predominantly covered by grass, shrubs and
28 scattered trees (Scholes & Archer, 1997). Amazonian savannas may have their origins
29 in remnants of pre-Andean vegetation cover, paleochannels of rivers and streams, or
30 humans successively clearing and burning forests over thousands of years (Clayton,
31 1961; Singh & Geissler, 1985). Regardless of their origins, the environmental stability
32 of tropical savannas is largely defined by ecological succession limited by regional
33 interactions between climate and adjacent forest resilience to seasonally irregular fire
34 events (Frost & Robertson, 1985; Bradley et al., 2017). In general, the stability of
35 Amazonian savannas is maintained by constant fire feedback, which limits processes
36 of ecological succession, even under favorable climate conditions for forest growth
37 (Staver, Archibald, & Levin, 2011).

38 Wildfire is often considered a natural disaster but differs from other destructive
39 phenomena (e.g. hurricanes and floods) in causing complex molecular changes in
40 ecosystems, which convert organic compounds into mineral products (Bond & Keeley,
41 2005). Such changes may reduce primary productivity, which triggers cascading
42 effects that affect energy and matter flow through trophic networks (Cochrane, 2003).
43 However, organism assemblages that experience seasonally irregular fire tend to be
44 highly resilient, and often recover quickly from fire events (Faria, Lima, & Magnusson,
45 2004), as the vegetation cover tends to regenerate rapidly (Cava, Pilo, Ribeiro, &
46 Durigan, 2017). In tropical savannas near Alter do Chão (eastern Amazonia, Pará,
47 Brazil), fire did not cause statistically significant short-term impacts on rodents (Layne,
48 Lima, & Magnusson, 2004) or lizards (Faria, Lima, & Magnusson, 2004). In fact, fire
49 can have indirect positive effects on these animals because it increases nutrient
50 availability. Some rodent species may benefit as fire induces grass-seed production

51 (Magnusson, Layme, & Lima, 2010), and some lizard species may find greater prey
52 availability (e.g. Coleoptera, Homoptera and Lepidoptera) in the first months after
53 habitats are burned (Brainthwaite, 1987; Griffiths & Christian, 1996; Diniz, Higgins, &
54 Morais, 2011).

55 Although short-term fire may have low impact on vegetation cover or animals
56 occupying Amazonian savannas, long-term effects are poorly known (Magnusson,
57 Layme, & Lima, 2010). It has been suggested that long-term fire may have beneficial
58 effects on ecosystem functioning because it keeps the carbon cycle in relative
59 equilibrium (Wardle et al., 2003). However, the extent (e.g. proportional size of burnt
60 areas) and frequency of fires may increase in response to climate change due to rising
61 temperatures and reduced rainfall and primary productivity, especially in areas
62 adjacent to urban agricultural areas (Cochrane & Barber, 2009). Therefore, in the long-
63 term, it is expected that fire may affect animal assemblages that are less resilient to
64 burning, and that fire-free time intervals, which are necessary for ecological succession
65 to recover vegetation cover, would be gradually shorter (Dale et al., 2001). This is
66 particularly critical in savannas because they provide good conditions for fire to spread
67 (e.g. temperature, fuel availability and wind). Consequently, biodiversity may be
68 indirectly affected by reduced primary productivity, changes in nutrient cycles, and
69 reduced habitat heterogeneity (Frost & Robertson, 1985).

70 Our study focused on investigating the effects of fire in the short term (1–5
71 years) and long term (21 years) on four lizard species occupying savannas in eastern
72 Amazonia (Alter do Chão, Santarém, Pará). Amazonian savanna lizards provide
73 interesting systems for testing fire effects, because the only refuges available for
74 lizards are ground holes, termite mounds and unburned shrubs and trees (Faria, Lima,
75 & Magnusson, 2004). However, as in the savannas of central Brazil (Costa, Pantoja,

76 Vianna and Colli, 2013), fire does not appear to cause massive mortality of lizards, and
77 the short-term effects can be restricted to small behavioral and demographic changes,
78 as in *Norops auratus* (Dactyloidae) in its foraging time and in the dispersion of
79 *Cnemidophorus lemniscatus* (Teiidae) to unburnt areas (Faria, Lima & Magnusson,
80 2004). Under such scenarios, population decline and long-term local extinction could
81 be expected not as a result of mortality, but rather of migration to areas providing more
82 favorable environmental conditions (Pianka, 1996) and less exposure to predators
83 (Attum & Eason, 2006).

84 Fire is potentially a direct predictor of spatial variation in lizard density in a
85 temporal snapshot, because it stimulates temporary migrations to adjacent habitats.
86 This assumption is based on the fact that reduced density in response to massive lizard
87 death by fire is unlikely (Singh, 2002; Costa, Pantoja, Vianna, & Colli, 2013), and
88 lizards tend to recolonize burnt areas throughout vegetation-cover recovery (Faria,
89 Lima, & Magnusson, 2004). However, ecological processes involved in fire-mediated
90 density-habitat relationships apparently vary as a function of fire intensity (Singh,
91 2002). At high intensities, fire may cause a temporary reduction in microhabitat
92 diversity, which would stimulate temporary migrations to adjacent habitats (McIlroy,
93 1978). At low intensities, fire may generate patch mosaics of burnt and unburnt
94 habitats, which temporarily increases spatial heterogeneity (Pianka, 1992). In this
95 case, density-habitat relationships are expected to be causally explained by
96 environmental heterogeneity filtering species locally, although these processes are
97 likely to be more dynamic over time in savannas than in forests (e.g. Rojas-Ahumada,
98 Landeiro, & Menin, 2012; Bueno, Bruno, Pimentel, Sanaiotti, & Magnusson, 2012;
99 Fraga, Ferrão, Stow, Magnusson, & Lima, 2018). Time intervals until lizards recolonize
100 burnt habitats are expected to vary interspecifically, because lizard species have

101 different physiological and behavioral responses to fire (Faria, Lima, & Magnusson,
102 2004; Costa, Pantoja, Vianna, & Colli, 2013; Duarte, Brown, & Forstner, 2017).
103 However, since effects of fire on lizard density may reflect effects of vegetation cover
104 as a proxy for availability of fleeing, foraging and especially thermoregulating sites, it
105 is plausible to deduce that environmental gradients quantifying vegetation cover are
106 efficient predictors of lizard density.

107 We tested the effects of fire and vegetation cover on lizard densities at two
108 distinct temporal scales. In the short-term, we tested the general hypothesis that lizard
109 densities are spatially structured in response to the proportion of areas burnt in the
110 previous one to five years. Rather than testing the immediate effects of fire on
111 population densities as in most studies (Costa, Pantoja, Vianna, & Colli, 2013; Duarte,
112 Brown, & Forstner, 2017), we focus on investigating time snapshots long enough that
113 vegetation cover has regenerated since the last fire season. We argue that the effects
114 of fire-shaped habitats should be detected after the period of recolonization of burnt
115 habitats, when lizard densities should be less biased by temporary migrations or
116 reduced detectability. Although individual fire events may have little effect, the
117 cumulative fire regime over the long term could affect lizard densities, so we also
118 investigated whether fire-induced habitat changes over 21 years predict changes in
119 lizard densities over that period.

120

121 **METHODS**

122 ***Study area and target-species***

123 The study area is located on the east bank of the Tapajós River, near the village
124 of Alter do Chão, Santarém, Pará (centroid coordinates 2°31' S, 55°00' W). This region

125 is covered by patches of savanna interspersed with fragments of secondary and gallery
126 forests (Faria, Lima, & Magnusson, 2004). The savannas near Alter do Chão vary in
127 the proportions of grass, shrub and tree cover (Magnusson, Lima, Faria, Victoria, &
128 Martinelli, 2001). The climate in the region is highly seasonal, with a rainy season
129 between January and June, and a dry season between July and December. Average
130 annual rainfall is 1,420 mm (mainly concentrated in the rainy season), and annual
131 temperature varied slightly from the average of 27.7 °C (Layme, Lima, & Magnusson,
132 2004).

