RESEARCH ARTICLE

Influence of vegetation regeneration and agricultural land use on lizard composition, taxonomic and functional diversity between different vegetation types in Caatinga domain, Brazil

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Abstract

Anthropogenic changes in habitats are one of the main threats to biodiversity. Understanding how species diversity and their functions are affected by these changes is crucial to assess environmental impacts. In this work, we aim to understand how lizard composition, taxonomic and functional diversity respond to differences in native vegetation regeneration stages (conserved vegetation and open secondary vegetation) and agricultural land use in different vegetation types (Caatinga sensu stricto, Cerrado sensu stricto and Relictual Humid Forest) in Caatinga domain, Brazil. In more degraded areas (open secondary vegetation and agricultural areas), we found a decline in species evenness, shown by greater dominance of few species. Moreover, we found a lower functional evenness in agricultural areas than in areas of conserved vegetation, which suggests that a smaller portion of functional traits present greater dominance in more anthropized areas. We did not detect any significant differences in species richness, but we did registered differences in species composition in Relictual Humid Forest. Contrary to our expectations, lizard abundance was also greater in more degraded areas, probably as a result of the increased abundance of species benefited by anthropization. In this work, we advance the knowledge of how anthropogenic changes influence lizard diversity and emphasize the importance of analysing different facets of diversity and different habitat environments to understand how anthropization affects patterns in community ecology.

KEYWORDS
agricultural areas, anthropic impacts, biodiversity loss, conservation, Squamata

INTRODUCTION

The conversion of pristine habitats into agricultural areas is one of the main ways of intensifying land use worldwide (Ellis et al., 2010). This often negatively impacts biodiversity (Moreira et al., 2020; Susi & Laine, 2021) through changes in conditions, resources, and interactions between organisms (Valladares et al., 2015). After use and consecutive land abandonment, it is expected that the regeneration of native vegetation will gradually recover the diversity and functioning of the environment, depending on factors such as previous land use and the type of native vegetation (Latawiec et al., 2016; Warring et al., 2016). Characterising different facets of biodiversity is an essential tool for analysing diversity patterns in community ecology (Carvalho et al., 2021; Hacala et al., 2021).

Taxonomic diversity encompasses traditional metrics such as species richness, abundance, and their interaction or distribution (e.g., species evenness and diversity indexes). In general, environmental impacts impair diversity metrics (e.g., Brown, 2001; Fenoglio et al., 2020; Flynn et al., 2009), but exceptions can occur, such as higher species richness (Sheil & Burslem, 2013) and species evenness (Biswas & Mallik, 2010) at intermediate disturbance levels, and increased abundance with disturbance (Flores et al., 2017). Metrics that consider species abundance, not just species richness, tend to change shortly after environmental changes, since even the lowest levels of disturbance can change population aspects before leading to species loss (Chapin III et al., 2000). Traditional metrics, however, do not take into account the identity of organisms, which can be attributed to species composition.

Knowing species identity through composition, helps us to reveal changes in diversity that other metrics, such as species richness, cannot reveal (Arnold et al., 2021). The identity of species, associated with knowledge of their life history (such as microhabitat use, diet and tolerance to environmental changes) helps us better understand the relationship between diversity and environmental aspects, such as responses to vegetation type or to anthropogenic changes (e.g. Costa et al., 2019). Through the assessment of species composition, however, it is not possible to aggregate together various characteristics of organisms and assess how they respond to environmental changes, which can be characterized by functional diversity (Mouchet et al., 2010).

In contrast to traditional metrics of diversity, functional diversity considers species characteristics by describing the distribution of functional traits (Mouchet et al., 2010; Petchey & Gaston, 2006). Functional diversity metrics can be negatively (e.g., in birds and mammals – Flynn et al., 2009; plants – Pakeman, 2011; birds – Almeida et al., 2016; anurans – Riemann et al., 2017; lizards – Berriozabal-Islas et al., 2017) or positively (e.g., plants – Pakeman, 2011 and lizards – Berriozabal-Islas et al., 2017) affected by environmental degradation. Response variation of functional traits can be influenced by aspects such as the investigated taxon (Matuoka et al., 2020; Scott et al., 2006), vegetation type (Biswas & Mallik, 2010), type of metric used (Villéger et al., 2010), or biogeographic region (Benício et al., 2021). Due to their particularities (e.g., functional redundancy – Walker, 1992), taxonomic and functional diversity may not respond concomitantly to environmental changes (Riemann et al., 2017; Song et al., 2014), evidencing the relevance of assessing these different facets of diversity together.

