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# Habitat Quality, Not Patch Size, Modulates Lizard Responses to Habitat Loss and Fragmentation in the Southwestern Amazon

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**ABSTRACT.**—As deforestation frontiers expand in the tropics, understanding species responses is critical to inform efficient land-use management policies. Here we evaluated lizard responses to changes in landscape, habitat patch, and quality in a deforestation frontier in southwestern Brazilian Amazonia. We first considered overall lizard assemblages and then two species subgroups of contrasting thermoregulation strategies. We sampled lizards at 21 forest patches (42–7,035 ha) subject to moderate habitat disturbance (e.g., cattle intrusion and selective logging). Based on 6,000 pitfall trap-days and 60,000 m of visual surveys, we recorded 215 individuals representing 15 species. Contrary to expectations, species richness and abundance were not explained by any of the variables considered, including matrix quality, proportion of forest cover, forest patch area and shape, age since isolation, arthropod biomass, canopy openness, litter volume, tree density, and fire history. However, the composition of persisting species was determined by the structural complexity of the adjacent matrix. The abundance of species that avoid direct sun exposure to regulate their body temperature increased under more-complex structures of adjacent matrix areas and decreased within patches more intensively affected by past fire events. Disturbance within forest patches likely decreased the patch-matrix contrast, contributing to the absence of forest area effects. Nevertheless, species-specific microhabitat requirements dictated part of the lizard species that were able to persist in the fragmented landscape. Strategies aiming to maximize lizard diversity should embrace retention of the habitat quality within forest patches and forest corridors/high-stature vegetation in at least some sites connecting forest remnants.

**RESUMO.**—À medida que as fronteiras de desmatamento se expandem nos trópicos, entender a resposta das espécies torna-se crítico para tomar medidas eficientes do manejo do uso do solo. Neste estudo, avaliamos as respostas da comunidade de lagartos a alterações ao nível da paisagem, fragmento e qualidade do habitat, numa fronteira de desmatamento no sudoeste da Amazônia brasileira. Primeiro consideramos toda a comunidade de lagartos e depois dois sub-grupos de espécies com comportamentos de termorregulação contrastantes. Amostramos os lagartos em 21 fragmentos (42 – 7.035 ha) sujeitos a níveis moderados de perturbação (por exemplo, invasão pelo gado e corte seletivo de madeira), utilizando armadilhas tipo-queda e busca ativa. No total, amostramos 6.000 armadilhas/dia e 60.000 m percorridos, respectivamente. Com base neste esforço, capturamos 215 indivíduos representando 15 espécies. Ao contrário do que esperávamos, nem a riqueza nem a abundância de espécies foram explicadas pelas das variáveis consideradas, incluindo qualidade da matriz, proporção de cobertura florestal, área e forma do fragmento florestal, tempo desde o isolamento, grau de abertura do dossel, vólum da liteira, densidade de árvores e histórico de fogos. No entanto, a composição de espécies foi determinada pela complexidade da matriz ao redor dos fragmentos. A abundância das espécies que evitam a exposição direta à luz solar para regular a sua temperatura corporal aumentou em fragmentos cercados por matrizes estruturalmente mais complexas e diminuiu em fragmentos anteriormente sujeitos a maior intensidade ao fogo. A perturbação dos fragmentos, ao diminuir o contraste estrutural com a matriz, provavelmente contribui para o fato de não terem sido observados quaisquer efeitos da área dos fragmentos. Ainda assim, a persistência de lagartos foi determinada por requerimentos espécie-específicos ao nível do micro-habitat. Estratégias que visem maximizar a diversidade de lagartos devem passar pela retenção da qualidade do habitat dos fragmentos, bem como de corredores/maior complexidade da estrutura da vegetação conectando remanescentes florestais.

Tropical forests host the highest levels of biodiversity but are also the largest current agricultural frontiers (Hansen et al., 2020). As a consequence of habitat loss and fragmentation, unprecedented changes in the remaining biodiversity have also been recorded (Laurance and Peres, 2006; Newbold et al., 2016). Over the last five decades, Amazonian forests have been rapidly converted into cattle pastures and cropland (Nobre et al., 2016). Currently, agricultural frontiers have expanded from neighboring savanna-like wooded biomes (Cerrado and Caatinga) into the Brazilian Amazon biome span an area >500 Mkm<sup>2</sup> (INPE, 2019). In the vast region known as the Amazonian ‘arc of

deforestation,’ variable-sized forest patches become isolated within cattle pastures and, to a lesser extent, mechanized monoculture (Fearnside, 2005).

Species diversity throughout fragmented tropical forest landscapes is dictated by both the remaining habitat amount (Fahrig, 2013) and landscape configuration, defined in terms of habitat patch area, isolation, and intensity of edge effects (Mendenhall et al., 2014; Bueno and Peres, 2019). Forest area affects both species richness and abundance by limiting population sizes, and the degree of isolation restricts species colonization rates (MacArthur and Wilson, 1967). In addition, habitat quality in either forest patch core areas or the surrounding open-habitat matrix may further dictate which species can persist under the newly created conditions. Within forest patches, edge effects alter vegetation structure (Malcolm,