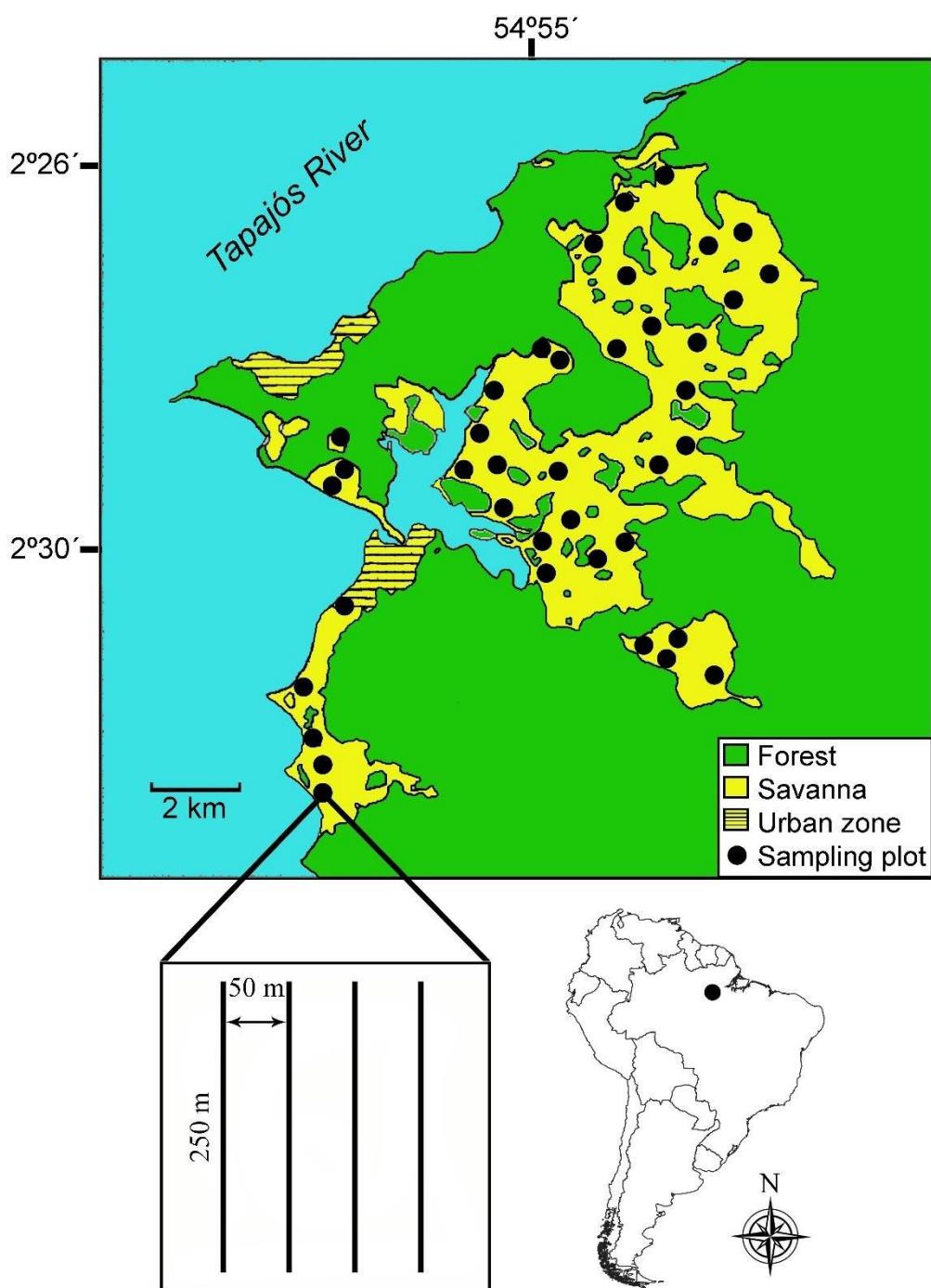
133 We sampled four species of diurnal lizards that are found in Amazonian
134 savannas and other areas with discontinuous vegetation cover. The Rainbow Whiptail
135 *Cnemidophorus lemniscatus* and the Amazon Racerunner *Ameiva ameiva* (Teiidae)
136 are terrestrial and active foragers (Magnusson et al., 1985). The former occupies
137 savannas, forest edges and farms in eastern Amazonia, while the latter is widely
138 distributed among different ecosystems in South America, including clearings in the
139 middle of primary forests and edges of paved roads (Vitt et al., 2007; Ribeiro-Júnior &
140 Amaral, 2016). Both species use underground holes to thermoregulate and spend little
141 time climbing in vegetation. The Striped Whiptail *Kentropyx striata* (Teiidae) and the
142 Grass Anole *Norops auratus* (Dactyloidae) are often considered to be terrestrial, but
143 use grass and shrubs, as well as termite mounds for thermoregulation. The former is
144 widely distributed in open habitats and flooded forests in Amazonia (Magnusson et al.,
145 1985), while the latter occupies sunny habitats covered by grassy vegetation from
146 northern South America to Costa Rica (Uetz, 2018).

147

148

149 **Lizard sampling**

150 We collected lizard density-data in 39 sampling plots, each covering 3.75 ha
 151 (250 x 150 m). Sampling was conducted along four 250 m long by 5 m wide transects
 152 through each plot. Transects were parallel and adjacent transects within each plot were
 153 spaced 50 m apart (Figure 1). The spatial distribution of the plots was systematically
 154 defined to cover 30,000 ha of savannas identified by satellite images, maintaining a
 155 minimum distance of 30 m from forest fragments (Magnusson, Lima, Albernaz,
 156 Sanaiotti, & Guillaumet, 2008).



170 **Figure 1.** Study area around the village of Alter do Chão, Santarém, eastern
171 Amazonian Brazil, where we sampled four lizard species to test the effects of fire and
172 vegetation cover on densities. The bottom-left detail shows the transect configuration
173 in each plot (black circles). Adapted from Faria, Lima, & Magnusson, 2004.

174

175 We counted lizards using daytime active visual search, with two simultaneous
176 observers in each plot. Observers walked side by side at 5 m from each other, moving
177 shrubs and grass bushes to stimulate lizard movement (Faria, 1999). Our sampling
178 protocol follows Faria, Lima, & Magnusson (2004), where they sampled all plots
179 between March and June. This period is appropriate for sampling lizards in savannas
180 because it is late in the rainy season, when the vegetation has largely recovered from
181 the last fire season. We surveyed only when the air temperature was $\geq 30^{\circ}\text{C}$ to reduce
182 the effects of false absences, since lizard activity is highly influenced by temperature
183 (Faria, Lima, & Magnusson, 2004). As the sampling plots are standardized in size and
184 configuration, and the sampling time and protocol was identical for all plots along all
185 years, we used numbers of individuals per species as a proxy for lizard density.

186 Different teams have counted lizards in the Alter do Chão savannas over time.
187 A. S. Faria, A. P. Lima and a field assistant collected data in 1998, I. Ghizoni and two
188 field assistants (W. Vasconcelos and W. Vasconcelos) collected data in 2002, and E.
189 Souza, P. Ganança, R. Fraga and two field assistants (E. Farias and L. Vasconcelos)
190 collected the data in 2019. We used a compilation of all this data in our analysis. The
191 ability to detect lizards varies between observers, but this does not affect our analyses
192 because comparisons are made within years (same observers) or based on
193 differences among years (same differences among observers across plots). All

194 observers were experienced and underwent training by Albertina Lima or William
195 Magnusson before surveys. Counts were undertaken when vegetation had recovered,
196 so vegetation density generally only varied subtly between plots. We assume that
197 differences in counts are mainly due to differences in lizard densities, but indicate
198 where conclusions could be influenced by differences in detectability.

199 The number of plots available has been reduced over time because of
200 expansion of urban areas over savannas. Also, we do not have data available for long-
201 term variation in vegetation cover across all plots. Therefore, our short-term analyses
202 based on data collected in 1998 and 2002 were based on 39 plots, and both short-
203 term analyses based on data collected in 2019 and long-term were based on 24 plots.

204 ***Measuring fire and vegetation cover***

205 Fire monitoring has been undertaken in the savannas of Alter do Chão over 21
206 years (1997 to 2018) by A. P. Lima. Data were usually collected yearly in January or
207 February, after the fire season in the region. For each plot, we represented the fire
208 history as the sum of proportional burnt areas among years, which were based on
209 binary presence or absence of burnt areas at regular intervals of 2 m along each
210 transect, in each plot.

211 Vegetation cover estimates were made by W. E. Magnusson and A. P. Lima in
212 1997, and R. Fadini, M. Cristo and J. M. Lima in 2017, being the second research team
213 trained by the first. Data were collected along transects from March to August at the
214 end of the wet season, when vegetation was already recovered from the previous
215 year's burns. A point-based plant cover estimate was obtained for each plot (Mantovani
216 & Martins, 1990), using a 2 mm x 1 m tall metal stick positioned every 2 m along the

217 transects. Although we recorded all plant species, we retained only shrubs and grasses
218 for analyses, as well as soil exposed (no vegetation touched). Therefore, the coverage
219 of each plant category (shrubs or grasses), and soil, was given by the percentage of
220 times it has touched the stick per plot.

221

222 **Data analysis**

223 To obtain an overview of changes in lizard densities over time, we used a
224 nonparametric Dunn's test to evaluate differences in lizard densities between paired
225 years, separately by species. For *A. ameiva* we used a Kruskal-Wallis test because
226 this species was not sampled in 1998.

227 Our tests are based on multiple linear models. Therefore, we preliminarily
228 plotted all independent variables (shrub, grass, exposed soil cover, and fire), applied
229 a Pearson's correlation test, and estimated variance-inflation factors (VIF) using the
230 car R-package (Fox & Weisberg, 2011) to check multicollinearity levels. We found that
231 exposed soil cover was highly correlated with grass (up to $r = -0.82$) and shrub cover
232 (up to $r = -0.69$) measured in 1998 and 2002. High collinearity was supported by high
233 VIF values for exposed soil (up to 48.30) on the inferential short-term models based
234 on data from 1998 and 2002, and also in the long-term model. To avoid statistical-
235 redundancy biases in the multiple models, we removed exposed soil cover from the
236 short-term models based on data from 1998 and 2002, as well as from the long-term
237 model. After removing this variable, we obtained $VIF \leq 3.55$ for all variables.

