

ORIGINAL ARTICLE

Recovery of lizard assemblages 10 years after reduced-impact logging in central-eastern Amazonia

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Abstract

Understanding changes in species composition due to human-induced habitat modification and environmental filtering is essential for formulating effective conservation strategies. Species turnover resulting from reduced-impact logging (RIL) is expected in the short term, generally with species adapted to open areas replacing those dependent on old-growth forest. However, little is known about how RIL activities influence assemblages after the perturbation ceased. We sampled lizards across an edaphic and vegetation-structure gradient in 64 plots in the Brazilian Amazon to test the hypothesis that changes in assemblage composition and proportion of heliothermic species are due to canopy openness resulting from ceased RIL activities and individual tree falls or to other environmental gradients. Contrary to expectations, canopy openness did not significantly affect the overall composition of lizard assemblages, but nearby unforested areas influenced assemblage composition, resulting in a higher proportion of heliothermic species. The composition of lizard assemblages was also significantly influenced by the distance to the nearest water body, vegetation height, and soil sand content. However, leaf litter height did not have a detectable impact on the composition of lizard assemblages. We conclude that short-term changes in species composition due to habitat modification by RIL do not persist in the long term after the perturbation ceases, and the assemblages may recover as vegetation regenerates.

[Correction added on 07 March 2025, after first online publication: Article title has been corrected in this version.]

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Although lizard species respond to spatial and temporal variation in environmental characteristics, we found evidence that lizard assemblages recover as reduced-impact logging (RIL) activities cease and vegetation regenerates.

Abstract in Portuguese is available with online material.

KEYWORDS

Alter do Chão, Amazon, environmental gradients, FLONA do Tapajós, habitat modification, heliothermic species, selective logging, species turnover

1 | INTRODUCTION

Human-driven modifications often lead to biodiversity loss and changes in local assemblage structure (Gibson et al., 2011; Iglesias-Carrasco et al., 2023). While some species disappear after forest modification, others colonize disturbed environments and increase in abundance (Lima et al., 2001; Thompson et al., 2016; Vitt et al., 1998). In the Amazon, the extent of forests altered by human activities is increasing, posing a growing threat to species dependent on old-growth forests. As people in the region pursue economic development, the need to explore sustainable alternatives that prioritize biodiversity conservation becomes ever more crucial. One such alternative is reduced-impact logging (RIL), which provides a possibility for natural-resource extraction while maintaining the forest. However, RIL may negatively affect the conservation of some biological groups (Castro et al., 2022; Putz et al., 2012; Slade et al., 2011).

Reduced-impact logging alters habitat structure, creating open areas that increase the incidence of solar radiation and directly impacts the local microclimate (Iglesias-Carrasco et al., 2023; Vitt et al., 1998). These changes have the potential to impact the abundance and distribution of animal species, although their vulnerability to environmental changes varies across taxa (Azevedo-Ramos et al., 2006; Lima et al., 2001). Following RIL activities, some species that depend on undisturbed forest conditions may experience population decline, while less-sensitive species tend to thrive and increase in numbers (Azevedo-Ramos et al., 2006; Castro et al., 2022; Goldingay et al., 1996; Vitt et al., 1998). In human-modified environments, it is generally expected that specialist forest species will be replaced by generalist species that exhibit greater resilience to disturbance, as long as the disturbed areas fall within their geographic range and are accessible through natural dispersal (Devictor et al., 2008).

The effects of RIL on animal species in the Amazon are still not well understood, with the few studies focusing primarily on mammals and birds (DeArmond et al., 2023; Henriques et al., 2008). Understanding of the effects of RIL on reptile assemblages is limited, and research on its impact on lizard species in the Amazon is scarce. Vitt et al. (1998) investigated the effects of RIL on lizard assemblages in the Amazon forest, but their analysis focused solely on the immediate influence soon after logging. That study suggested that clearings formed by RIL activities could have a negative impact

on lizard assemblages as they allow heliothermic lizard species that rely on solar exposure to regulate their body temperature to enter the forest, posing a threat to non-heliothermic species. Lizards maintain a close relationship with ambient temperature, with heliotherms representing extreme cases on a spectrum ranging from thermoconformers to active thermoregulators. While heliotherms heavily depend on solar exposure to regulate their body temperature, other lizards can passively or actively adjust their internal temperature. Besides the RIL activities carried out through selective logging of commercial tree species by companies or for the subsistence of local residents, natural clearings likely attract species of heliothermic lizards (Vitt et al., 1997).