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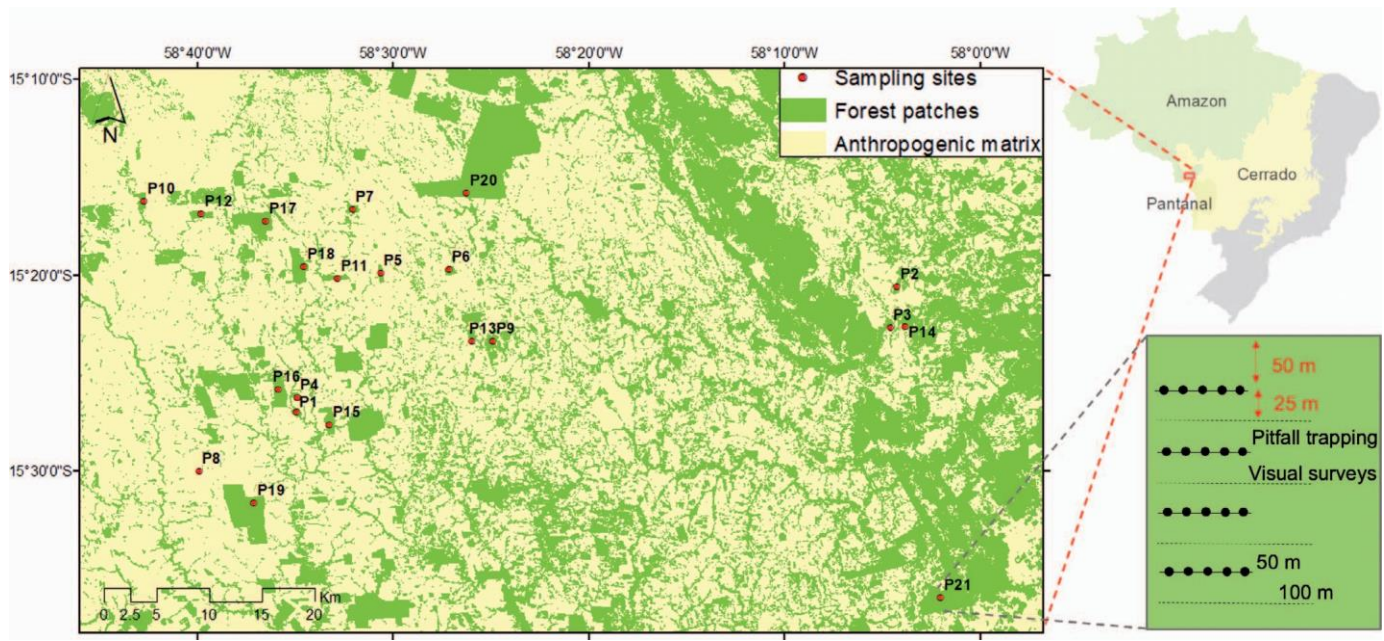


FIG. 1. Location of the 21 forest patches surveyed within the Jaurú and Cabaçal river basins, Mato Grosso, southern Brazilian Amazon. Patches surveyed are numbered according to Supplementary Table S1. Inset map shows the location of the study area (red rectangle) within the Brazilian Amazon biome. The sampling site inset illustrates the sampling design used at each forest patch in terms of pitfall trapping and intensive visual searches. Distances between traps are indicated in the figure. See main text for a detailed description of the sampling design.

1994), eventually reducing the availability of trophic and structural resources. Habitat deterioration is further boosted in more-irregularly shaped patches (i.e., those with proportionally longer perimeters in relation to the patch area; Benchimol and Peres, 2015a) and additive human disturbance (e.g., burning and logging; Barlow et al., 2016). Matrix areas surrounding forest patches limit individual dispersal across the landscape according to their degree of hostility (Driscoll et al., 2013), which is often expressed by the structural complexity of vegetation (Prevedello and Vieira, 2010; Santos-Filho et al., 2012). Ultimately, species persistence depends on intrinsic ecological traits in adjusting to novel habitat conditions (Cabrera-Guzman and Reynoso, 2012; Lion et al., 2016). For instance, novel environmental features of disturbed sites can often benefit synanthropic generalists at the expense of strict forest habitat specialists (Devictor et al., 2008; Newbold et al., 2014; Palmeirim et al., 2017a).

Lizards, and reptiles in general, include the most threatened and least studied terrestrial vertebrate taxa (International Union for Conservation of Nature [IUCN], 2015). Lizards are ectothermic species, relying on specific microhabitats and microclimatic conditions and, in Amazonian lizards, typically exhibit low dispersal capacity (Garda et al., 2013). The habitat specificity of lizards is expected to render them particularly sensitive to habitat disturbance (Gibbons et al., 2000; Vitt and Caldwell, 2014). Amazonian lizard assemblages are usually species-rich and structurally complex (Ávila-Pires, 1995). Interspecific niche partitioning usually operates on the basis of food and microhabitat types, which are closely linked to species metabolism (Vitt et al., 1999). To maintain suitable body temperatures as diurnal forest species, heliophile species expose themselves to direct sunlight while heliophobe species avoid direct exposure to sunlight (Vitt et al., 1998). Warm-adapted lizards also tend to be larger-bodied generalist species that prey on a variety of arthropods and smaller vertebrates (Martins, 1991; Ávila-Pires, 1995). Despite the mounting evidence on the

ecological impacts of habitat loss and fragmentation worldwide, proportionally fewer studies have been focused on squamate reptiles in tropical forests (Gardner et al., 2007), where deforestation frontiers are currently expanding (INPE, 2019). Such understanding has therefore great potential to enhance the effectiveness of habitat management actions.