238 To test the effects of short-term fire and vegetation cover on lizard densities we
239 used Generalized Linear Models (GLM) implemented in R (R Core Team 2019). In
240 general, lizard density data were asymmetric and approximated a theoretical negative

241 binomial distribution (see histograms in supplemental material S1). Therefore we used
242 the MASS R-package (Venables & Ripley, 2002) to set up multiple GLMs in order to
243 account for negative binomial distribution (`glm.nb` function).

244 We implemented GLMs following the general formula $\text{lizard density} = a + b_1(\text{shrub cover}) + b_2(\text{grass cover}) + b_3(\text{exposed soil cover}) + b_4(\text{fire})$, excluding the
245 highly correlated *exposed soil cover* when necessary. We set up the GLM models to
246 test the effects of the independent variables measured in periods shortly before the
247 lizard-sampling period, and according to data availability. We obtained three short-term
248 sampling snapshots that are based on lizard densities estimated in 1998, 2002 and
249 2019. To test non-random variation in estimated lizard density in 1998, we used
250 vegetation cover and fire data collected in 1997. For estimated lizard densities in 2002,
251 we used vegetation cover measured in 1997 and fire measured in 2001. For estimated
252 lizard densities in 2019, we used vegetation cover measured in 2017, and the sum of
253 fire measured in 2017 and 2018. We summed over these years because the number
254 of plots that burned in 2018 ($N = 2$) was too low for meaningful analysis.

256 To test long-term effects of fire and vegetation cover on lizard densities we also
257 used GLM implemented in R. We used the difference in lizard density (Δ density)
258 between 2019 and 1998 for *C. lemniscatus*, *K. striata* and *N. auratus*, and differences
259 between 2019 and 2002 for *A. ameiva* (this species was not sampled in 1998). As
260 predictor variables, we used differences in shrub and grass cover between 1997 and
261 2017, and the sum of the proportional burned areas over the 21 years sampled (18
262 years for *A. ameiva*). The general GLM formula was given by $\Delta \text{lizard density} = a + b_1(\Delta \text{shrub cover}) + b_2(\Delta \text{grass cover}) + b^3(\text{summed fire})$, where Δ denotes *current - past*.

265 **RESULTS**266 ***Sampling overview***

267 Our total lizard sample was composed of 1,697 individuals, distributed in 522
 268 sighted lizards in 1998 (excluding *A. ameiva*), 550 in 2002 and 625 in 2019. The
 269 Rainbow Whiptail, *C. lemniscatus*, was consistently the most frequently sampled
 270 species, with relative frequencies of at least 80%. The other species occurred at
 271 minimum frequencies of 45%, although densities and frequencies tended to increase
 272 for *K. striata* and *N. auratus* from 2002. A detailed overview of lizard sampling is shown
 273 in Table 1.

274

275 **Table 1.** Summary of lizard sampling over three surveys of plots in Amazonian
 276 savannas. The species (Sp) sampled were *Cnemidophorus lemniscatus* (Cl),
 277 *Kentropyx striata* (Ks), *Norops auratus* (Na) and *Ameiva ameiva* (Aa). N = total number
 278 of individuals, AD = average density, Freq = frequency relative to number of sampling
 279 plots (%), - = unavailable data.

Sp	1998				2002				2019			
	N	Range	AD	Freq	N	Range	AD	Freq	N	Range	AD	Freq
Cl	413	0–33	10.59	85	362	0–42	9.28	80	340	1–44	11.96	100
Ks	32	0–5	0.82	45	38	0–4	0.97	45	77	0–5	2.37	70.83
Na	77	0–10	1.97	62.5	79	0–9	2.02	67.5	160	1–9	5.71	100
Aa	-	-	-	-	71	0–9	1.92	67.5	48	0–4	1.67	70.83

280

281 Dunn's and Kruskal-Wallis tests (Table 2) showed that *C. lemniscatus* and *A.
 282 ameiva* densities did not change significantly among sampling times ($P > 0.12$ in all
 283 cases). Those species have similar thermoregulation modes, and do not often climb
 284 the vegetation to thermoregulate. However, *K. striata* and *N. auratus* densities

285 increased from 2002 ($P < 0.001$ in all cases). Both species climb the vegetation to
 286 thermoregulate, although they may also use termite mounds.

287

288 **Table 2.** Summary of Dunn's (Z) and Kruskal-Wallis (X^2 , only for *A. ameiva*) test
 289 outputs comparing densities among four lizard species sampled in savannas in eastern
 290 Amazonian Brazil between sampling times. Bolded P values show cases in which the
 291 null hypothesis was rejected.

293

Species	Sampling	Z or X^2	P
<i>Cnemidophorus lemniscatus</i>	1998 – 2002	1.84	0.12
	1998 – 2019	-0.26	0.79
	2002 – 2019	-2.11	0.10
<i>Ameiva ameiva</i>	2002 – 2019	0.01	0.91
	1998 – 2002	0.20	0.83
<i>Kentropyx striata</i>	1998 – 2019	-3.64	< 0.001
	2002 – 2019	-3.84	< 0.001
<i>Norops auratus</i>	1998 – 2002	1.05	0.29
	1998 – 2002	-5.40	0.37
	1998 – 2019	-4.67	< 0.001
	2002 – 2019	3.62	< 0.001

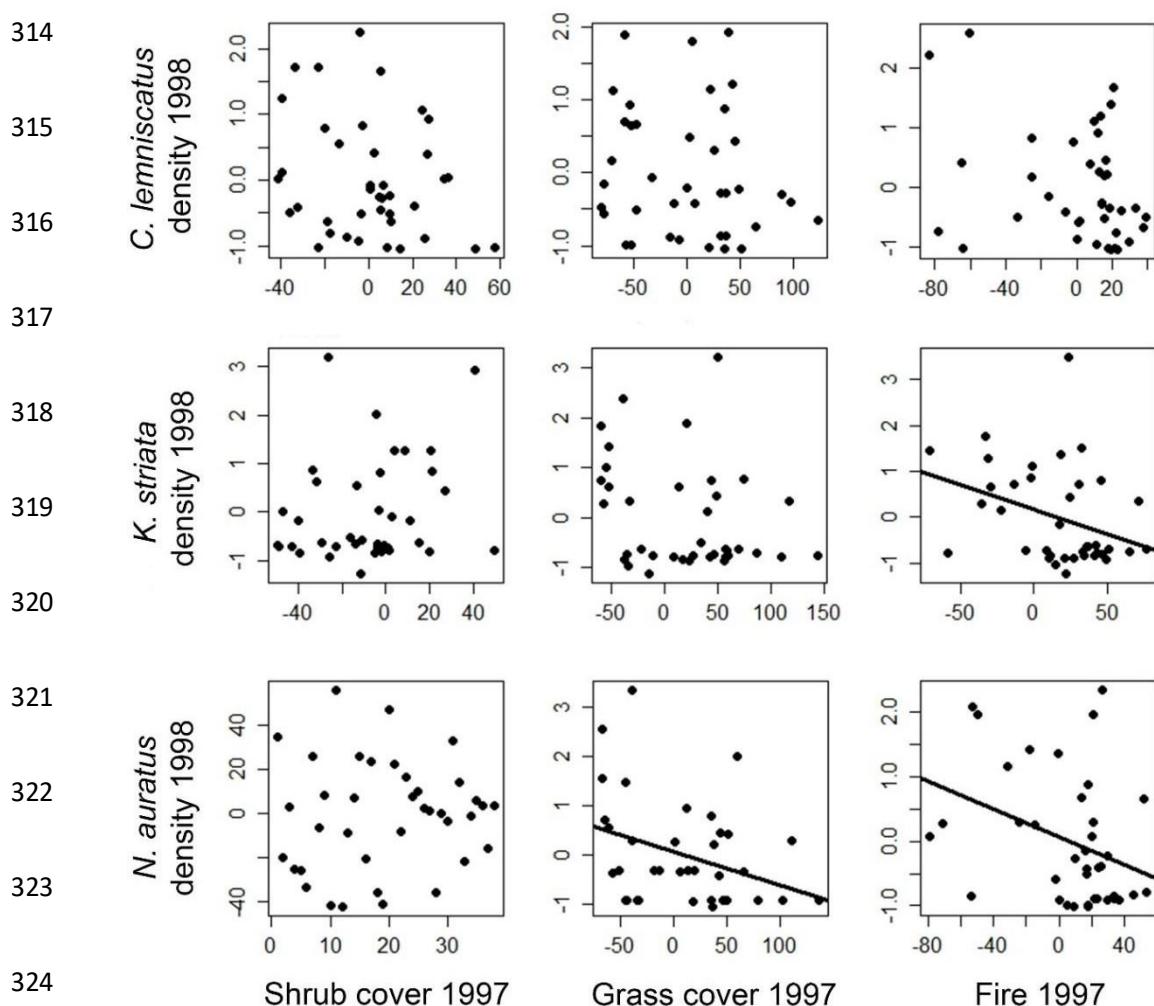
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300