However, local changes do not always result in differences at larger scales. For example, Baccaro et al. (2012) showed that the presence of dominant ants on baits reduced the number of other species at a scale of a few dozen meters, but this effect was not detectable in sampling units measuring 250m in length. For lizards, at the local scale, biotic interactions and environmental filters may affect assemblage composition, but at regional scales, historical factors, such as geographical barriers, may be better predictors of assemblage composition (Peixoto et al., 2020). Nevertheless, RIL practices do not result in the complete removal of forest cover, and the movement of lizards between clearings and non-clearings does not necessarily have a significant impact on the composition of assemblages at larger scales. Additionally, if natural open areas are too scarce or too distant from the location disturbed by RIL, some open-area lizard species may be absent after the disturbance, as the closed forest could act as a barrier for species that specialize exclusively in open areas. Additionally, changes in species composition due to habitat modification by RIL could be short-term, and the assemblages may recover as vegetation regenerates (Iglesias-Carrasco et al., 2023; Lima et al., 2001). Lima et al. (2001) found that the effect of selective logging on heliothermic species was more pronounced in the short term and diminished over time (after 9 years). This suggests that the effects of selective logging are more apparent shortly after RIL ceases and become less relevant for conservation as time progresses, likely due to habitat regeneration.

In addition to activities that lead to forest modification, such as RIL, environmental factors influence the composition of lizard species, with different species associated with specific habitats (Faria et al., 2019; Peixoto et al., 2020; Souza et al., 2021), and turnover

in local lizard assemblages is expected due to environmental filtering (Faria et al., 2019; Peixoto et al., 2023; Peixoto et al., 2020). In unexploited forest environments, environmental gradients related to vegetation and soil structure (Peixoto et al., 2020, 2023), leaf litter height (D'Cruze & Kumar, 2011; Fauth et al., 1989), and distance from water bodies (Faria et al., 2019; Peixoto et al., 2020) determine the availability of sites for foraging, resting, shelter, and thermoregulation, and they may influence the structure of local lizard assemblages through environmental filtering and competition.

The lack of understanding of the changes in biological assemblages resulting from human modifications in the environment, as well as the influence of environmental heterogeneity on these assemblages, represents a challenge for the effective implementation of conservation strategies (Gardner et al., 2007; Iglesias-Carrasco et al., 2023). Additionally, it is crucial to explore viable alternatives for resource exploitation that can effectively conserve biodiversity. In this study, we sampled lizards across an edaphic and vegetation-structure gradient in 64 plots in Brazilian Amazonia to test the hypotheses that changes in assemblage composition and proportion of heliothermic species are due to canopy openness resulting from ceased RIL activities and individual tree falls, or to other environmental gradients (proximity to unforested areas, vegetation height, natural soil variation, distance to water bodies, and leaf-litter height). We expected that changes in species composition and the proportion of heliothermic species would be associated with the formation of clearings caused by RIL and proximity to unforested areas.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area is situated in central-eastern Amazonia, near the east bank of the lower Tapajós River (Figure 1). It comprises continuous and fragmented semideciduous forests, surrounded by a savanna matrix, within an Environmental Protection Area (APA) near the village of Alter do Chão, as well as continuous forest in the Tapajós National Forest (TNF), which covers 527,319 hectares (ICMBio, 2019). The TNF is a forest area that falls under the IUCN category VI, indicating a protected area with sustainable use of natural resources (Dudley et al., 2010). The mean annual temperature is relatively stable at about 25.5°C throughout the year. However, precipitation exhibits pronounced seasonality, with a distinct 4-month dry season from August to November. The average annual rainfall between 1971 and 2016 was 1820 mm (ICMBio, 2019).

Currently, the management of TNF includes low-impact timber harvesting, which is restricted to areas defined by a management plan established by the Brazilian government in collaboration with local communities organized into a cooperative (Brocardo et al., 2023), the Mixed Cooperative of the Tapajós National Forest (COOMFLONA). Since 2005, COOMFLONA has been conducting logging activities in the north-central part of TNF, using reduced-impact logging techniques. Additionally, local people living in TNF

extract wood for subsistence purposes and occasionally use fire for land clearing, which is assumed to have only a small impact.