Here we investigate the responses of lizard assemblages to habitat loss, fragmentation, and the consequent degradation in habitat quality in a highly fragmented landscape in southwestern Brazilian Amazonia. We surveyed lizard assemblages across 21 remaining forest patches of different sizes that were subject to moderate levels of habitat disturbance (e.g., cattle intrusion and selective logging). We first examined the combined effects of landscape (matrix quality and proportion of forest cover), habitat patch (area, age since isolation, and shape), and habitat quality in terms of food (arthropod biomass) and structural resources (canopy openness, litter volume, tree density, and fire history) within forest patches on lizard species richness, abundance, and composition. Across the gradient of fragmentation severity, we expected lizard species richness and abundance to be negatively affected, with concomitant changes in species richness. We then assessed species-specific responses across the same gradient in terms of thermoregulation strategy, expecting heliophile and heliophobe species to either increase or decrease in abundance, respectively.

## MATERIAL AND METHODS

**Study Sites.**—Lizard assemblages were surveyed throughout a vast deforestation frontier located in the basins of Jaurú and Cabaçal rivers, tributaries of the Paraguay River, in southwestern Mato Grosso, Brazil ( $15^{\circ}15'6''S$ ,  $58^{\circ}42'56''W$  and  $15^{\circ}33'43''S$ ,  $58^{\circ}00'17''W$ ; see Fig. 1). Large-scale human disturbance in the region took place in 1960s. In 2004, only 14.4% (or 518.5 km<sup>2</sup>) of the original amount of forest cover remained across the entire landscape because of forest conversion, primarily into cattle

pastures. The study area is characterized by a forest cover similar to that in other seasonally dry parts of Amazonia and best described as seasonal submontane semideciduous forest on eutrophic red-yellow podzolic soils (Oliveira et al., 1982) at elevations of 100–500 m a.s.l. (Amaral and Fonzar, 1982). The climate is seasonal tropical with marked wet and dry seasons and a mean annual precipitation of 1,330 mm. Annual temperature reaches 38°C, with mean maximum and mean minimum temperatures of 24.98°C and 20.8°C, respectively (Resende et al., 1994).

We surveyed diurnal lizard assemblages at 21 forest patches that had been previously selected to include a range of patch sizes (42–7,035 ha), proportion of forest cover (1–90% considering a 1-km<sup>2</sup> buffer), and age since isolation (0–35 yr). Habitat within forest patches was characterized by variable intensities of anthropogenic disturbance, including cattle intrusion, selective timber extraction, and surface fires. All surveyed forest patches were surrounded by a nonnative habitat matrix consisting of cattle pasture varying in grass sward height, which resulted from variation in the intensity of cattle overgrazing and stocking density. Any large tract of continuous forest larger than 5,000 ha was entirely absent from this region, further precluding their inclusion in this study as a comparative baseline.

**Lizard Sampling.**—We sampled lizards twice in both the wet and dry seasons at nine forest patches (Patches 1–9), once in the wet season at four patches (Patches 10–13) and once in the dry season at eight patches (Patches 14–21; Supplementary Table S1). To do so, we used both linear transects of pitfall traps and visual searches. Each pitfall transect was 50 m long and contained five, 24-L plastic buckets placed every 10 m. Buckets were shaped as a truncated cone (i.e., 37-cm height, 30-cm diameter at the open top, and a 26-cm-diameter bottom) and buried to their rims into the ground and linked at ground level by an 80-cm-height (plastic) silt-fence stapled to wooden stakes. The guide fence was buried 5 cm into the soil (Supplementary Fig. S1). At each sampling site, we deployed a total of four pitfall transects 50 m apart from each other so that the first transect was 50 m distant from the edge and the fourth transect was 200 m (see Fig. 1). During the rainy season, we placed pieces of Styrofoam in the buckets to prevent animals from drowning, and buckets were periodically emptied of water. We daily checked and emptied pitfall traps.

We additionally carried out visual searches, further ensuring that diurnal arboreal lizards were properly sampled (Cechin and Martins, 2000). Our visual surveys consisted of active searches for lizards conducted by one person walking very slowly (~5 m/min) along a 100-m transect, and included the careful examination of tree trunks up to 1.5-m high and the leaf-litter within a 5-m strip on each side of the transect. At each sampling site (patch), we sampled a total of four visual survey-transects, located between the pitfall trapping transects, so that the first visual survey-transect was located at 75 m from the edge and the fourth at 225 m. Each transect was surveyed twice, at the third and seventh days of the pitfall-trapping sessions, between 0900 h and 1200 h. Sampling effort amounted to a total of 6,000 pitfall-days and surveyed a cumulative distance of 60,000 m.

**Landscape, Patch, and Habitat Quality-related Variables.**—At the landscape scale, we measured the degree of matrix complexity surrounding forest patches (matrix) and the proportion of forest cover (cover). Matrix was characterized based on the vegetation sward height of the cattle pasture. We considered five classes of

equal sward height intervals, ranging from one, for shortly cropped pasture shorter than 20 cm, which was often associated with overgrazed ranches, to five in the case of large expanses of *colonião* grass (*Panicum maximum*) taller than 200 cm. To do so, we established four, 100-m transects in the matrix surrounding each sampling patch, each transect 50 m apart from the patch edge and at a roughly 90° angle from the patch center. Along each transect, we measured vegetation sward height at five equidistant points, so that matrix is defined as the mean sward height ( $n = 20$ ) at each sampling site. Cover corresponded to the proportion of primary and secondary forest cover within an external 1-km buffer from the perimeter of each forest patch. We extracted cover using Landsat imagery available for the study area and period using the ArcGIS software (ESRI, Redmonds, California; <https://www.esri.com/en-us/home>). We also used the Landsat imagery and software (National Aeronautics and Space Administration [NASA], Washington, DC; <https://landsat.gsfc.nasa.gov/>) to obtain the land-use configuration of the study area as shown in Figure 1.