301 **Short- and long-term effects of fire and vegetation cover**

302 In the short-term, we found few significant relationships ($P \leq 0.05$) between
 303 predictor variables and lizard densities, despite lizard responses to fire and vegetation
 304 cover varying greatly among species and sampling years. We found negative effects
 305 of fire on *K. striata* density ($R^2 = 0.19$, $P = 0.01$) in 1998 (Figure 2) and in 2019 ($R^2 =$
 306 0.55, $P = 0.03$), but not in 2002 ($P = 0.35$). We also found weak negative effects of
 307 grass cover ($R^2 = 0.08$, $P = 0.03$) and fire ($P = 0.03$) on *N. auratus* densities in 2004,

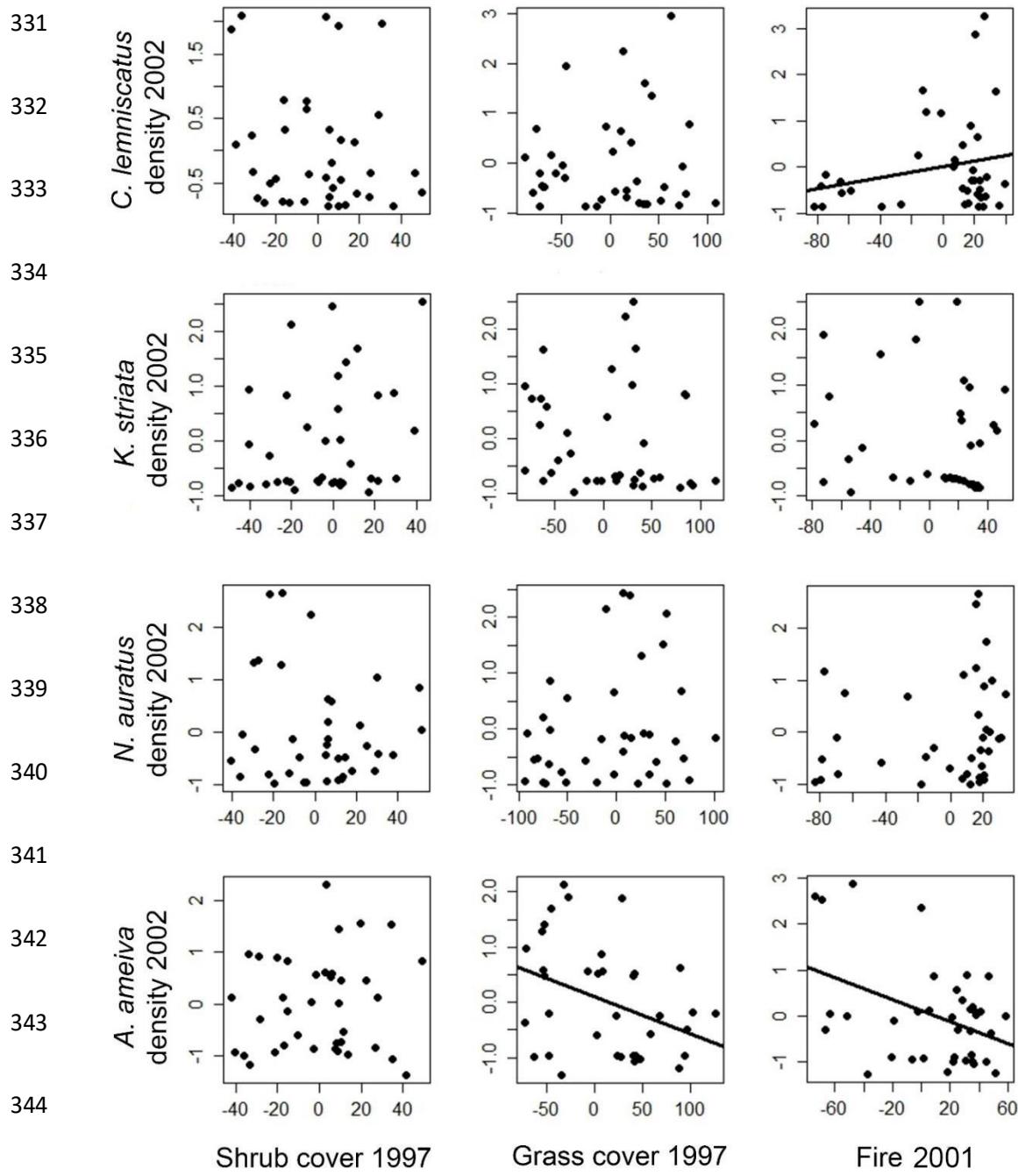
308 but not in 2002 ($P \geq 0.22$) or 2019 ($P \geq 0.17$). In 2002 (Figure 3), fire positively affected
 309 *C. lemniscatus* density, but the relationship was weak ($R^2 = 0.04$, $P = 0.04$). In 2019
 310 (Figure 4), *K. striata* density was positively affected ($R^2 = 0.55$) by shrub ($P = 0.003$),
 311 grass ($P = 0.009$) and exposed soil cover ($P = 0.02$), and *N. auratus* density was
 312 positively affected by shrub cover ($R^2 = 0.36$, $P = 0.05$). Detailed outputs from the short-
 313 term GLMs can be found in Table 3.



325
 326 **Figure 2.** Partials plots derived from multiple generalized linear models showing short-
 327 term effects of fire and vegetation cover on densities of four lizard species sampled in

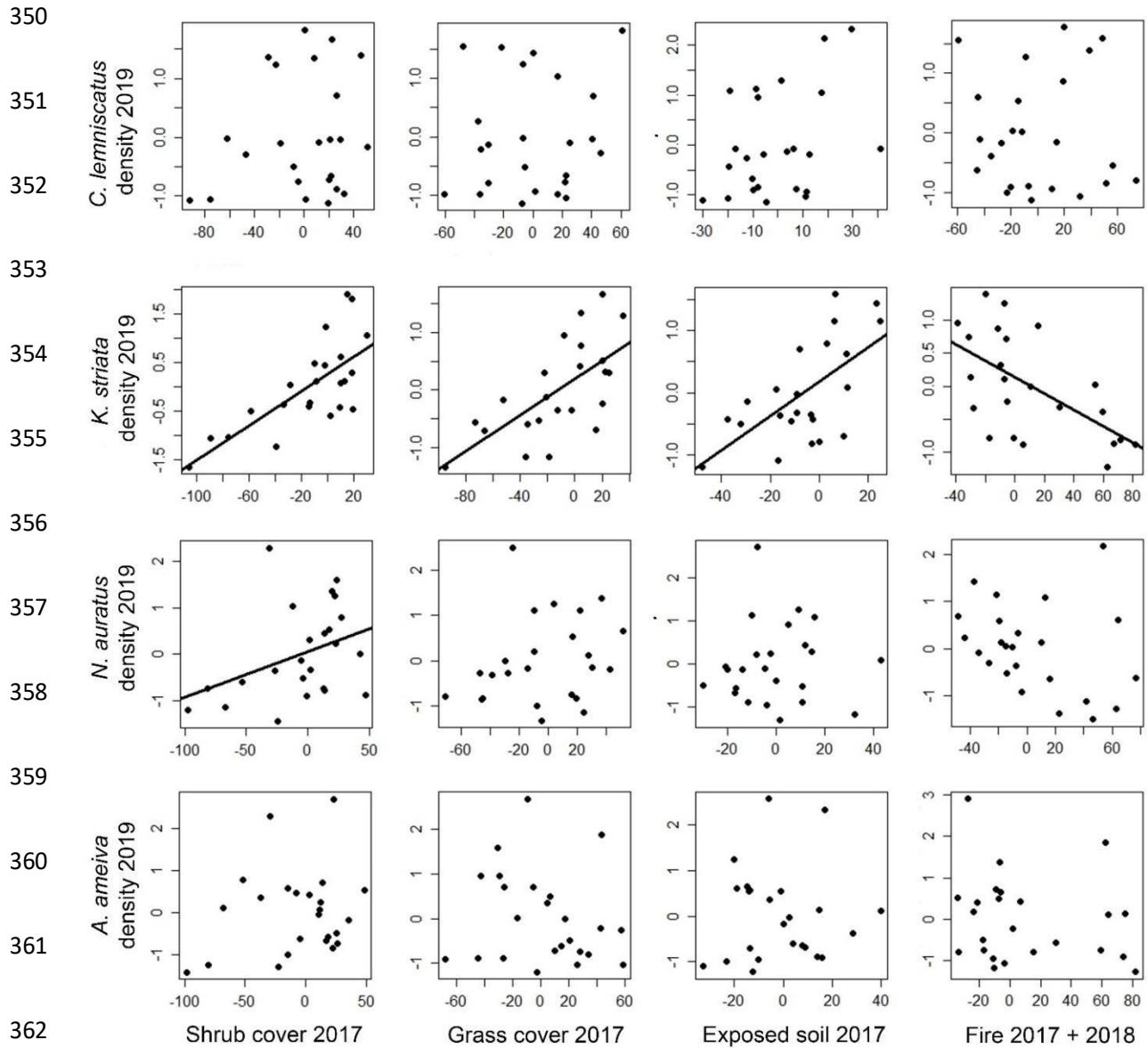
328 Amazonian savannas in 1998. Only statistically significant ($P < 0.05$) relationships are
 329 represented by lines.