Lizards (Squamata) are good models for testing the effect of anthropogenic disturbances, as they respond to changes such as fragmentation (Walkup et al., 2017), reduction of habitat heterogeneity (Pianka, 1967), and land use for agriculture (Janiawati et al., 2016). However, studies considering joint taxonomic and functional diversity responses in this taxon

are still scarce (e.g., Berriozabal-Islas et al., 2017). Likewise, little is known regarding possible functional and taxonomic diversity variations due to anthropogenic disturbance in the Caatinga domain for animals (except Arnan et al., 2018 – ants). Much of the environment has been altered by anthropogenic activities, with approximately 63% of the region formed by anthropogenic ecosystems (Silva & Barbosa, 2017). The term "domain" for the Caatinga helps to encompass the various types of vegetation found in its region, considered ecologically and evolutionarily heterogeneous (Queiroz et al., 2017). The predominant vegetation type in the region is a Seasonally Dry Tropical Forest (Caatinga sensu stricto). Other vegetation types encountered in the domain, but to a lesser extent including the Tropical Savanna (Cerrado sensu stricto) and Relictual Humid Forest (Moro et al., 2015). The search for patterns among different environments contributes to better predictions on how the biodiversity aspects can be affected by disturbances (e.g., Biswas & Mallik, 2010).

We evaluate how changes in stage of native vegetation regeneration and agricultural land use affects lizard assemblages composition, functional and taxonomic diversity considering different vegetation types in Caatinga domain (Caatinga sensu stricto, Cerrado sensu stricto and Relictual Humid Forest). We used diversity metrics widely explored in diversity studies in different groups of organisms (e.g., fish – Villéger et al., 2010; plants – Sitters et al., 2016; lizards – Berriozabal-Islas et al., 2017; birds – Matuoka et al., 2020; amphibians – Moreira et al., 2020). To represent taxonomic diversity, we used species richness (number of species), species evenness (species abundance distribution, Pielou, 1966) and abundance (total number of individuals in the investigated taxon – lizards). To represent functional diversity, we used functional richness (FRic, volume in the trait space occupied by the species, Villéger et al., 2008), functional evenness (FEve, species abundance distribution in functional space, Villéger et al., 2008) and functional divergence (FDiv, how much the taxa differ within each attribute category, Mason et al., 2005).

We predict that, the metrics will show a lower value in open secondary vegetation and agricultural areas than conserved vegetation. This is justified for species richness because more degraded environments can support a limited set of species (Scott et al., 2006, but see Biswas & Mallik, 2010), for abundance because more degraded environments may have fewer resources and thus harbour fewer organisms (Biaggini & Corti, 2015; Scott et al., 2006), for FRic because species in more degraded areas tend to present more similar traits, and thus, lower FRic (Mouillot et al., 2013), for FEve because more similar traits in more degraded areas can lead to a greater clustering of species abundance in the functional space and thus lower FEve (Villéger et al., 2008, but see Berriozabal-Islas et al., 2017), for FDiv because due to homogenization, more degraded environments may present a smaller proportion in the distribution of species abundance as more extreme functional attributes (Mouillot et al., 2013), and for species evenness because more degraded environments tend to be dominated by fewer species (Tu et al., 2020). In addition, we also investigated whether species composition changes between the different regeneration stages of vegetation, as well as agricultural areas.

MATERIALS AND METHODS

Study area

Three protected areas and surrounding areas in Brazil were sampled: Aiuaba Ecological Station (AES; 6°41′03.4″ S, 40°12′52.3″ W), Sete Cidades National Park (SCNP; 4°06x03.0″ S, 41°42′09.1″ W) and Ubajara