At the patch scale, we estimated forest patch size (area), shape (shape), and age since isolation (age). Area corresponds to the total forest area of each patch and we previously log-transformed ( $\log_{10} x$ ) this variable. We calculated shape for each forest patch based on the index proposed by Laurance and Yensen (1991) following the equation:

$$SI = \frac{P}{2\sqrt{A}}$$

where SI is the shape index,  $P$  is the patch perimeter (m), and  $A$  is the patch area (ha). In a perfect circle,  $SI = 1.0$ , whereas more-irregular shapes have higher values. We also calculated area and shape using ArcGIS. We obtained the time since isolation for each patch (age) through semistructured interviews with willing local residents who had lived next to, and had been familiar with, the postisolation history of each forest patch for at least 15 yr.

Lizard responses to habitat loss and fragmentation are closely related to their thermal biology, which is further linked to microhabitat use (Vitt and Caldwell, 2014). In that sense, we measured a set of habitat variables that, as hypothesized, may affect species persistence in remaining forest patches, including tree density (tree), canopy openness (canopy), litter volume (litter), and fire history (fire). At each sampling site, we obtained tree, canopy, and litter by averaging the respective values obtained at each pitfall trap ( $n = 20$  traps/sampling site) in addition to each live-trap station simultaneously used to survey small mammals ( $n = 40$  stations/sampling site; for further details on small mammal traps see Santo-Filho et al., 2012). Including the habitat measurements obtained near live-trap stations further allowed us to better characterize each sampling site. We quantified ‘tree’ by counting all arborescent palm and nonpalm trees  $\geq 30$  cm in diameter at breast height (DBH) within a 6-m radius centered at each pitfall trap or live-trap station. We estimated canopy considering the proportion of canopy gaps obtained from readings taken directly above each trap using a wire-mesh grille (50 × 50 cm) containing 100 hollow 0.25-cm<sup>2</sup> squares. We measured litter next to each pitfall trap by transferring the litter collected within a 0.5-m<sup>2</sup> quadrat into a transparent plastic box (40 × 32 × 21 cm). The height of this box was marked every 1 cm to allow for litter depth readings. Prior to readings, we performed a standardized leaf-litter volume compaction procedure in which a 2-kg wooden

block of nearly the same size as the box opening was gently dropped on top of the litter. Similarly to age, we obtained fire history at each sampling site based on interviews with local residents, followed by field verification *in situ* at each forest patch in which direct signs of fires (e.g., charred trees) were recorded.

We accounted for lizard food availability by quantifying arthropod biomass (arthropod). We measured this variable using 2-L pitfall traps containing a 300-ml solution of 5% formaldehyde and 10 ml of transparent detergent that remained in the field during eight consecutive days. We sampled arthropods at each sampling site using 18 pitfall traps deployed along the same visual-survey transects. Arthropod samples (insects, arachnids, and myriapods) obtained from individual pitfall traps were weighed using a high-precision (0.0001 g) scale once all excess water had been removed using absorbent filter paper. In nine patches (Patches 1–9), arthropods sampling was carried out twice, in both the dry and wet seasons. At these patches, we estimated arthropod by summing the values obtained at each pitfall trap ( $n = 18$  traps) and averaging the biomass between the two seasons. In the remaining 12 patches surveyed, we sampled arthropods once and quantified that by summing the values obtained at each pitfall trap.

**Data Analysis.**—We evaluated the accuracy of lizard sampling using the coverage estimator ( $\hat{C}_n$ ) recommended by Chao and Jost (2012), which estimates the proportion of the total number of individuals in an assemblage that belongs to the species represented in the sample. Overall, our lizard trapping was reasonably accurate in relation to our sampling effort ( $>0.50$ ), averaging  $0.76 \pm 0.28$  of sample coverage per site. For Patches 16 and 19,  $\hat{C} = 0$  and, given the poor sampling representativeness therein, those sites were excluded from subsequent analyses (Supplementary Table S1). For the remaining patches, species richness was given by the number of species observed. Species composition was examined using nonmetric multidimensional scaling (NMDS) ordination based on the quantitative Bray-Curtis similarity matrix of species composition using the ‘vegan’ R package (Oksanen et al., 2020). The first two NMDS axes allowed us to preserve the original dissimilarities under a reduced number of dimensions (stress = 0.17). The first NMDS axis was then used to derive scores used as a proxy of species composition in further analyses.

Any potential effect of survey season on species richness and abundance was tested using a Wilcoxon paired test considering the nine patches (Patches 1–9) that were sampled twice, once in the wet and again in the dry season. No differences were observed between seasons for both species richness ( $U' = 9.5$ ,  $P = 0.495$ ) and abundance ( $U' = 15.5$ ,  $P = 0.779$ ). In subsequent analyses, species abundance was standardized according to sampling effort (i.e., by doubling the number of individuals recorded in patches surveyed only once).