330



346 **Figure 3.** Partials plots derived from multiple generalized linear models showing short-
 347 term effects of fire and vegetation cover on densities of four lizard species sampled in

348 Amazonian savannas in 2002. Only statistically significant ($P<0.05$) relationships are
 349 represented by lines.



363
 364 **Figure 4.** Partials plots from multiple generalized linear models showing short-term
 365 effects of fire and vegetation cover on densities of four lizard species sampled in
 366 Amazonian savannas in 2019. Only statistically significant ($P<0.05$) relationships are
 367 represented by lines.

368

369 The GLM outputs usually made ecological sense, since species that climb
 370 vegetation to thermoregulate (*K. striata* and *N. auratus*) were sometimes positively
 371 affected by vegetation cover and negatively affected by fire. The same model returned
 372 significant positive effects of exposed soil cover on *K. striata* density.

373 Although we found some ecologically supported statistical relationships, an
 374 overall analysis of the GLM outputs revealed that the relationships tested were
 375 generally weak (see R^2 values in Table 3) or inconsistent among sampled years. This
 376 finding is supported by the fact that less than 30% of the P values from individual
 377 independent variables lead us to reject the GLM null hypothesis. Therefore, it is
 378 reasonable to generalize that nonrandom lizard density regarding the measured
 379 independent variables is generally limited to a few sampling snapshots, and short-term
 380 fire and vegetation cover generally have minor effects on lizard densities.

381

382 **Table 3.** Summary of the main results from generalized multiple linear models used to
 383 test short-term effects of fire and vegetation cover on densities of four lizard species,
 384 which were sampled in Amazonian savannas over three different periods. Undefined
 385 values were due to lack of sampling or removal of highly correlated variables. Bold P-
 386 values show cases in which the null hypothesis was rejected.

Species	Variable	1998		2002		2019	
		$R^2 = 0.05$	P	$R^2 = 0.04$	P	$R^2 = 0.17$	P
<i>C. lemniscatus</i>	Shrub	-1.50	0.13	0.88	0.37	1.14	0.25
	Grass	-0.95	0.33	0.53	0.59	0.52	0.60
	Soil	-	-	-	-	1.83	0.06
	Fire	-1.70	0.08	2.07	0.04	-0.87	0.86
		$R^2 = 0.19$		$R^2 = 0.04$		$R^2 = 0.55$	
		Shrub	1.53	0.12	1.59	0.11	2.91
							0.003

<i>K. striata</i>	Grass	-1.71	0.08	-0.92	0.35	2.58	0.009
	Soil	-	-	-	-	2.31	0.02
	Fire	-2.32	0.01	-0.92	0.35	-2.12	0.03
		$R^2 = 0.08$		$R^2 = 0.08$		$R^2 = 0.36$	
<i>N. auratus</i>	Shrub	0.33	0.73	-0.82	0.40	1.88	0.05
	Grass	-2.14	0.03	1.58	0.11	1.15	0.24
	Soil	-	-	-	-	-0.31	0.75
	Fire	-2.07	0.03	1.21	0.22	-1.36	0.17
<i>A. ameiva</i>	Shrub	-	-	0.29	0.76	1.14	0.25
	Grass	-	-	-2.32	0.02	-0.94	0.34
	Soil	-	-	-	-	0.02	0.97
	Fire	-	-	-2.53	0.01	-1.94	0.23

387

Our results in the long-term showed low predictive power of fire and vegetation cover for changes in densities of most lizard species (Figure 5). The GLMs had little predictive power for *C. lemniscatus* ($P = 0.51$) or *K. striata* ($P = 0.21$). For these species, differences in lizard densities were randomly distributed over accumulated fire gradients and differences in vegetation cover (Figure 3). For *N. auratus*, the GLM explained 24% of the variation in density differences between years, but shrub cover was the only predictor variable that significantly contributed to the model ($P = 0.02$). The positive relationship suggests that the availability of thermoregulation sites resulting from 21 years of fire-induced habitat change affects *N. auratus* density. The GLM for *A. ameiva* was the best-fitted model ($P = 0.005$) and explained 48% of the variation in density differences. This finding was mainly associated with negative effects of grass cover ($P = 0.04$), and the positive effects of accumulated fire over time ($P = 0.0006$). Overall, sites that have been historically maintained open by fire has favored high lizard densities. The long-term GLM results are summarized in Table 4.

402

403 **Table 4.** Summary of the main results from generalized multiple linear models used to
 404 test long-term effects of fire and vegetation cover on differences in densities of four
 405 lizard species between 2019 and 1998. Bold P-values show cases in which the null
 406 hypothesis was rejected.

Species	Variables	t	P	R²
<i>C. lemniscatus</i>	Shrub	1.30	0.20	
	Grass	-0.76	0.45	0.10
	Fire	0.82	0.42	
<i>K. striata</i>	Shrub	1.58	0.13	
	Grass	0.47	0.64	0.19
	Fire	1.67	0.11	
<i>N. auratus</i>	Shrub	2.37	0.02	
	Grass	0.95	0.35	0.24
	Fire	0.24	0.80	
<i>A. ameiva</i>	Shrub	1.52	0.14	
	Grass	-2.12	0.04	0.48
	Fire	4.04	0.0006	

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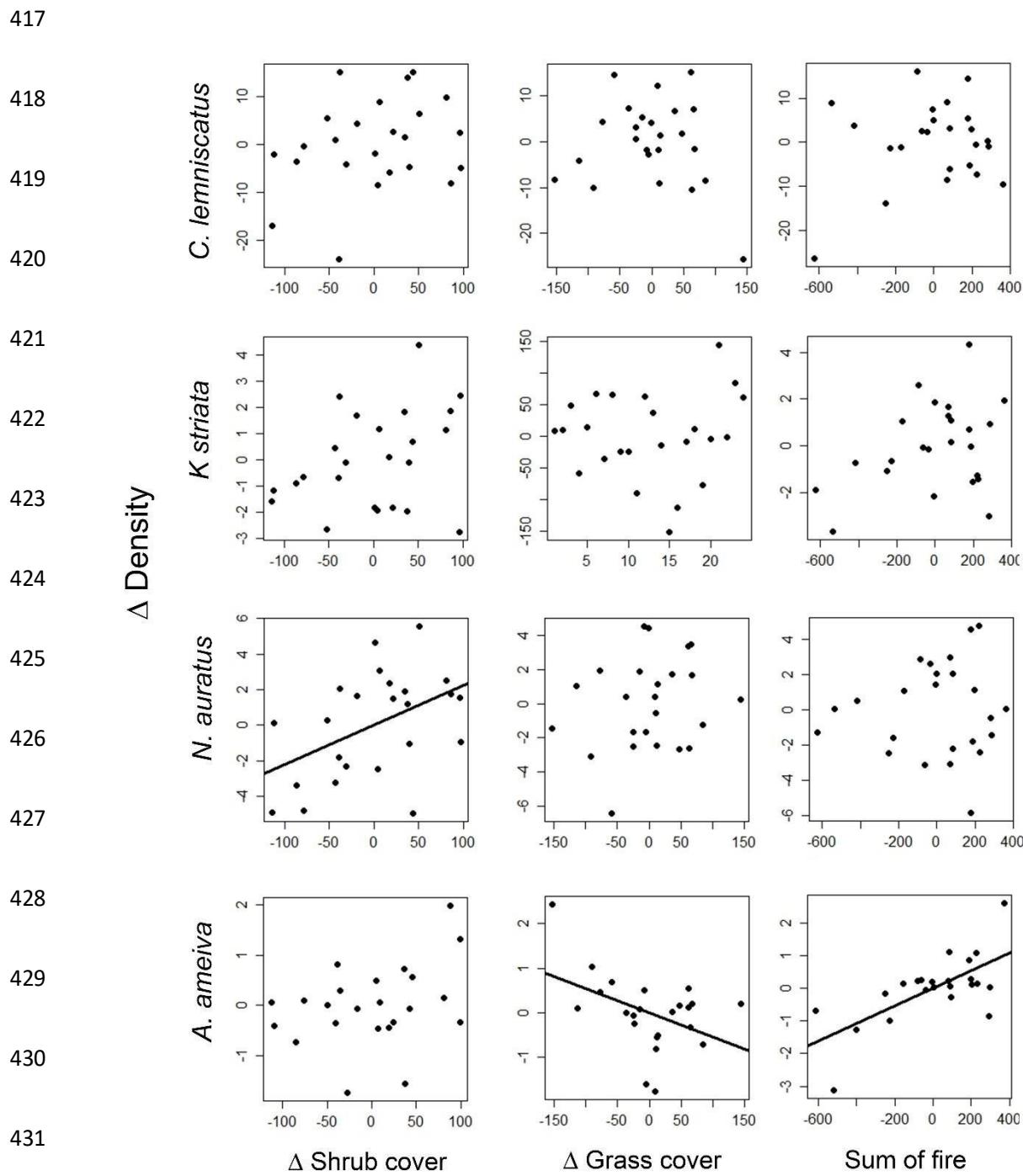
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416



433 **Figure 5.** Partials plots from multiple generalized linear models showing long-term
 434 effects of accumulated fire (sum of proportions of burned areas over 21 years) and
 435 differences in vegetation cover between 2017 and 1997 on differences between
 436 current and past densities of four lizard species sampled in Amazonian savannas. Only
 437 statistically significant ($P < 0.05$) relationships are represented by lines.