National Park (UNP; 3°50′31.2″ S, 40°54′00.5″ W; Figure 1a). The AES is located in the state of Ceará, in the municipality of Aiuaba, with an average annual rainfall of 568.4 mm and an average altitude of 466 m (IPECE – Aiuaba, 2017). The rainy season is from February to April, the climate is Tropical Hot Semi-arid, and the predominant vegetation is the shrub-tree Caatinga (IPECE – Aiuaba, 2017). The SCNP is located in the northeast of the state of Piauí, in a marginal area of Cerrado sensu stricto in the transition with Caatinga sensu stricto, with an average annual rainfall of 1337 mm and an altitude between 100 and 280 m. The rainy season is from January to May, and the region's climate is classified as Dry Sub-humid. The predominant vegetation is open Cerrado (Santos, 2018). The UNP is located northwest of the state of Ceará. In Relictual Humid Forest areas, the altitude is approximately 847.5 m, and the average annual rainfall is 1483.5 mm. The rainy season is from January to April, and the climate is Tropical, Sub-humid (IPECE – Ubajara, 2017). In the Caatinga sensu stricto areas, the altitude is about 121 m, and the average annual rainfall is 1139.2 mm. The rainy season is concentrated from January to April, and the climate is Tropical Hot Semi-arid and Tropical Hot Semi-arid Mild (IPECE – Frecheirinha, 2017).
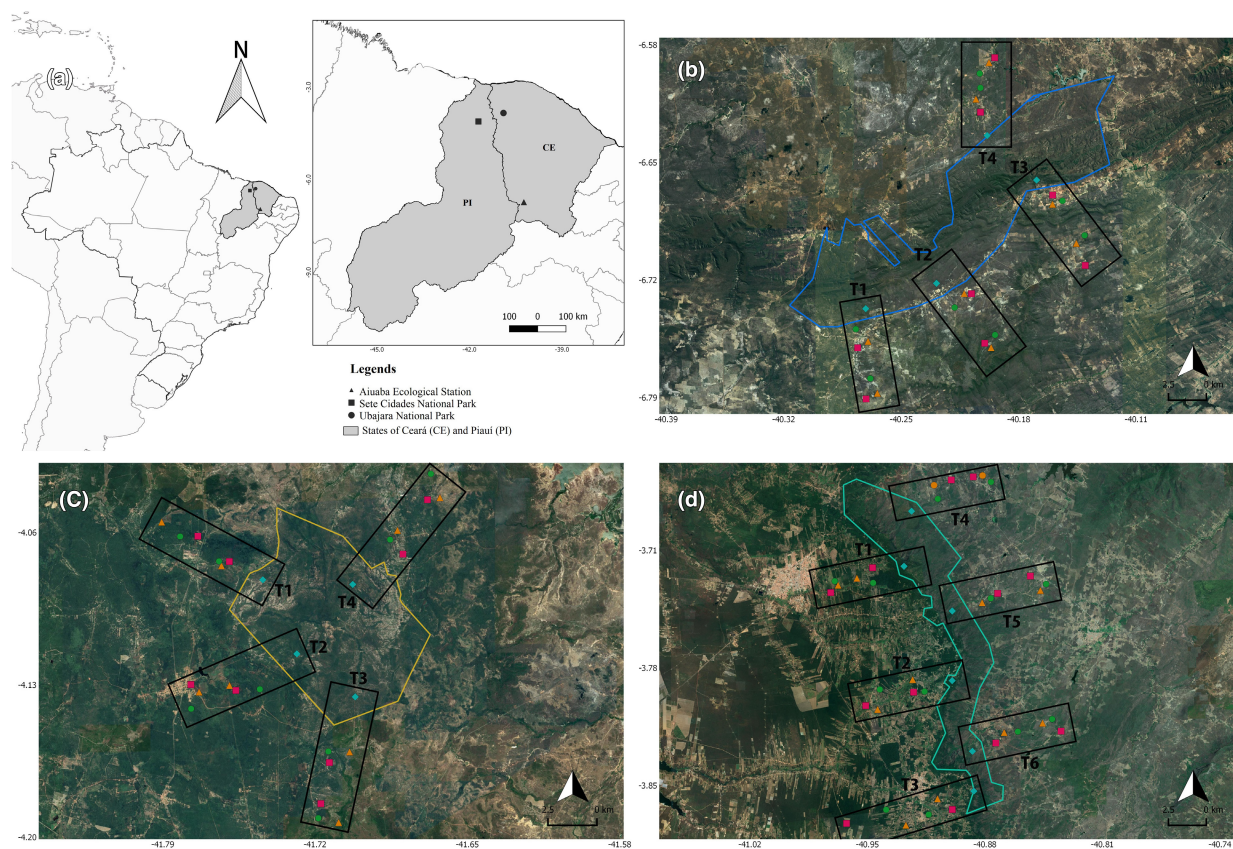
FIGURE 1 Location of protected areas in Brazil (a) and distribution of sampling points across protected areas and their surroundings in Aiuaba Ecological Station (b), Sete Cidades National Park (c) and Ubajara National Park (d). Blue diamond – conserved vegetation within protected areas; Green circle – conserved vegetation without protected areas; Orange triangle – open secondary vegetation; Pink square – agricultural areas. T – transect. In UNP transects 1, 2 and 3 are areas of Relictual Humid Forest, and transects 4, 5 and 6 are areas of Caatinga.

Sample design, classes of native vegetation regeneration and land use

Initially, we built maps for each protected area and respective surrounding areas. In each area we delimited four transects (minimum distance of 3 km from each other), except in UNP, where we delimited three transects in Relictual Humid Forest and three transects in Caatinga. For each transect, we delimited three circles, starting from the inside to the outside of the protected area, with a radius of 1 km each, to select the points within each radius. The circles serve to delimit the dispersion of points in each transect (transects are marked with a rectangle in Figure 1b-d). Within the demarcated sampling radius, we used the statistical method of random stratification to select sampling points representing different levels of vegetation degradation (conserved vegetation within protected areas, conserved vegetation without protected areas, open secondary vegetation and agricultural areas). For this purpose, a 500 x 500 m grid on each circle, in which all patches of the same land cover class were enumerated, taking into account the vegetation's density and colour, considering areas with higher plant density in a more advanced stage of regeneration and with lower density in earlier stages. The mapping was done through a supervised classification and then refined with the OpenLayers Plugin tool in QGis with Google satellite images. Supervised classification uses algorithms to classify the pixels of an image in order to represent the evaluated classes. After this process, the classes were confirmed with field visits and with the use of an unmanned aerial vehicle (UAV). We used the "random" function in Excel to randomly select the points for each class. We repeated this procedure for all classes and recorded geographic coordinates of the selected points in GPS for field location.