Given the importance of forest patch size to examine species extinction dynamics in fragmented landscapes (Watling and Donnelly, 2006), we first examined the isolated effects of patch size ( $\log_{10} x$ ) on species richness, abundance ( $\log_{10} x$ ), and composition (NMDS axis 1) using Generalized Linear Models (GLMs) fitted with a Gaussian distribution. The combined effects of patch, landscape, and habitat quality-related metrics on the same three response variables were then examined using GLMs with a Gaussian distribution. To control for high levels of variable interdependence, a Pearson correlation matrix was performed. The variable cover was highly correlated with Area ( $r \neq 0.70$ ) and further excluded from the analysis. In addition,

multicollinearity was tested by calculating the Variance Inflation Factor (VIF) of each independent variable (Dormann et al., 2013). No variables were observed to be moderately redundant ( $VIF > 4$ ), so the nine uncorrelated variables were retained in subsequent analyses. For each of the three response variables describing lizard diversity, species richness, standardized abundance ( $\log_{10} x$ ), and species composition (NMDS<sub>1</sub>), a candidate model set was constructed using all additive combinations of the nine explanatory variables, and models were ranked based on their Akaike Information Criterion, corrected for small sample sizes (AICc: Burnham and Anderson, 2002), using the MuMIn R package (Bartoń, 2016). If only one plausible model was obtained ( $0 < \text{DAICc} < 2$ ,  $\text{DAIC} = \text{AIC}_i - \text{AIC}_{\min}$ , in which  $i = i^{\text{th}}$  model), results were presented for that ‘best’ model. If multiple plausible models were obtained, a model averaging was performed using those models to account for model uncertainty in multimodel inference. Explanatory variables were previously standardized ( $x = 0$ ,  $r = 1$ ) to place coefficient estimates on the same scale.

The separate responses of species with contrasting thermoregulation strategies were further analyzed. Species classification (i.e., heliophile or heliophobe) was based on the information available in Ávila-Pires (1995) in terms of species behavior, preferred habitat, and body temperature. The same modeling approach as before was repeated but with consideration of the standardized abundance of both heliophile and heliophobe species ( $\log_{10} x$ ). All analyses were carried out in R environment (R Development Core Team, 2018).

## RESULTS

Across the 21 forest patches surveyed, we recorded 215 lizards representing 15 species, 14 genera, and 7 families, including nine heliophile ( $n = 101$  individuals, 47.0%) and six heliophobe species ( $n = 114$ , 53.0%). The number of species per patch surveyed ranged from one to nine ( $4.5 \pm 1.8$  species). The most commonly recorded species were the heliophobe *Gonatodes hasemani* ( $n = 47$ ; 21.9% of individuals) and the heliophile *Copeoglossum nigropunctatum* ( $n = 39$ ; 18.1%), while the only nonnative species in the Amazon biome we found, the heliophile *Stenocercus caducus*, was the most widespread species, occurring at 90.5% of the patches ( $n = 19$ ). Three heliophile species were recorded only once (i.e., *Micrablepharus maximiliani*, *Kentropyx calcarata*, and *Polychrus cf. liogaster*; Table 1; Supplementary Table S2).

Across the gradient of habitat loss and fragmentation, forest patch area failed to explain any of the measures of lizard diversity considered—species richness, abundance ( $\log_{10} x$ ), and composition (NMDS<sub>1</sub>; Supplementary Fig. S2 and Table S3). According to the ordination diagram on lizard species composition, no patch segregation based on their forest area was observed (Fig. 2). Furthermore, additional variables considered at either the patch or landscape scales, and those related to habitat quality, were uninformative in explaining lizard species richness and abundance (Fig. 3A–B, Supplementary Table S4). Nevertheless, the identity of species persisting in the fragmented landscapes was predicted by the level of habitat quality in the surrounding matrix vegetation ( $b_{\text{MATRIX}} = 0.154$ ,  $P = 0.004$ ; Fig. 3C, Supplementary Table S5).

When species abundance of either heliophile or heliophobe species was considered separately (Fig. 3D–E), past fire intensity negatively affected heliophobe species ( $b_{\text{FIRE}} = -0.214$ ,  $P = 0.006$ ; Supplementary Table S6), although heliophiles also declined to



TABLE 1. Abundance and occupancy of the 15 species recorded across 21 forest patches within the Jaurú and Cabaçal river basins, Mato Grosso, southern Brazilian Amazon, including their thermoregulation strategy (sourced from Ávila-Pires 1995).

| Family           | Species                               | Thermoregulation strategy | Species abundance  |      | No. of fragments occupied |
|------------------|---------------------------------------|---------------------------|--------------------|------|---------------------------|
|                  |                                       |                           | No. of individuals | %    |                           |
| Gekkonidae       | <i>Gonatodes hasemani</i>             | Heliophobe                | 47                 | 21.9 | 15                        |
|                  | <i>Gonatodes humeralis</i>            | Heliophobe                | 9                  | 4.2  | 6                         |
| Gymnophthalmidae | <i>Bachia dorbignyi</i>               | Heliophobe                | 4                  | 1.9  | 4                         |
|                  | <i>Rondonops biscutatus</i>           | Heliophobe                | 6                  | 2.8  | 2                         |
|                  | <i>Iphisa elegans</i>                 | Heliophile                | 22                 | 10.2 | 10                        |
|                  | <i>Micrablepharus maximiliani</i>     | Heliophile                | 1                  | 0.5  | 1                         |
|                  | <i>Cercosaura eigenmanni</i>          | Heliophobe                | 22                 | 10.2 | 12                        |
| Hoplocercidae    | <i>Hoplocercus spinosus</i>           | Heliophile                | 3                  | 1.4  | 1                         |
| Polychrotidae    | <i>Norops fuscoauratus</i>            | Heliophobe                | 12                 | 5.6  | 5                         |
|                  | <i>Polychrus</i> cf. <i>liogaster</i> | Heliophobe                | 1                  | 0.5  | 1                         |
| Scincidae        | <i>Copeoglossum nigropunctatum</i>    | Heliophile                | 39                 | 18.1 | 12                        |
| Teiidae          | <i>Ameiva ameiva</i>                  | Heliophile                | 10                 | 4.7  | 4                         |
|                  | <i>Kentropyx calcarata</i>            | Heliophile                | 1                  | 0.5  | 1                         |
|                  | <i>Salvator merianae</i>              | Heliophile                | 2                  | 0.9  | 2                         |
| Tropiduridae     | <i>Stenocercus caducus</i>            | Heliophile                | 36                 | 16.7 | 19                        |

some degree at burned sites. Unlike heliophiles, heliophobe abundance increased in forest patches that were surrounded by a more complex vegetation structure ( $b_{\text{MATRIX}} = 0.216$ ,  $P = 0.008$ ; Fig. 4). In addition, heliophile abundance further showed a trend toward declining in patches containing a higher tree density ( $b_{\text{TREES}} = -0.164$ ,  $P = 0.087$ ; Fig. 3E).