438 **DISCUSSION**

439 Fire and seasonal fire-induced vegetation cover do not consistently affect
440 density of individual lizard species in either the short and long term. Significant effects
441 of fire and vegetation cover on lizard density estimates were restricted to a few short-
442 term sampling snapshots, and there were few significant effects of predictor variables
443 in the long-term. Although fire potentially changes habitat structure at different
444 spatiotemporal scales, and consequently affects microclimate and the availability of
445 thermoregulation sites for lizards (Miranda, Ricci-Leitão, & Rocha, 2010; Sato et al.,
446 2014; Costa, Pantoja, Souza, Queiroz, & Colli, 2019), spatiotemporal effects of such
447 changes in the Alter do Chão savannas are apparently dependent on further
448 unmeasured factors, which vary over time. Therefore, our findings suggest that
449 changes in lizard densities over 21 years are more likely to be caused by multiple
450 factors acting on different short-term snapshots than by accumulated fire-induced
451 changes in habitat structure.

452 In the short term, we found that the effects of fire and vegetation cover on lizard
453 density were not consistent across different sampling snapshots. A combination of
454 lizard and vegetation-cover resilience and rapid habitat regeneration has driven rapid
455 recolonization by lizards that may have dispersed from adjacent habitats (Braithwite,
456 1987) or stayed hidden in shelters during fire (Costa, Pantoja, Vianna, & Colli, 2013).
457 After an extensive fire event in the Alter do Chão savannas a few months after our
458 sampling, we observed many *N. auratus* on or near termite mounds surrounded by
459 burnt vegetation, indicating that termite mounds are important shelters for this species
460 during fire. Fire effects and vegetation cover appear to be dependent on specific
461 conditions of a given sampling snapshot. Such conditions may involve random or
462 nonrandom fluctuations in lizard density and fire intensity, as we have shown by the

463 increase in the densities of two species that climb the vegetation to thermoregulate (*K.*
464 *striata* and *N. auratus*).

465 Although our general short-term findings do not indicate that fire and vegetation
466 cover are good predictors of lizard densities, the occasionally significant relationships
467 between lizard densities and the independent variables we measured may have
468 biological significance. *Kentropix striata* density was negatively affected by fire (1998
469 and 2019), and positively affected by vegetation cover and exposed soil in 2019. Since
470 this species climbs plants to thermoregulate and forages on exposed soil (Magnusson
471 et al., 1985), our findings suggest lizard density dependent on habitat quality, and
472 spatial structure mediated by environmental filtering (Garda et al., 2012). Additionally,
473 the estimated densities of *N. auratus*, which also climbs plants to thermoregulate
474 (Faria, Lima, & Magnusson, 2004), was negatively affected by fire in 1998, and
475 positively affected by shrub cover in 2019. The negative relationship between grass
476 cover and *N. auratus* density in 1998 is probably best explained by biased detectability
477 in sites with high grass cover, since the camouflage of this species is very efficient in
478 the savanna grasses. Therefore, we have identified some evidence of environmental
479 filtering spatially structuring lizard densities, although the size of the environmental
480 gradient regions occupied by each species varied greatly over time.

481 In the long term, changes in habitat structure induced by the accumulated fire
482 effects over 21 years had little effect on species-habitat relationships in our study
483 system. This finding seems contradictory to the significant effects of fire on lizards from
484 savannas in central Brazil (Costa, Pantoja, Souza, Queiroz, & Colli, 2019). However,
485 the fire in that study was quantified as categories of suppression levels, while we
486 measured proportions of burned areas by wild, uncontrolled fire. A potential problem
487 of controlling fire in tropical savannas is artificially changing fire-mediated species-

488 habitat relationships, which may be positive, negative or negligible, depending on
489 species biological traits (Faria, Lima, & Magnusson, 2004; Costa, Pantoja, Souza,
490 Queiroz, & Colli, 2019). For instance, we found that variation in shrub cover over time
491 has favored high densities of *N. auratus*, which is consistent with the increase in
492 density of this species since 2002. This finding suggests that the availability of
493 thermoregulation sites for *N. auratus* has increased over time, indicating that
494 vegetation cover regeneration has been favored by fire-free periods increasing over
495 time.

496 For most of the sampled species, changes over time in lizard density were
497 random with respect to long-term fire and fire-mediated changes in habitats. However,
498 accumulated fire over time positively affected *A. ameiva* density, for which changes in
499 grass cover caused negative effects. This species is often considered to be habitat-
500 generalist (Aoki, Piatti, Landref-Fillho, & Souza, 2011; Abrahão-Morato, 2012) when
501 habitats are described as static snapshots (e.g. categorical levels, continuous
502 gradients measured only once). *Ameiva ameiva* shows high levels of ecological
503 plasticity and occupies very distinct ecosystems (Colli, 1991; Aoki, Piatti, Landref-
504 Fillho, & Souza, 2011; Abrahão-Morato, 2012). However, we have shown that
505 quantifying habitats through landscape dynamics over time may reveal predictors of *A.*
506 *ameiva* density. Specifically, the largest differences in *A. ameiva* density occurred in
507 plots that historically had larger proportions of burned areas and exposed soil, which
508 is consistent with the species biology. *Ameiva ameiva* is a relatively large heliotherm
509 that occupies open habitats and may benefit from the relatively high availability of prey
510 in areas with more frequent burning (Colli, 1991). Interestingly we found no evidence
511 that the species density has changed over time, suggesting that lizard densities
512 change spatially, along temporally changing habitats. Therefore, long-term effects of

513 fire and vegetation cover on *A. ameiva* density should be interpreted considering
514 complex interactions among different spatiotemporal scales.

515 We found that short-term fire-mediated changes in habitat quality do not
516 consistently affect lizard density, and that long-term fire-mediated changes in lizard
517 spatial structure are not necessarily associated with changes in lizard density over
518 time. These findings are consistent with relatively negligible short- and medium-term
519 effects of fire on lizards from the Alter do Chão savannas (Faria et al., 2004) and
520 indicate that the biodiversity of Amazonian savannas is well adapted to seasonal fire.
521 Therefore, reforesting savannas to reduce the effects of climate change on the Planet
522 (Bastin et al., 2019) is not advisable, since the spatial structure of biodiversity
523 occupying savannas may be anthropogenically changed by the extinction of seasonal
524 fire. Savannas are locally rare ecosystems in Amazonia, and biologically
525 complementary to surrounding forests, as resident species must necessarily be well-
526 adapted to water and thermal stress (Barbosa, 2007; Plotkin & Riding, 2011). The
527 lizards sampled in the Alter do Chão savannas do not occur in the surrounding forests
528 or are restricted to clearings and edges. Therefore, Amazonian savannas should be
529 protected because they contain unique biodiversity, and conservation programs should
530 be more focused on protecting the surrounding forests, which act as natural barriers
531 against the spread of fire.

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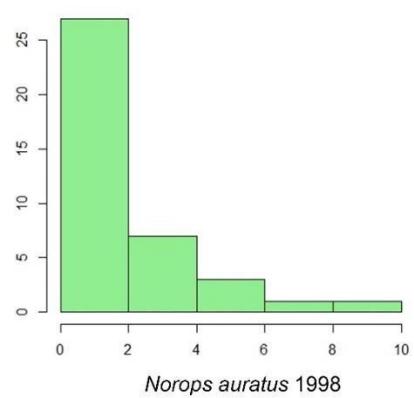
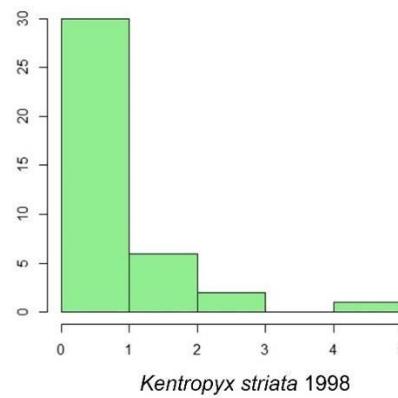
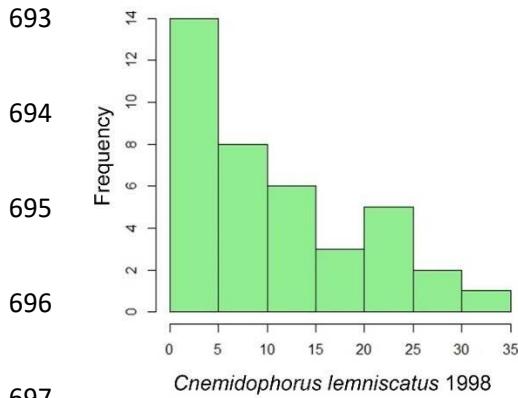
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689 **SUPPLEMENTARY MATERIALS**

690 **S1.** Histograms showing the distribution of short-term densities of lizard species
 691 sampled on 39 plots (light green and pink) and 26 plots (light blue) in the Alter do Chão
 692 savannas (eastern Amazonian Brazil).