We established seven sampling points in each transect: one in conserved vegetation within protected area, two in conserved vegetation without protected areas, two in open secondary vegetation and two in agricultural areas (Figure 1b-d). The points taking into account the regeneration stage of native vegetation and land use. The regeneration stage of native vegetation is latter in conserved vegetation and earlier in open secondary vegetation. Agricultural areas represent land use (Appendix S1). Each point had a minimum distance of 500 m from the other points in the same transect (Figure 1b–d). We sampled 28 points in the areas with four transects and 21 points in the areas with three transects, totaling 98 points. We used QGIS v 2.18.19 (QGIS Development Team, 2019) for map production, classification and demarcation of points.

In traditional subsistence agriculture in northeastern Brazil (slash-and-burn), soil preparation involves falling the vegetation, removing the fallen logs, burning the remaining vegetation (fallen branches, trunks, herbs), and then planting crops (Oliveira et al., 2020). Irrigation is used in some regions to keep crops growing throughout the year, such as in the Planalto da Ibiapaba, Ceará (Girão et al., 2001), where the areas of Relictual Humid Forest assessed in this area are located. The agricultural areas in Caatinga and Cerrado were abandoned in the dry period, but they were irrigated in the Relictual Humid Forest. Therefore, we visited abandoned agricultural areas in the Caatinga and Cerrado but cultivated areas in the Relictual Humid Forest during the dry season. All agricultural areas were cultivated in the rainy season (Appendix S1). The crops in Caatinga and Cerrado were predominantly maize, maize with beans, maize with cassava, in the Relictual Humid Forest, maize with beans in addition to cultivars (avocado, passion fruit, banana, tomato).

Sampling of lizards

We sampled the species during the daytime (between 8 and 17 h). Nocturnal animals were sighted in rest areas (e.g., under tree barks). At each point we moved away from the vegetation edges for at least 50 m, entering the forest, except in agricultural areas, which were sometimes small fragments; thus, we also sampled the vegetation edges in the latter. We sampled lizards for 60 min at each point of conserved vegetation outside protected areas, open secondary vegetation and agricultural areas, and 120 min in conserved areas within protected areas, as these had a lower number of points than the other categories (Figure 1b-d). We used visual encounter surveys (VESs) as the sampling method (Crump & Scott Jr., 1994). We explored most microhabitats used by lizards, such as rocks, tree trunks, fallen logs, on the ground, under tree bark and in leaf litter (e.g., Werneck et al., 2009). To help explore the litter, we used rakes.

We performed three expeditions in each protected area and surroundings between 2018 and 2020, two in the rainy season and one in the dry season, to cover different conditions encountered throughout the year. We sampled the AES (Caatinga) in April 2018, and March and September 2019; the UNP (Caatinga) in April and September 2019, and February 2020; the UNP (Relictual Humid Forest) in April and September 2019, and February 2020; and the SCNP (Cerrado) in May and November 2019, and February 2020. A previous study found little divergence in the species richness and abundance of Caatinga lizards between the dry and rainy seasons (Passos et al., 2016). The total sampling effort taking into account all researchers in the field was 290 h and 20 min at AES and surrounding areas (Caatinga); 331 h and 10 min at SCNP (Cerrado) and surrounding areas; 238 h and 26 min at UNP (Caatinga) and surrounding areas and 250 h and 43 min at UNP (Relictual Humid Forest) divided between the four land cover classes, totaling 859 h and 56 min.