2.2 | Sampling design

In the southern portion of the study region, inside the Tapajós National Forest (TNF), we sampled 40 plots distributed across four research modules established as part of the Brazilian Program for Biodiversity Research (PPBio) for biodiversity monitoring. These modules follow the Rapid Assessment and Long-term Ecological Research (RAPELD) system (Magnusson et al., 2013). Each module is 1 km in width and 5 km in length. Within each module, there are 10 evenly spaced 250-m-long plots that follow terrain contours (Magnusson et al., 2013). The minimum distance between plots in the same module is 1 km. Two of the modules are situated in the northern region of TNF and are 5.6 km apart. One is located in an area where selective logging occurred in 2012–2014, and the other is closer to a traditional community and experienced limited impact from subsistence wood extraction. The other two modules are located in the southern region, 56 km from the northern modules and are 7.3 km apart (Figure 1). The southern modules contain old-growth forest and have not been subjected to logging activities.

In the north of the study area, inside the Alter do Chão APA, we also surveyed 24 plots, 19 located in forest fragments surrounded by a savanna matrix and five in continuous forest (Figure 1). Although these plots were 250 m long, they did not follow the terrain contour. However, since the area was relatively flat, this deviation resulted in minimal differences in variability within each plot. The minimum distance between plots was 723 m. Therefore, we sampled a total of 64 plots, with 10 of these plots located within an area that has been subjected to RIL 10 years ago.

We collected up to two voucher specimens for some species, adhering to specimen collection and preservation protocols authorized by ICMBio/SISBIO license n° 76,445–1. No endangered species were collected.

2.3 | Lizard-data collection

We sampled each plot three times, once in 2020 and twice in 2021, all during the dry season between October and December of each year.

We sampled lizards through active visual search, with two observers positioned 10 m apart. The observers walked slowly through the plots, and every lizard sighted in the plot was counted. Additionally, to detect species that inhabit the leaf litter, such as gymnophthalmids, we raked leaf litter in a 2-m strip along the centerline of the plot. Sampling in the leaf litter was undertaken in the reverse direction after visual search. Our sampling was conducted during daylight hours, typically between 09:30 h and 15:00 h, in the absence of rain. We sampled only at temperatures >26°C since lizards are more active at higher temperatures. The average searching