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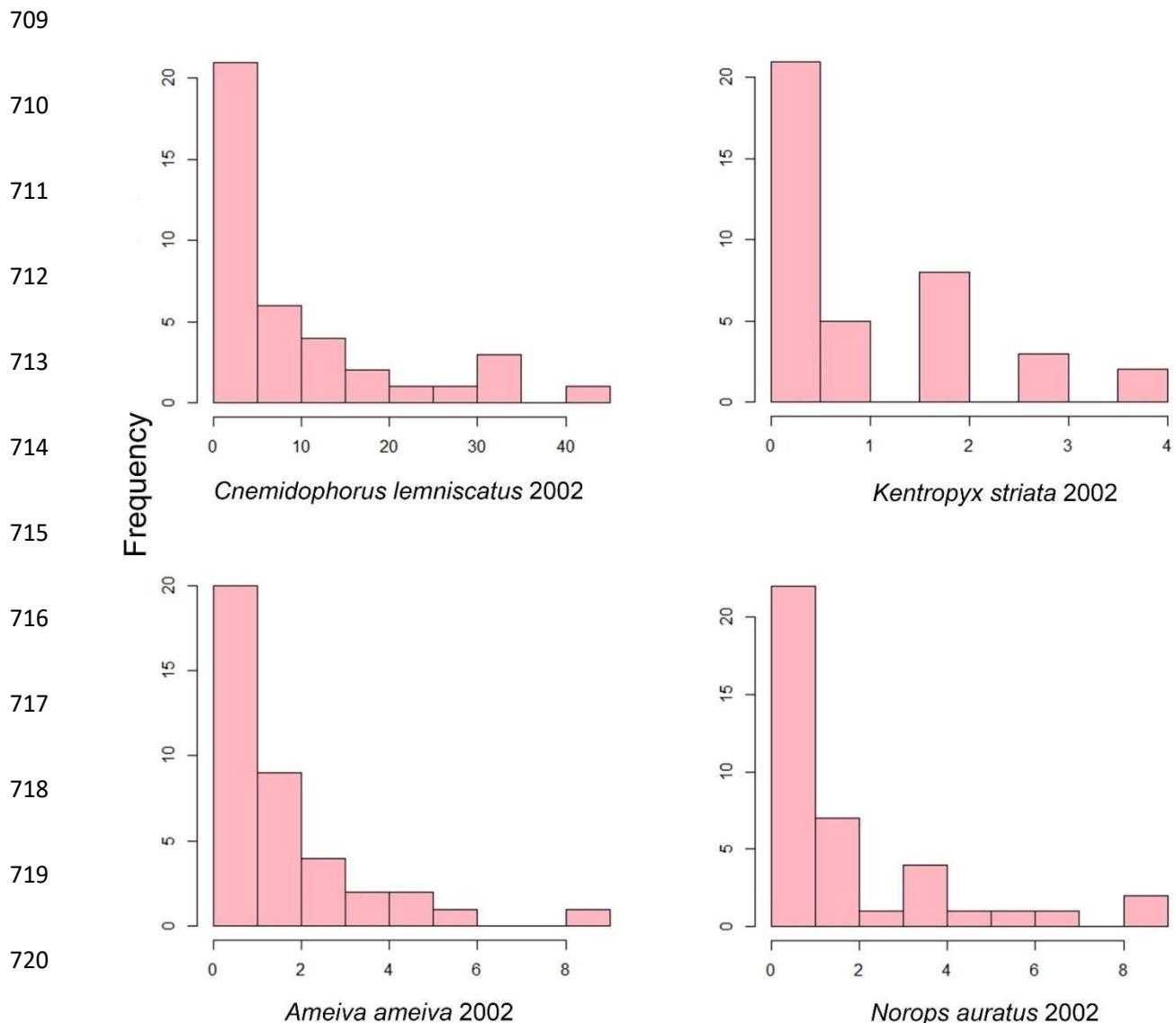
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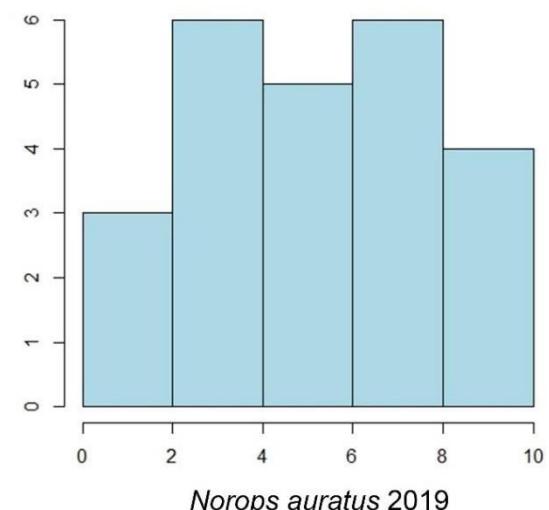
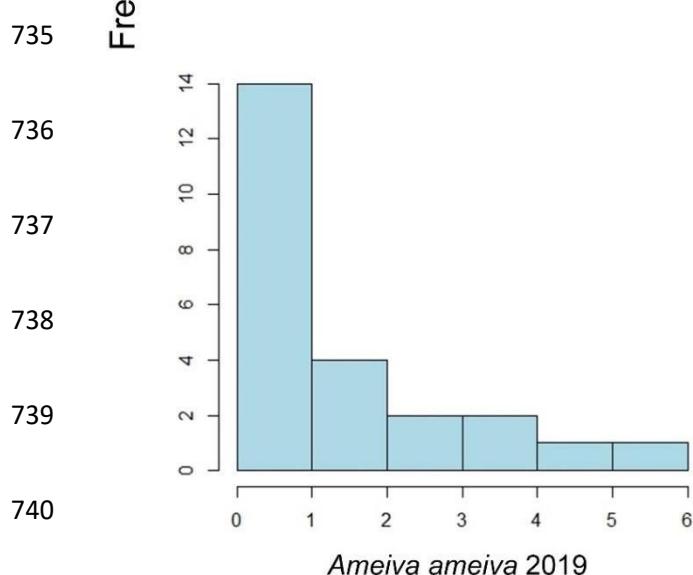
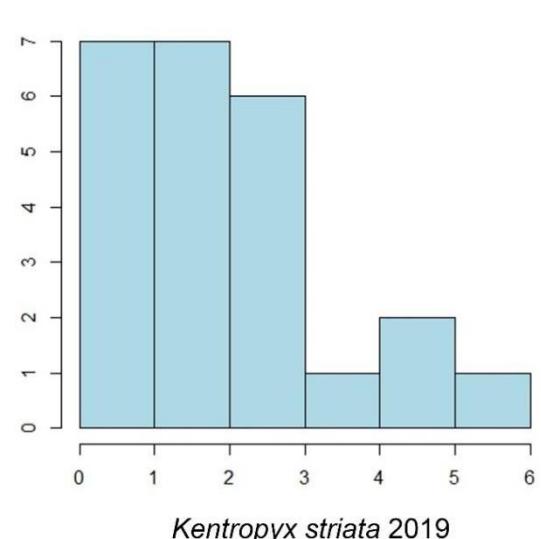
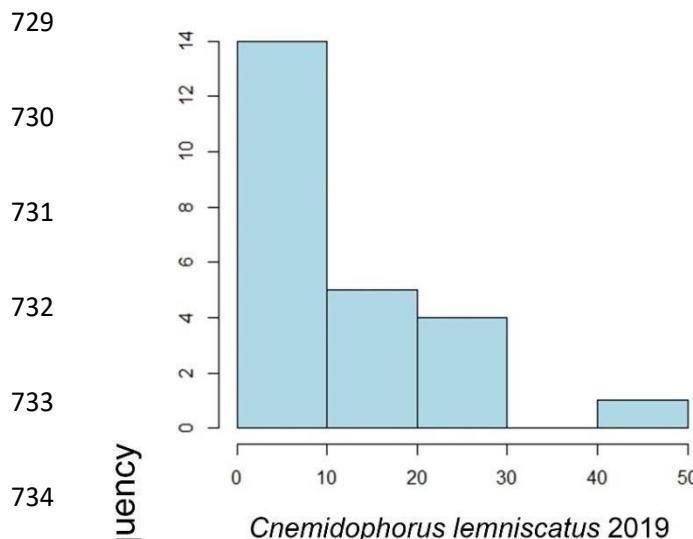
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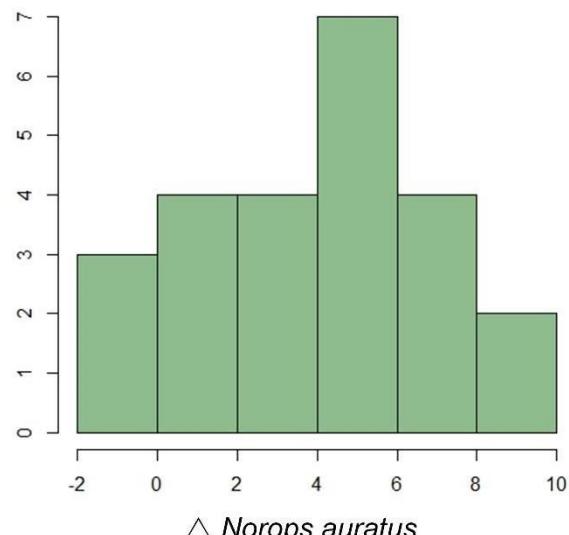
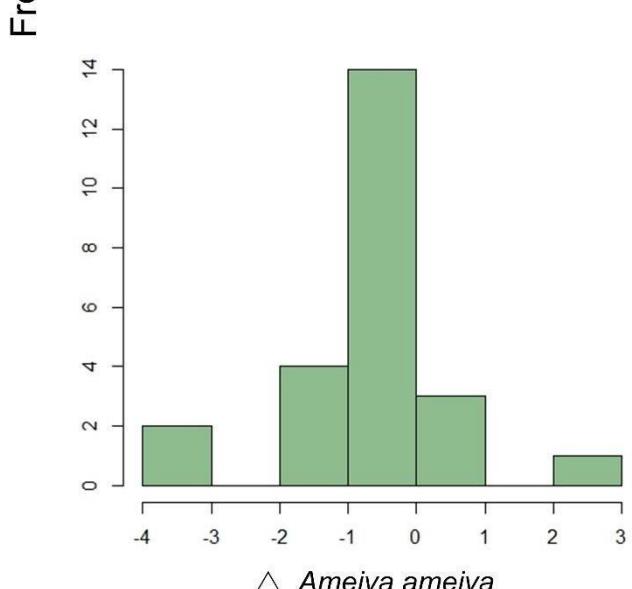
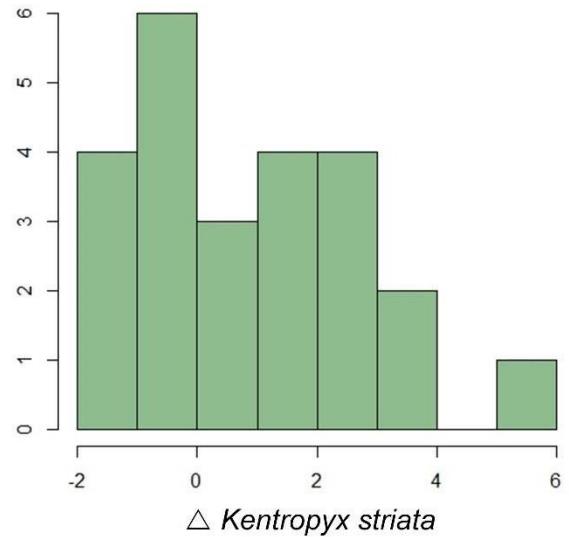
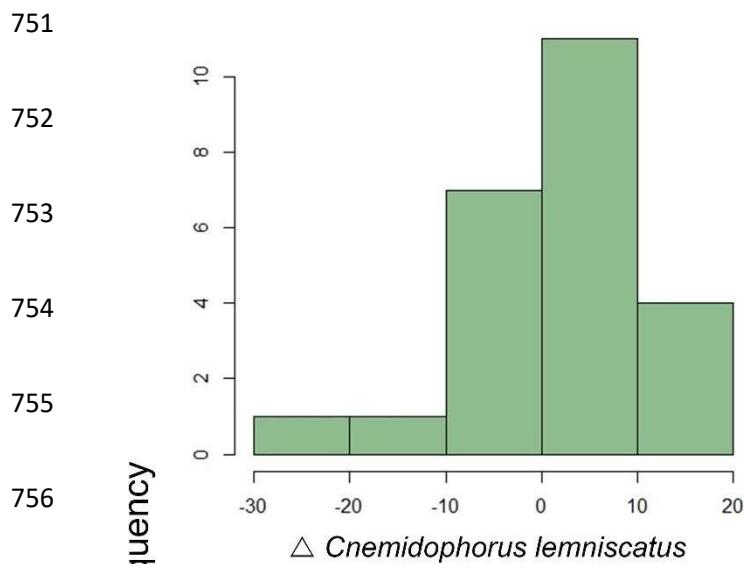
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748 **S2.** Histograms showing the distribution of density differences (current – 21 or 18 years
 749 ago) in four lizard species sampled in 24 plots in the Alter do Chão savannas (eastern
 750 Brazilian Amazon). Differences are represented by Δ .