Taxonomic and functional diversity

To identify the lizard species, we carried out specific diagnoses, considering the geographic distribution of the species and using specific literature for identifications (e.g. Arias et al., 2018; Castro et al., 2019; Costa et al., 2018; Passos et al., 2011; Recorder et al., 2014; Ribeiro-Júnior, 2015; Ribeiro-Júnior & Amaral, 2016; Roberto & Loebmann, 2016; Rodrigues et al., 2006; Vanzolini et al., 1980). To estimate functional diversity (Petchey, 2003; Riemann et al., 2017), we considered traits related to niche (spatial, temporal and trophic) complementarity in resource partition, as well as characteristics that influence growth and reproduction (Rosenfeld, 2002). We recorded the following traits: foraging type (active forager, sit-and-wait, and intermediate forager), diet (insects/arthropods, herbivorous, omnivorous), habit (terrestrial, arboreal, arboreal-terrestrial, fossorial/semi-fossorial, saxicolous, generalist), activity period (diurnal, nocturnal), average SVL (males) and the average number of eggs per litter (Appendix S2). These traits were used in previous studies with lizards (e.g., Vidan et al., 2019) and proved adequate for identifying functional diversity variations with changes in land use (Berriozabal-Islas et al., 2017). We obtained the information for each species by consulting the literature (Appendix S2). When unavailable, we used data collected in the field. Some animals were collected to measure functional traits (collecting permit no 68 031–1 and 72 762, Instituto Chico Mendes de Conservação da Biodiversidade – ICMBio). After capture we recorded the snout-vent length (SVL) with a calliper (precision 0.1 mm). The collected specimens were euthanized with a lethal injection of 2%

lidocaine chloridate, fixed in 3.7% formaldehyde, and preserved in 70% alcohol. We deposited the specimens at the Regional Center of Ophiology at the Federal University of Ceará (NUROF).

Statistical analyses

We pooled the data of each class of native vegetation regeneration and land use in each transect, totaling 16 sampling units in areas with four transects (AES and SCNP) and 12 sampling units in areas with three transects (UNP). This aggregation was necessary to equalize the sampling effort between categories, due to the differences in the number of points in conserved vegetation within protected areas (Figure 1b-d). Furthermore, we built sample-based rarefaction curves using the same sampling units described above to evaluate the sampling efficiency. We estimated the expected species richness using richness estimators (Chao 2 and Jackknife 1) to assess the sample sufficiency in each category. In this case, we used each field visit as a sampling unit at each point.

To test our prediction of changes in taxonomic and functional diversity, we built mixed models using the categories (conserved vegetation, open secondary vegetation and agricultural areas) and its interaction with the type of vegetation as explanatory variables, and the diversity metrics (species richness, species evenness, abundance, FRic, FEve and FDiv) as response variables. From this broad model, we simplified it using the AIC method (select models with lower AIC value) and retained the most parsimonious model.

As conserved areas inside and outside protected areas represent a more advanced stage of regeneration, we group them together for comparison with the other classes (open secondary vegetation and agricultural areas). We used the fitdistrplus R-package (Delignette-Muller & Dutang, 2015) to find the best fit distribution of the data used in our models. We used linear mixed models (LMM–lme4 R-package, Bates et al., 2015), or generalized linear mixed-effects model (GLMM–lme4 R-package, Bates et al., 2015, glmmTMB – glmmTMB R-package, Brooks et al., 2017), depending on the fit of the data, with the transects as a random effect nested within the study vegetation type. We then use post-hoc tests (lmerTest R-package, Kuznetsova et al., 2017) to assess the differences between each category pair. We performed an analysis for each response variable.

To test whether there are differences in species composition between different classes of vegetation regeneration and land use we performed a non metric multidimensional scaling (NMDS–vegan R-package, Oksanen et al., 2022) with 100 randomizations and one dimension, using the Bray–Curtis distance. From the NMDS, we obtained ordering scores that convey the compositional differences between the different classes of vegetation regeneration and land use. We then applied the scores as a response variable in a mixed linear model (lmm), using the categories of vegetation regeneration and land use (conserved vegetation, open secondary vegetation and agricultural areas) and its interaction with the type of vegetation as explanatory variables, and the ordering scores of the NMDS as response variables. From this broad model, we simplified it using the AIC method (select models with lower AIC value) and retained the most parsimonious model. We then use post-hoc tests (lmerTest R-package, Kuznetsova et al., 2017) to assess the differences between each category pair. To build the figures from the NMDS we used the same models, however with two dimensions.

To assess whether the response variables are correlated or not, and thus whether they can be assessed individually, we calculated Pearson

correlations coefficients for data with normal distribution and Spearman correlations coefficients for non-normally distributed data. Conventionally, correlations of 0.1 to 0.3 are considered weak, 0.4 to 0.6 moderate, and 0.7 to 1.0 strong (Dancey & Reidy, 2006). We calculated FRic, FEve and FDiv in FD R-package (Laliberté et al., 2014). We stimated the species richness in the software EstimateS 9.1.1 (Colwell, 2013), and calculated species evenness in Past 3.04 (Hammer et al., 2001). All statistical analyzes that used R packages and the production of Figures 2 and 3 were performed in R Statistical Software (v. 4. 1. 2; R Core Team, 2021). The R scripts used in the analyses are available in Figshare online repository (see data availability statement).