#### DISCUSSION

Over the last three decades, the Amazonian ‘arc of deforestation’ has left behind a vast patchwork of forest and nonforest areas, in which forest remnants are becoming increasingly isolated and more degraded (Fearnside, 2005; Nobre et al., 2016). Despite the wide range of forest patches included in our study (varying in size nearly 10-fold), we failed to detect any species-area relationship. In fact, the effects of forest area, or any other variables at the patch and landscape scales, were uninformative in explaining any of the diversity metrics considered. However, habitat quality, particularly in terms of fire history within forest patches and the complexity of

vegetation surrounding forest patches, determined the persistence of heliophobe lizard species under highly disturbed conditions.

Island Biogeography Theory (MacArthur and Wilson, 1967) has been extensively used to explain species diversity persisting in fragmented landscapes (Haila, 2002), with forest area generally exerting a strong effect on species diversity (Watling and Donnelly, 2006). Across the southwestern Amazonian deforestation frontier, however, forest lizards did not show the typical species-area relationship. In fact, our findings diverged from previous tropical lizard community studies in not showing the typical habitat area effects. For instance, forest area effects explained between 10% and 80% of the lizard species richness persisting in forest patches similarly isolated by a pasture matrix (see compilation of studies in Palmeirim et al., 2017b).

In our study, lizard assemblages were instead determined primarily by the quality the surrounding matrix. Likewise, small mammal assemblages in the same study sites failed to respond to forest patch area but were also predicted by the quality of the open-habitat matrix of cattle pastures (Santos-Filho et al., 2012). In our study system, forest patches were subject to some degree of timber extraction and cattle intrusion from the nearby pasture matrix. In particular, cattle intrusion, which is facilitated by the absence of fences delimiting matrix pastures, resulted in the marked removal of the understory vegetation, trampling of seedlings and saplings, and soil compaction. In northern Mato Grosso, cattle intrusion similarly affected the composition of forest-dependent mammals across remnant riparian forest corridors (Zimbres et al., 2017). The substantial levels of forest patch degradation increased the patch-matrix structural similarity, which likely reduces the relative importance of forest patch area for residual lizard assemblages. The absence of large tracts of undisturbed forest throughout the study landscape also contributed to the lack of a species-area relationship given that species-rich baseline areas are no longer available and a historical extinction filter may have already eliminated the most-sensitive species throughout the entire landscape (Bueno and Peres, 2020). For instance, Palmeirim et al. (2017b) recorded up to 12 lizard species (70.6% of the total number of species recorded in that study) in continuous forest sites in the central Amazon that was comparable only to the largest insular forest patches surveyed (>500 ha). Although it is possible that the more vulnerable

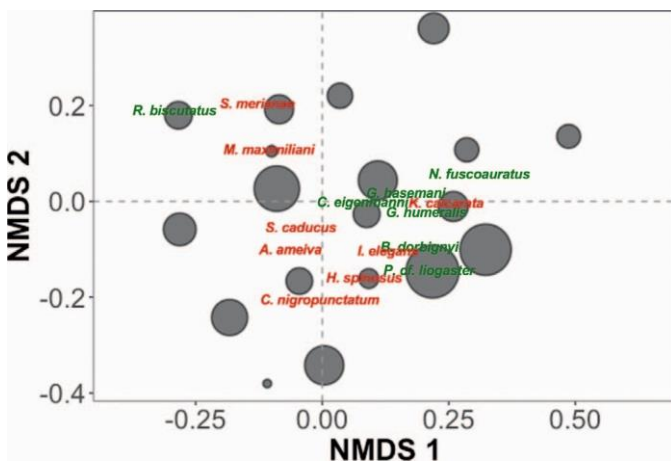


FIG. 2. Nonmetric Multidimensional Scaling (NMDS) ordination plot based on the Bray-Curtis similarity matrix of lizard species composition representing both 21 surveyed forest patches and 15 recorded lizard species. Site symbols are sized proportionally to forest patch size. Species names are colored according to species thermoregulation strategy: heliophile (in red) and heliophobe (in green; for complete species names, see Table 1).