Comments addressed to the program coordination (optional)

This well-designed study demonstrates that lizards in the savanna at Alter do Chão are, both in the short- and long-term, pretty darn resistant to fire. This is a really neat result, and to many, will seem counter-intuitive. The lizard fauna of these savannas is depauperate compared with adjacent forest. Although a few additional species occur in these savannas (e.g., *Gymnophthalmus*, *Iguana*), the four species chosen make up the core of the savanna lizard fauna, and forest is pretty much a barrier for three of them. Moreover, with the possible exception of *N. auratus*, these lizards are not microhabitat specialists that would be stranded (without microhabitats) following a fire—they can either move or enter retreats (e.g., termite mounds). Adding to this result is the fact that burned patches in savanna apparently recover to savanna. Thus, from the lizard's point of view, habitat change is relatively short-lived. Again, a very nice study with important results.

I collected in a cerrado patch in southern Rondônia in 1985 just after a fire swept through burning virtually all of the grass and smaller shrubs. What struck me was how common lizards were after the fire, and all were using termite nests. *Kentropyx striata*, and *Norops meridionalis* were in nearly every termite mound. We also collected several *Ameiva parecis*, which was undescribed at the time, also using termite nests. The thesis by Erika dos Santos Souza demonstrates that lizard populations do well following fire in open habitats, and her results no doubt will apply to many cerrado habitats as well.

Final recommendation

I - Approved ()

indicates that the reviewer fully approves the dissertation without corrections or with minimum corrections

II - Approved with Corrections (X)

indicates that the reviewer approves with minor appointed corrections, but the dissertation does not need to return for a second review

Note: I made a few very minor suggestions directly on the manuscript. Very nice job!

III - Major Review ()

indicates there is a significant need to rewrite the dissertation, and that the reviewer wants to receive a second, reviewed, version to make a final decision

IV - Failed ()

indicates that the dissertation is not fit for a masters degree

Reviewer

Name: Laurie J. Vitt, Professor and Curator Emeritus

Date: January 30, 2020

Signature:

A handwritten signature in black ink, appearing to read "Laurie J. Vitt".

Comentários à coordenação do PPGBEEs:

A dissertação está ótima, com planejamento e execução impecáveis, bem como muito bem escrito. Devido a qualidade do trabalho e experiência dos autores envolvidos, provavelmente o manuscrito será aceito com poucas correções. Assim, fiz alguns apontamentos mínimos no documento anexo e parabenizo tanto o PPGBEEs quanto a discente e seus orientadores.

Avaliação final do projeto de dissertação de mestrado**I - Aprovado (X)**

indica que o revisor aprova a dissertação em correções ou com correções mínimas

II - Aprovado com Correções ()

indica que o avaliador aprova o projeto com correções extensas, mas que a dissertação não precisa retornar ao avaliador para reavaliação

III - Necessita Revisão ()

indica que há necessidade de reformulação do trabalho e que avaliador quer reavaliar a nova versão da dissertação antes de emitir uma decisão final

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indica que a dissertação não é adequada, nem com modificações substanciais

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Assinatura: 

Comentários à coordenação do PPGBEES:

Prezados,

A dissertação que eu avaliei está muito bem escrita e estruturada. O fato de o arquivo ter vindo em formato .docx facilita a inserção de comentários, correções e sugestões. Sugiro que mantenham esse padrão.

A introdução está coerente, clara, objetiva e bem embasada na literatura. Os materiais e métodos também. Apenas alguns ajustes são necessários nessas seções. Todos eles estão anotados no arquivo.

Os resultados trazem dados novos e relevantes, e certamente é um trabalho com uma grande contribuição ao conhecimento da fauna neotropical e os efeitos do fogo em áreas de savana. Os dados abrangem não só uma amostragem adequada, como também temporalmente abrangente. Certamente tudo isso torna os resultados e conclusões mais robustos.

O trabalho também tem grande relevância social, uma vez que discute um tema complexo que são os efeitos do fogo. No documento em anexo eu sugiro aos autores que pensem mais a respeito da forma como eles discutem os resultados. Sobretudo, porque temos visto discussões acaloradas e polêmicas sobre o fogo na Amazônia nos últimos anos.

Os resultados e a discussão estão coerentes e claros. Sugiro aos autores ressaltar que o trabalho foca em 4 espécies que são generalistas e adaptadas a alterações ambientais em maior ou menor grau. Entretanto, as savanas amazônicas possuem espécies que são sensíveis a alterações ambientais ou localmente endêmicas, e portanto, cada espécie pode ser afetada em maior ou menor grau pelos efeitos do fogo. Com o crescimento da área urbana ao redor de Alter do Chão, as áreas de escape ou de fonte de espécimes para recolonização da área afetada pelo fogo, pode se extinguir, e futuramente tornar a área suscetível a extinção local.

As referências devem ser padronizadas de acordo com as normas da revista.

A quantidade e a qualidade das figuras são adequadas.

Finalmente, recomendo a aprovação da dissertação com apenas algumas sugestões de correções que podem ser acatadas ou não pelos autores. Nada que comprometa a qualidade final do trabalho.

Algumas dúvidas que tive e poderiam ser facilmente contornadas através de uma conversa com os autores eu incluí no arquivo da dissertação.

As minhas sugestões ao texto estão inclusas no arquivo em anexo.

Avaliação final do projeto de dissertação de mestrado**I - Aprovado (X)**

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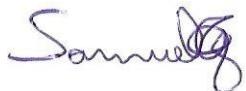
IV - Reprovado ()

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