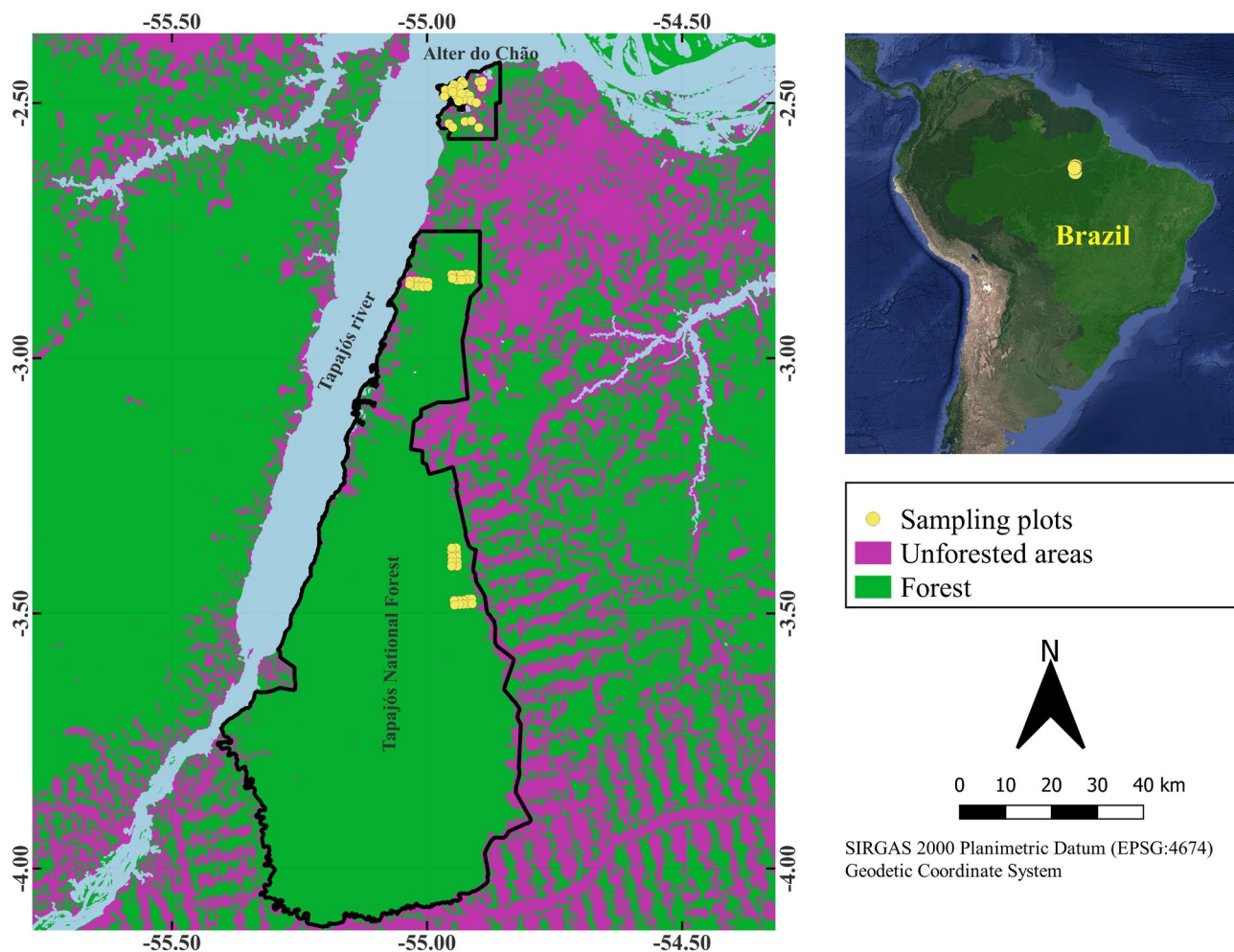


FIGURE 1 Study area in central-eastern Amazonia, showing the location of 64 sampling plots, each 250m long. Color should be used for printed figures.

time in each plot was 60min. This method has proven to be highly effective in sampling lizard assemblages in the Amazon rainforest (Faria et al., 2019; Peixoto et al., 2020, 2023).

2.4 | Environmental variables

In order to assess the spatial heterogeneity in habitat suitability, we measured seven environmental predictors in each plot: canopy openness, vegetation height, proportion of unforested areas in the landscape, quantity of clay and sand, leaf litter height, and distance to the nearest water body. The sampling methods followed the protocols established by PPBio (<http://ppbio.inpa.gov.br>). We selected variables considering structural habitat differences that reflect historical distinctions between the northern (with savannas present) and southern (dominated by forests) portions of our study area. Additionally, our variables quantify continuous gradients along the transition between dense forests and forest surrounded by savannas.

We used data collected by a portable Light Detection and Ranging (LIDAR) device (Model LD90-3100VHS-FLP, Riegl, Horn,

Austria), which employs laser scanning to measure variables that quantify canopy openness (our local-clearing index) and average vegetation height in the plots (see Torralvo et al., 2020, 2021). We estimated canopy openness by calculating the percentage of sky shots, which represents the number of emitted pulses that do not return to the apparatus. Clearings arose as a consequence of individual tree falls or selective removal.

Measures of unforested areas, the proportion of open areas in the landscape, were obtained in a previous study (Torralvo et al., 2020, 2021) by using a satellite-based layer with 30m×30m pixels made available through the MapBiomas project (Souza et al., 2020, see full description in <http://mapbiomas.org>), which summarized the data on area without forest until 2019. Using the raster R package (Hijmans, 2020), we extracted the proportions of areas without forest within 500-m buffers around each plot. In our study region, unforested areas are predominantly found in the northern part. These open areas are mainly composed of savanna areas surrounding forest fragments, while a smaller portion is the result of deforestation, primarily driven by subsistence activities by local communities. The savannas act as dispersal barriers for almost all lizard species in the

region, although 80% of the heliothermic species (*Copeoglossum nigropunctatum*, *Ameiva ameiva*, *Kentropyx calcarata*, and *Kentropyx striata*) occur in both forested and savanna environments.

Soil collection and analyses were carried out following the PPBio protocol (available at <https://ppbio.inpa.gov.br/manuais>). We used data on the quantity (g/kg) of clay and sand (sum of fine and coarse sand) to 5 cm from the surface. Leaf litter height was measured with a ruler at six points separated by 50-m intervals in each plot, and the mean values per plot were used in the analyses. We measured the distances from each plot to the nearest water body using the Euclidean distance matrix tools of QGIS 3.16.2 software (QGIS Development Team, 2020), applied to combined hydrographic shapefiles from public repositories (IBGE, 2021). Summaries of all measured environmental variables are given in Table 1.

2.5 | Data analysis

Considering that the spatial variation in the abundance of species plays a fundamental role in the structure of assemblages, we used generalized linear models on high-dimensional data to investigate the impact of environmental variables on the abundance of all species. The analyses were conducted using the `manyglm` function from the `mvabund` R package (Wang et al., 2020). This approach allows for hypothesis testing and avoids the confounding of node and link effects that can arise from mis-specified mean–variance relationships (Warton et al., 2012). The statistical significance of the final model was evaluated using Wald's test and PIT-trap resampling with 999 iterations in the `anova.manyglm` function. We used in the analyses the sum of the number of individuals of each species recorded in the surveys of each plot.