RESULTS

In total, we recorded 23 lizard species distributed in 11 families: Gekkonidae (4 spp.), Phyllodactylidae (2 spp.), Sphaerodactylidae (1 spp.), Mabuyidae (3 spp.), Dactyloidae (1 spp.), Iguanidae (1 spp.), Leiosauridae (1 spp.), Polychrotidae (1 spp.), Tropiduridae (3 spp.), Gymnophthalmidae (3 spp.) and Teiidae (3 spp.; Appendix S3). The rarefaction curve tended to stabilize, indicating that the sampling was adequate, suggesting that our sampling effort was satisfactory (Appendix S4).

In the Caatinga areas studied, we found 17 lizard species (14 in AES and 13 in UNP). Among them, *Tropidurus jaguaribanus* Passos et al., 2011 and *Vanzosaura multiscutata* (Amaral, 1933) are endemic to the Caatinga (Mesquita et al., 2017). *Tropidurus hispidus* (Spix, 1825) was the most abundant species in conserved areas and in open secondary vegetation
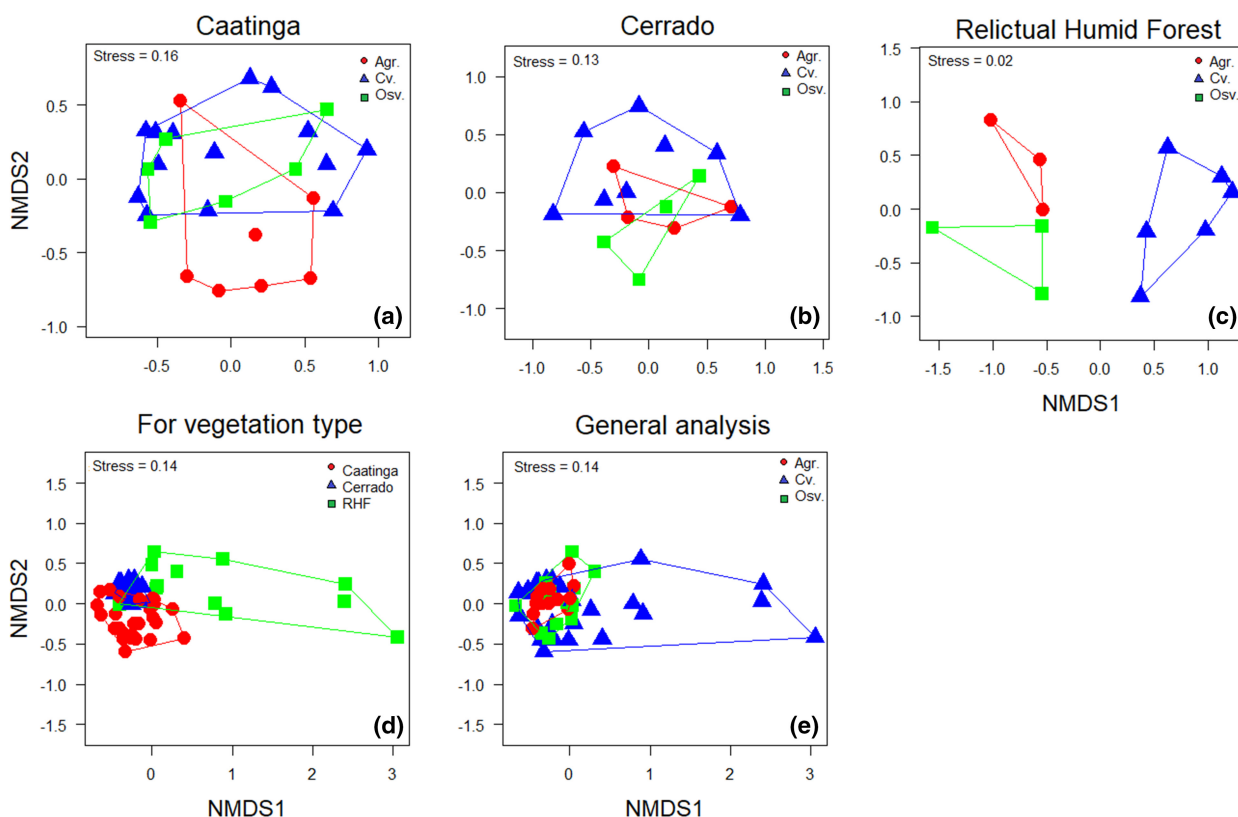
FIGURE 2 Non-metric multidimensional scaling (NMDS) graphics for vegetation type, and taking into account the different stages of regeneration of native vegetation and agricultural land use, in general analysis and for each vegetation type investigated. AGR, agricultural areas; CV, conserved vegetation; OSV, open secondary vegetation.)
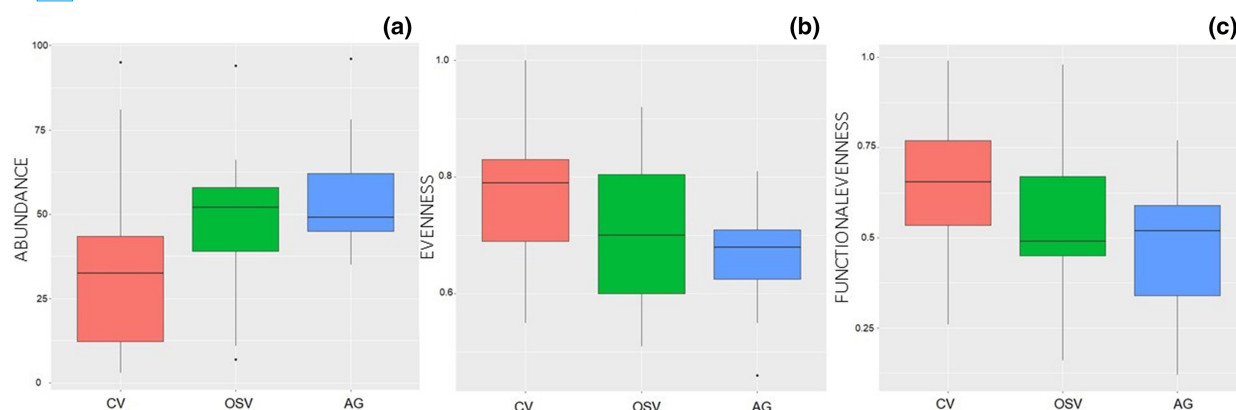
FIGURE 3 Abundance (a), species evenness (b) and functional evenness (c) in the different stages of vegetation regeneration and agricultural areas. AG, agricultural areas; CV, conserved vegetation; OSV, open secondary vegetation.