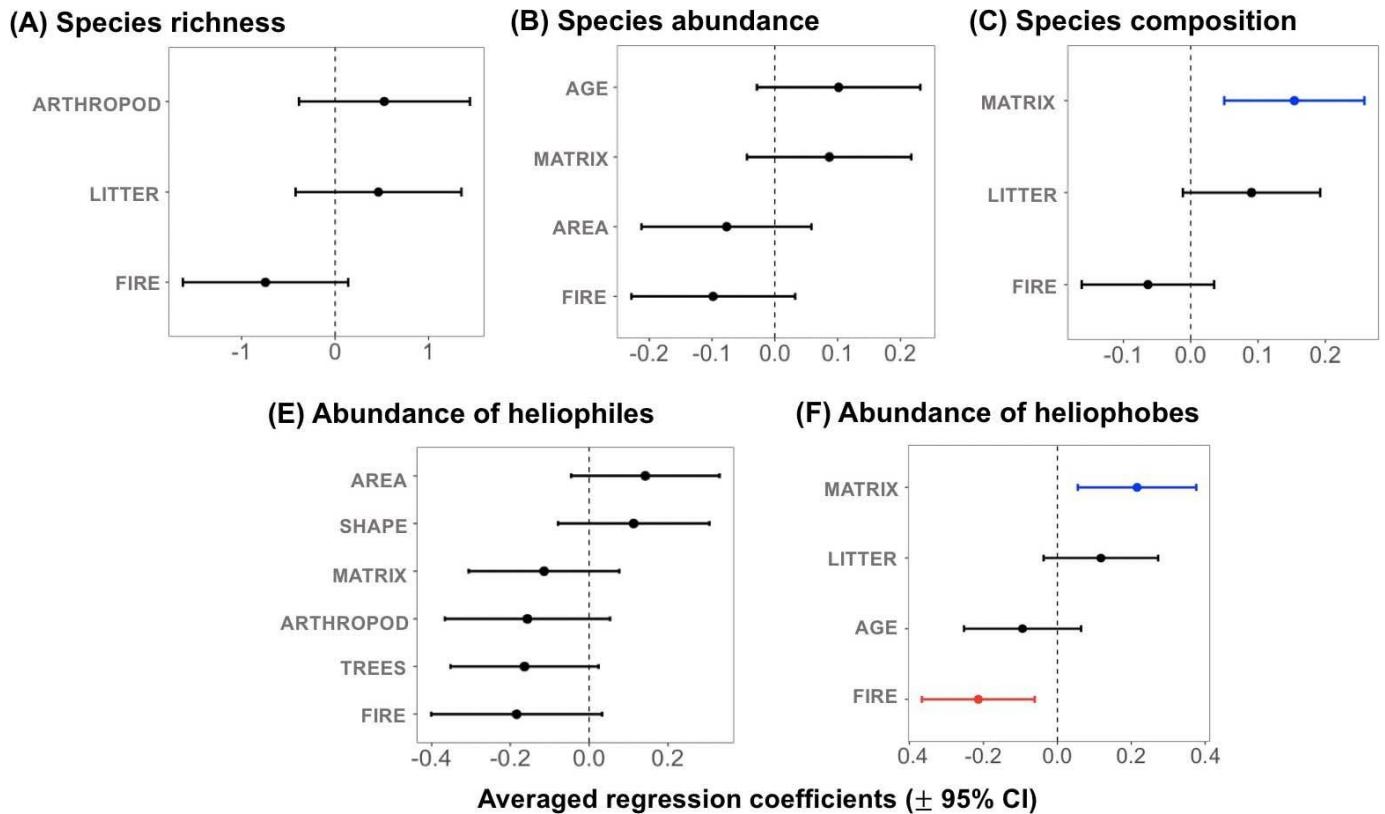


FIG. 3. Estimates of averaged models and their 95% confident intervals for predictors of (A) species richness, (B) species abundance ( $\log_{10} x$ ), (C) species composition (denoted by the NMDS axis 1), and (D) abundance of heliophile and (E) heliophobe individuals ( $\log_{10} x$ ). Predictors included matrix complexity (matrix), forest cover (cover), years since patch isolation (age), patch shape (shape), litter depth (litter), tree density (trees), arthropod biomass (arthropod), canopy openness (canopy), and presence of fire (fire). Statistically significant negative and positive coefficients are color-coded in red and blue, respectively.

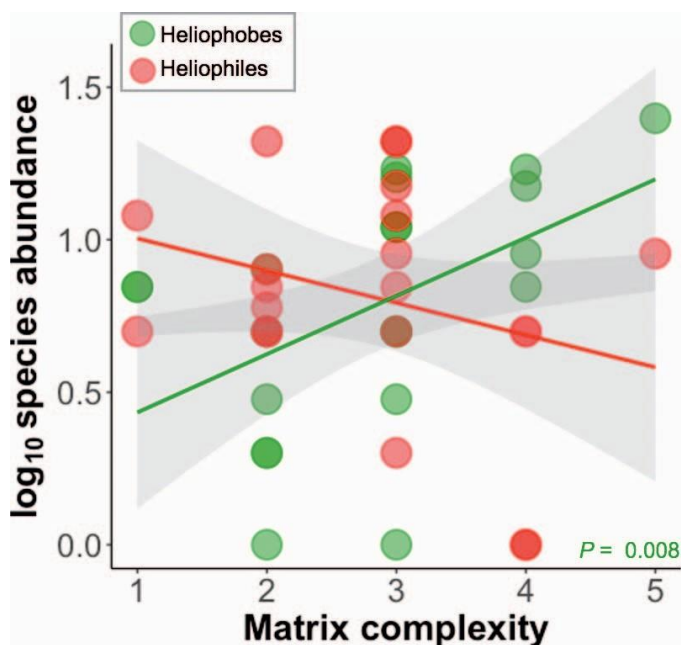


FIG. 4. Relationships between the species abundance of heliophile (red circles) and heliophobe individuals (green circles;  $\log_{10} x$ ) and degree of vegetation complexity in the matrix surrounding surveyed forest patches. Line represents the adjusted model and shaded area represents the 95% confidence region.  $P$ -values are indicated for the strongest relationships (i.e.,  $P < 0.05$ ).

lizard species had already been extirpated from this region, we were only able to compare our results with other studies that also lacked appropriate intact forest controls. That was the case of a study recording a total of 11 lizard species in a nearby Amazonian forest landscape (Ávila and Kawashita-Ribeiro, 2011) and a Cerrado scrubland landscape within the state of Mato Grosso that recorded 14 species (dos Santos et al., 2011).