For the proportion of heliothermic species in each plot (e.g., *Ameiva ameiva*, *Cnemidophorus lemniscatus*, and *Kentropyx striata*), we used generalized linear models. Definitions of the species as heliothermic or non-heliothermic were based on studies by Diele-Viegas et al. (2019) and Vitt et al. (2008).

Due to the clustering of unforested areas in the northern region of our study area, spatial autocorrelation effects could complicate the interpretation of the results (see Torralvo et al., 2021), so we tested for spatial autocorrelation in the residuals produced by the multiple linear and generalized linear models for species composition and proportion of heliothermic species using Moran's I global test with the R package `ape` (Paradis & Schliep, 2019).

We log-transformed the variable “Distance to water bodies” to obtain normal residual distribution in the analyses for both species composition and proportion of heliothermic species. To assess multicollinearity among environmental variables, we calculated the variance inflation factor (VIF) using the R package `car` (Fox et al., 2012). Some soil-related predictor variables were redundant, with VIF values exceeding 14 for clay and sand content, while the other variables exhibited VIF values below 2.7 in the model. To mitigate the high redundancy among variables (high clay content indicates low soil sand content, and vice versa), we excluded clay content from the model. After the exclusion of clay content, VIF values ranged from 1.04 to 2.57. Therefore, the final variables included together in both the linear model of species composition and the generalized linear model of the proportion of heliothermic species were canopy openness, vegetation height, proportion of unforested areas in the landscape, quantity of soil sand content, leaf litter height, and distance to the nearest water body (Table 1).

3 | RESULTS

We recorded 1795 individuals belonging to 19 species and eight families (Table 2). *Gonatodes humeralis* and *Chatogekko amazonicus*, from the *Sphaerodactylidae* family, were the most abundant species, and they were found in 98.4% and 82.81% of the surveyed plots, respectively. In contrast, we encountered *Arthrosaura reticulata*, *Bachia cf. flavescens* (*Gymnophthalmidae*), and *Cnemidophorus lemniscatus* (*Teiidae*) in only one plot each.

Of the five heliothermic species we sampled, three (60%) were sampled in clearings within densely forested areas (*Ameiva ameiva*, *Kentropyx calcarata*, and *Copeoglossum nigropunctatum*) and have therefore been successful in colonizing the logged areas. Among the remaining species, *Cnemidophorus lemniscatus* was found at the forest edges where RIL operations were conducted. Therefore, this species could occupy clearings if changes imposed by RIL practices made forest habitats sufficiently open.

3.1 | Species composition and proportion of heliothermic species

Contrary to our expectations, the degree of canopy openness in the plots, as measured by our local-clearing index, did not have a

TABLE 1 Minimum (Min), maximum (Max), mean and standard deviation (SD) values of environmental variables measured in 64 plots in western Pará, central-eastern Amazonia.

Gradient	Min	Max	Mean	SD
Canopy openness (%)	9.67	28.99	19.02	5.13
Unforested areas (>30 m × 30 m)	0	53.35	7.81	13.93
Soil sand content (g/kg)	26.00	928.00	608.49	322.68
Distance to water bodies (m)	91.59	5.702	1.554	1.443
Litter height (cm)	0.80	3.63	2.01	0.62
Vegetation height (m)	15.20	77.60	44.20	12.00

TABLE 2 Lizard species found in 64 sampling plots in western Pará, central-eastern Amazonia.

Family/species	Ab	Frequency (%)
Dactyloidae		
<i>Dactyloa punctata</i> (Daudin, 1802)	8	10.94
<i>Norops fuscoauratus</i> (D'Orbigny, 1837)	97	59.38
<i>Norops ortonii</i> (Cope, 1868)	12	14.06
<i>Norops trachyderma</i> (Cope, 1875)	29	34.38
Gymnophthalmidae		
<i>Arthrosaura reticulata</i> (O'Shaughnessy, 1881)	2	1.56
<i>Bachia cf. flavescens</i> (Bonnaterre, 1789)	1	1.56
<i>Cercosaura ocellata</i> (Wagler, 1830)	18	23.44
<i>Iphisa aff. elegans</i> (Gray, 1851)	2	3.12
Leiosauridae		
<i>Enyalius leechii</i> (Boulenger, 1885)	6	7.81
Phyllodactylidae		
<i>Thecadactylus rapicauda</i> (Houttuyn, 1782)	9	14.06
Scincidae		
* <i>Copeoglossum nigropunctatum</i> (Spix, 1825)	42	43.75
Sphaerodactylidae		
<i>Chatogekko amazonicus</i> (Andersson, 1918)	398	82.81
<i>Gonatodes humeralis</i> (Guichenot, 1855)	1040	98.44
Teiidae		
* <i>Ameiva ameiva</i> (Linnaeus, 1758)	8	7.81
* <i>Cnemidophorus lemniscatus</i> (Linnaeus, 1758)	2	1.56
* <i>Kentropyx calcarata</i> (Spix, 182)	91	51.56
* <i>Kentropyx striata</i> (Daudin, 1802)	5	7.81
Tropiduridae		
<i>Plica plica</i> (Linnaeus, 1758)	13	18.75
<i>Plica umbra</i> (Linnaeus, 1758)	12	17.19