(relative abundance–42.63% and 29.88%, respectively). *Ameivula pyrrhogularis* (Silva & Avila-Pires, 2013) was the most abundant in agricultural areas (relative abundance–46.99%). We did not register a significant difference in species composition between none of the different classes of vegetation regeneration and land use in the Caatinga (Agricultural areas vs. conserved vegetation – Est = −0.005; t-value = −0.06, p = 0.94; Agricultural areas vs. open secondary vegetation–Est = 0.01, t-value = 0.17, p = 0.86; Conserved vegetation vs. open secondary vegetation–Est = 0.02, t-value = 0.26, p = 0.79, Figure 2a).

In the Cerrado areas studied, we registered 14 species, without endemisms. *Tropidurus hispidus* was the most abundant species in conserved vegetation (relative abundance–31.11%), and *Ameivula pyrrhogularis* was the most abundant species in open secondary vegetation and agricultural areas (relative abundance–43.54% and 45.14%, respectively). We did not register a significant difference in species composition between none of the different classes of vegetation regeneration and land use in the Cerrado (Agricultural areas vs. conserved vegetation – Est = −0.001; t-value = −0.01, p = 0.98; Agricultural areas vs. open secondary vegetation–Est = −0.009, t-value = −0.07, p = 0.94; Conserved vegetation vs. open secondary open vegetation–Est = −0.007, t-value = −0.07, p = 0.94, Figure 2b).

In the sampled areas of the Relictual Humid Forest, we recorded 12 species. We found typical species from the Relictual Humid Forest of northeastern Brazil, such as *Enyalius bibronii* Boulenger, 1885, and forest species as *Norops fuscoauratus* (D'Orbigny, 1837 in Duméril & Bibron, 1837; Appendix S3). The most abundant species in preserved areas was *Coleodactylus meridionalis* (Boulenger, 1888; relative abundance–32.5%), in open secondary vegetation was *Brasiliscincus heathi* (Schmidt & Inger, 1951; relative abundance–32.5%) and in agricultural areas was *A. pyrrhogularis* (relative abundance −41.35%). We recorded a significant difference in species composition between agricultural areas and conserved vegetation (Est = −0.79; t-value = −6.61, p < 0.001) and between conserved vegetation and open secondary vegetation areas (Est = 0.83; t-value = 6.93, p < 0.001), but not between agricultural areas and open secondary vegetation (Est = 0.03; t-value = 0.22, p = 0.78, Figure 2c).

Species composition between study areas differed between Caatinga and Relictual Humid Forest (Est = −0.32; t-value = −5.17, p < 0.001) and Cerrado and Relictual Humid Forest (Est = −0.30; t-value = −4.49, p < 0.001), but did not differ between Caatinga and Cerrado (Est = −0.01; t-value = −0.27, p = 0.78, Figure 2d). Taking into account all study areas together, the composition differed between agricultural areas and conserved

vegetation (Est = −0.28; t-value = −4.52, $p < 0.001$), and between conserved vegetation and secondary open vegetation (Est = 0.28; t-value = 4.72, $p < 0.001$), but did not differ between agricultural areas and open secondary vegetation (Est = 0.01; t-value = 0.21, $p = 0.82$, Figure 2e). The stress value for this NMDS analysis was 0.17.