Lizard dependency on specific microhabitats and microclimatic conditions renders them highly vulnerable to habitat disturbance (Garda et al., 2013; Vitt and Caldwell, 2014). Therefore, despite the overall levels of disturbance within forest patches, our results suggest that some variation in habitat quality played a major role in determining lizard assemblages across the fragmented landscape. In particular, the abundance of heliophile individuals was limited by the structural complexity of the surrounding matrix. Overall, matrix quality surrounding forest patches tends to play a critical role in determining the persistence of vertebrate species in fragmented landscapes (Gascon et al., 1999, Pfeifer et al., 2017), and species-specific responses have often been observed (Debinski and Holt, 2000). In fact, in the Amazon biome, heliophobe species were expected to be particularly sensible to habitat quality because those maintain lower body temperatures (averaging  $\sim 27.78^{\circ}\text{C}$  for all heliophobe species in the assemblage), and actively seek shaded microhabitats, whereas heliophile species maintain higher body temperatures ( $\sim 36.18^{\circ}\text{C}$ ) that are regulated by exposure to understory sun-flecks (Vitt et al., 1998). In this case, a more complex vegetation structure in the surrounding pasture matrix likely facilitates the movement of heliophobe species

between forest patches, which eventually increases their occupancy and/or abundance therein. Interestingly, although not statistically significant, heliophile species showed a trend toward a decrease in abundance in patches with higher tree density, where direct sunlight exposure also is expected to be lower. Different lizard responses according to their thermoregulation mode have been similarly observed in other fragmented landscapes, in which heliophobe abundance decreased toward smaller and more habitat-degraded fragments (Almeida-Gomes and Rocha, 2014; Palmeirim et al., 2017b), or in the aftermath of logging, in which heliophiles also increased in abundance (Lima et al., 2001).

Furthermore, heliophobe species were also affected by habitat quality within forest patches, as dictated by the history of previous accidental or intentional fire events. It is likely that previous occurrence of fires contributed to an increase in heat penetration and desiccation into the understory (Scheffers et al., 2016). Such habitat alterations might be unfavorable for species that are less tolerant of a wide spectrum of environmental conditions. Variations in local fire history might then explain why only heliophobe species abundance was significantly affected by forest fragmentation. Surface fires are also an important driver of bird and mammal species loss in other Amazonian fragmented forest landscapes (Lees and Peres, 2006; Benchimol and Peres, 2015b).

Given the relentless expansion of the Amazonian ‘arc of deforestation,’ different forest-climate equilibrium states may eventually be reached (Nobre et al., 2016) such that remaining closed-canopy forest fragments will likely gradually decay into poor-quality forest habitats (Sampaio et al., 2007). The degradation of habitat could be further amplified by additional anthropogenic disturbance including bovine cattle intrusion, roundlog and firewood extraction, and wildfires. Ongoing anthropogenic disturbance could explain why forest area was not an important predictor of forest lizard diversity in our study region. Instead, the wider context of habitat quality within and around forest patches played an important role in determining which species, and groups of species traits, were able to persist. Our findings highlight the importance of accounting for variability in habitat quality in both forest and nonforest habitats (Lindenmayer and Franklin, 2002). Strategies aiming to maximize diversity of squamate reptiles in heavily deforested and disturbed fragmented landscapes should envisage maintaining adequate microhabitat conditions and at least a minimal amount of functional connectivity between forest patches. To do so, management actions within forest patches should curb timber extraction and prevent cattle intrusion; for example, by placing adequate fences delimiting pastures. Moreover, the persistence of forest-dependent heliophobe lizard species will require preventive suppression of surface fires and the resulting habitat degradation within forest patches, in addition to maintaining more structurally complex interstitial matrix areas throughout the entire fragmented landscape. Integrating the different management measures by local governments is critical to safeguard the long-term diversity of lizards and other forest vertebrate taxa across tropical deforestation frontiers.

#### ETHICS STATEMENT

This study was carried out in a landscape of rapid deforestation and where very few biodiversity surveys have been carried out. For this reason, an additional aim of the data collection obtained here was to inform local biodiversity,

including molecular analysis, resolving local taxonomy. To date, given the lack of systematic surveys, the specimens collected in this study represent a major contribution for the understanding of the local herpetofauna in a hyper-diverse region representing a transition zone between the Amazon biome and the Cerrado and Pantanal biomes. For those reasons, we planned a maximum of 10 individuals of voucher specimens per species were collected at each forest patch surveyed (but this maximum number was not reached for any species or patch). Animal trapping, handling, and euthanasia followed the guidelines of the Brazilian Ministry of Science, Technology and Innovation (Campos et al., 2016), which are in agreement with those indicated in the Guidelines for Use of Live Amphibians and Reptiles in Field Research by the Herpetological Animal Care and Use Committee (2004). Our study was also approved by the appropriate Brazilian government agency (Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis, permit numbers 033/02, 004/03, 129/203, and 057/04). Accordingly, lizards were initially anesthetized with an inhaled agent (5% isoflurane) and subsequently administered 0.5–2 ml of a solution containing 2% lidocaine hydrochloride in the intra-abdominal portion. Animals were deposited at both the National Institute of Amazonian Research (Instituto Nacional de Pesquisas da Amazônia; INPA) and the State University of Mato Grosso (Universidade do Estado de Mato Grosso; UNEMAT).

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#### SUPPLEMENTARY DATA

Supplementary data associated with this article can be found online at <http://dx.doi.org/10.1670/20-145.s1>