Note: Heliothermic species are indicated with an asterisk (*). (Ab) is the total number of individuals found, and frequency (%) is based on the number of plots in which each species was found.

significant effect on the overall composition of lizard assemblages (Wald=4.478, $p=.149$), with many species, such as *Gonatodes humeralis*, *Norops fuscoauratus*, and *Copeoglossum nigropunctatum* occurring at similar abundances throughout the gradient (Figure 2a). In addition, canopy openness did not affect the proportion of heliothermic species ($p=.13$), although 80% of heliothermic species in the study area were encountered in forested areas.

However, as predicted, unforested areas in the buffer zone significantly affected assemblage composition (Wald=6.385, $p=.002$), with many species, such as *Cnemidophorus lemniscatus*, *Kentropyx striata*, and *Enyalius leechii*, exhibiting localized distributions, with higher abundances at one end or the other of the environmental

gradient (Figure 2b). About 70% of the species occurred exclusively or with significantly higher abundance in plots far from unforested areas, with 37% of the total species occurring only in plots with exclusively forested areas in the buffer zone. In contrast, two species (*Cnemidophorus lemniscatus* and *Kentropyx striata*) were exclusively found in plots with high proportions of unforested areas in the buffer zone, and both are heliotherms (Figure 2b). Other species, such as *Copeoglossum nigropunctatum*, *Gonatodes humeralis*, *Norops ortonii*, and *Cercosaura ocellata*, did not appear to respond to the proportion of unforested areas, as they occurred with similar abundances along the gradient (Figure 2b). Similarly, the proportion of heliothermic species was positively affected by the proportion of unforested areas, indicating the availability of thermoregulation sites as a driver of lizard assemblages ($p=.005$).

The composition of lizard assemblages was also significantly influenced by the distance to the nearest water body (Wald=5.344, $p=.016$), vegetation height (Wald=6.057, $p=.002$), and soil sand content (Wald=5.578, $p=.008$). However, leaf litter height (Wald=3.745, $p=.472$) did not have a detectable impact on the composition of lizard assemblages (Figure S1). In contrast, the proportion of heliothermic species, while increasing with soil sand content ($p=.01$), was not affected by the remaining variables ($p>.16$ in all cases).

Most species exhibited localized distributions along the measured gradients, displaying significantly higher abundances at one end or the other of the environmental gradients (Figure S1). Only *Gonatodes humeralis*, *Cercosaura ocellata*, *Copeoglossum nigropunctatum*, and *Norops ortonii* had relatively consistent abundances across all gradients (Figure S1).

The spatial autocorrelation tests conducted on the residuals of both multiple models, for species composition and the proportion of heliothermic species indicated that the results were unaffected by geographic distance (Moran's I $p=.19$ for the species-composition model and 0.40 for the proportion-of-heliothermic species model). These findings indicate that the observed patterns of assemblage structure are primarily shaped by environmental filtering, leading to assemblage turnover, rather than being influenced by distances between plots.

4 | DISCUSSION

Our results showed that, although many of the lizard species we sampled are widely distributed in Central-Eastern Amazonia, at the local scale, species are filtered by environmental gradients and by the amount of unforested areas nearby. Contrary to our expectations based on the study by Vitt et al. (1998), we did not find evidence that clearings formed by RIL activities and individual tree falls affect species composition or the proportion of heliothermic species at the plot scale (250 m).

Clearings formed by selective logging might impact species composition, favoring the presence of heliothermic species, and consequently, have a negative effect on species typically associated with forest (Vitt et al., 1998). However, these effects were observed in

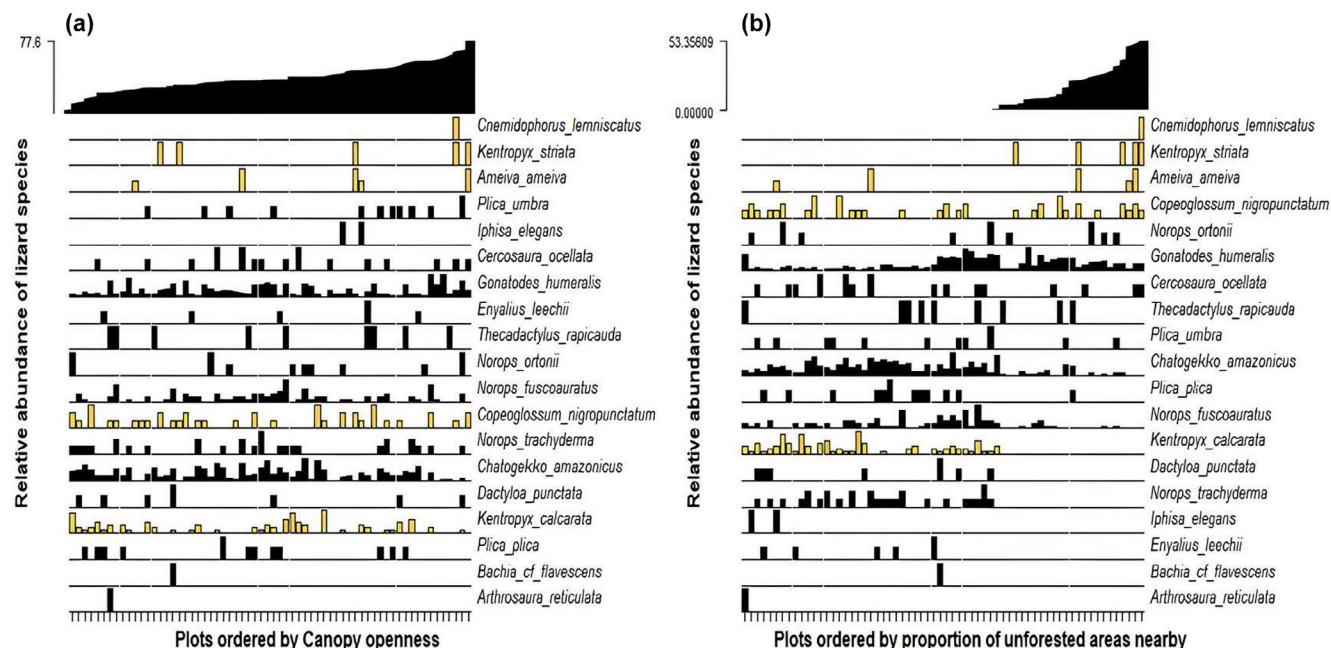


FIGURE 2 Direct ordination of plots along gradients of canopy openness (a) and nearby unforested areas measured by proportion of open areas in the landscape (b). The height of the rectangles denotes species relative abundances, and blank spaces indicate species absence. The yellow rectangles represent heliothermic species. Color should be used for printed figures.

the short term, as the study of Vitt et al. (1998) examined the effects of selective logging on lizard assemblages 1 year after RIL activities. In contrast, we did not detect effects of clearings in the long term, 10 years after RIL activities ceased, and species appear to reassemble as vegetation regenerates (Iglesias-Carrasco et al., 2023; Lima et al., 2001). Our findings support Lima et al. (2001), who evaluated densities of three heliothermic lizard species after selective logging in an Amazon forest and found that the densities of the species increased in the medium term (4 years after selective logging). However, several years after the RIL had ceased (10 years), the effect was less pronounced and not detected for all species.

Vitt et al. (1998) also found a higher concentration of heliothermic lizards in recently established clearings resulting from RIL activities than in natural clearings or continuous forest areas. Natural clearings have a less pronounced impact on lizard microhabitats due to the preservation of understory vegetation, which moderates temperature, provides shade, and creates diverse microhabitats for various lizard species, including a layer of fallen leaves (Vitt et al., 1998). In contrast, RIL clearings lack understory vegetation and have fewer fallen leaves on the ground, resulting in a reduced number of microhabitats for non-heliothermic lizards (Vitt et al., 1998). Our findings suggest that, over time, as vegetation regenerates in RIL-formed clearings, new microhabitats appear and become inhabited by non-heliothermic species that were not present in the recently open areas.

While the open areas resulting from RIL activities and individual tree falls may not impact species composition and the proportion of heliothermic species several years after the reduced-impact logging had ceased, our findings highlight that the presence of unforested areas near our sampling units led to increased species turnover and

the prevalence of heliothermic species. Forest lizard species, such as *Dactyloa punctata*, *Norops trachyderma*, and *Enyalius leechii*, were replaced by heliothermic species, such as *Ameiva ameiva*, *Copeoglossum nigropunctatum*, and *Kentropyx striata* (Figure 2b). This result was expected since heliothermic species prevail in unforested areas, being adapted to open environments with heightened sunlight exposure and elevated temperatures. This result emphasizes the importance of maintaining large forested areas to protect forest species (Gibson et al., 2011).

Our results also showed that soil texture influenced both species turnover and the proportion of heliothermic species, with a higher proportion of heliothermic species in plots on sandier soils. Soil texture has the potential to shape reptile assemblages by affecting the availability of invertebrates (Nielsen et al., 2010), which contribute to the diet of most lizard species (Vitt et al., 2008). Sandier soils can also influence the movement of some species, which may move more effectively in sandier environments, and sandier soil may facilitate predator evasion through sand burrows. The increased proportion of heliothermic species in sandier soils may be related to the thermoregulation of these species, as sandier soils tend to have higher temperatures than clay-rich soils. In our study area, sandy regions are primarily situated near savanna areas. Therefore, soil texture determines both vegetation cover and the spatial structure of lizard assemblage composition.

Our findings indicate that vegetation height is a determinant of lizard species composition; however, it did not affect the abundance of heliothermic species. In our study, areas with taller vegetation had higher abundance of arboreal species (e.g., *Plica plica*, *Enyalius leechii*, *Norops trachyderma*). These areas provide greater vertical stratification, favoring arboreal species; they use high perches for

foraging, resting, and thermoregulation. In contrast, areas with lower vegetation had higher abundances of terrestrial species (e.g., *Cnemidophorus lemniscatus*, *Kentropyx striata*, and *Bachia* cf. *flavescens*). Tall vegetation is primarily found in areas covered by old-growth forest in our study area, highlighting the importance of these environments in determining spatial variation in arboreal-species abundance.

The composition of lizard assemblages was also significantly influenced by the distance to the nearest water body for many species, but this variable had no apparent impact on heliothermic species. Water-body distances play a crucial role in shaping reptile assemblages in the Amazon region (De Fraga et al., 2011; Faria et al., 2019; Moraes et al., 2016), especially for lizards (Faria et al., 2019; Peixoto et al., 2020). Distance from a water body reflects a variety of interacting variables, including microclimate, nutrient availability, vegetation cover, and edaphic structure (Peixoto et al., 2020).

Despite the spatial variation in leaf litter depth (0.8–3.63 cm) across our plots causing significant variation in food and shelter availability for small-bodied terrestrial lizards, such as Gymnophthalmidae species (Faria et al., 2019), contrary to expectations, this variable did not influence assemblage composition or proportion of heliothermic species. While litter depth is generally considered crucial for determining shelter availability, egg deposition sites, and foraging opportunities for terrestrial species, particularly fossorial ones (Fauth et al., 1989; Vitt et al., 2007), it appears not to be a significant factor for species turnover in our study region. Nevertheless, the study by Faria et al. (2019) found that litter depth did impact lizard composition in another forest in the Amazon region. This suggests that the impact of litter depth on lizard species composition should not be generalized, and the specific characteristics of each Amazon region should be considered.

Our results indicate that certain environmental variables influence the species composition of lizards. The distribution of many species, particularly those non-heliothermic forest dwellers, is primarily affected by nearby areas devoid of forests. Areas with a higher proportion of unforested areas are concentrated around the village of Alter do Chão, to the north of our study area (Fadini et al., 2021; Torralvo et al., 2021), which has been experiencing intense anthropogenic pressure, primarily driven by real estate speculation. Although the sampled area in Alter do Chão is not currently directly threatened by deforestation, it is within an Environmental Protection Area, a category of reserve which is supported by Brazilian environmental legislation but has limited effective power to control urban growth and other land uses (Françoso et al., 2015). In contrast, to the south of our study area lies the Tapajós National Forest, a category of reserve that legally permits sustainable use by traditional communities, such as RIL.

There are few economic alternatives that do not require deforestation currently available in the Amazon, and selective logging is one of them (Putz et al., 2012). Our data indicate that selective logging may be a viable and environmentally superior alternative for conserving forest-dependent lizard assemblages compared to activities that lead to deforestation. Although lizard assemblages respond to spatial

and temporal variation in environmental characteristics, we found evidence that lizard assemblages recovered as vegetation regenerated after reduced-impact logging ceased in the Tapajós FLONA.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.n02v6wx6g>.

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