Regarding diversity metrics, for abundance and species evenness, the most parsimonious model included the influence of regeneration stage of vegetation and land use as a significant variable (Table 1), however without interaction effect with the study area (variable called "habitat" in Table 1), which does not allow us to predict these results for each vegetation type. In general, however, conserved areas showed lower abundance (Figure 3a) and greater species evenness (Figure 3b) than secondary open vegetation areas (species evenness–Est = 0.07, t-value = 2.50, $p < 0.01$; abundance–Est = −21.42, t-value = −4.14, $p = 0.001$) and agricultural areas (species evenness–Est = 0.10, t-value = 3.74, $p < 0.001$; abundance–Est = −15.56, t-value = −2.92, $p = 0.005$). Secondary open vegetation and agricultural areas did not differ in abundance (Est = −5.86, t-value = −0.96, $p = 0.34$) or species evenness (Est = 0.03, t-value = 0.89, $p = 0.37$) each other.

For functional evenness, conserved areas had higher values than agricultural areas (Est = 0.15, t-value = 2.56, $p = 0.01$, Figure 3c). There were no differences between conserved areas and secondary open vegetation (Est = 0.11, t-value = 1.82, $p = 0.07$), and secondary open vegetation and agricultural areas (Est = 0.04, t-value = 0.59, $p = 0.55$). For variables that also showed in their more parsimonious model differences in data between different vegetation types (abundance and evenness, Table 1), the results are presented in Appendix S5.

We found no significant differences in species richness, FRic and FDiv (Table 1) between the different stages of vegetation regeneration and agricultural areas. The species richness recorded at each categories was generally close to those showed by the richness estimators used (Appendix S3). Correlations between response variables were generally weak (correlation coefficient between 0.1 and 0.3). In only one case was it

TABLE 1 The most fitted model for each response variable from the more complex model: response variable~land use classes*habitat + (1|area/transect), where "land use class" are the different stages of native vegetation regeneration (conserved vegetation, secondary open vegetation and agricultural areas), and "habitat" are the different vegetation types (Caatinga, Cerrado and Relictual Humid Forest).

Response variable	Best fit model (response ~ explanatory variable)	AIC	Explanatory variable	df	Chi^2	p-value
Species richness	Species richness ~ habitat	228.75	Habitat	2	3.1	0.21
Species evenness	Species evenness ~ land use class + habitat	−98.164	Land use class	2	16.01	**<0.001**
			Habitat	2	8.61	**0.01**
Abundance	Abundance ~ land use class + habitat	457.4	Land use class	2	19.94	**<0.001**
			Habitat	2	19.75	**<0.001**
Functional richness	Functional richness ~ habitat	−0.36	Habitat	2	2.77	0.24
Functional evenness	Functional evenness ~ land use class + habitat	−19.45	Land use class	2	7.68	**0.02**
			Habitat	2	4.25	0.11
Functional divergence	Functional divergence ~ habitat	−45.32	Habitat		3.81	0.14
Species composition	NMDS scores ~ land use class*habitat	−14.33	Land use class * habitat	4	52.93	**<0.001**
			Land use class	2	16.07	**<0.001**
			Habitat	2	66.93	**<0.001**

Significant p-values in bold.

moderate (correlation coefficient between 0.4 and 0.6 – between species evenness and abundance; Appendix S6).

DISCUSSION

Effects of changes in stages of native vegetation regeneration and agricultural land use on taxonomic diversity and species composition

Species richness did not change between the regeneration stages of native vegetation or in agricultural areas. It is still controversial whether reptile species richness reflects changes in land use because it may not decrease in some areas (Cordier et al., 2020). Thus, species richness alone should be interpreted with caution when used as a metric to assess the effects of environmental impacts, because it does not consider the characteristics of the organisms (e.g., functional traits) that describe their relationship with the environment (Ouchi-Melo et al., 2018). Despite lack of changes in species richness in all vegetation types, we detected changes in species composition, which mainly occurred from conserved areas to more degraded areas (open secondary vegetation and agricultural areas).

In Relictual Humid Forest areas studied, species turnover reflects the loss of forest species and colonization by generalist, more tolerant to open and disturbed environments, and widely distributed species (for example, *Ameiva ameiva*–Benício et al., 2019; Vitt & Colli, 1994; Appendix S3). Species found in pristine areas of Relictual Humid Forest, which have lower temperatures and radiation levels (Vitt et al., 2003), such as *Copeoglossum nigropunctatum* (Spix, 1825) and *C.meridionalis* were absent in more disturbed areas. In the Amazonian tropical rainforest, *C.nigropunctatum* populations are associated with open areas, but this lizard usually inhabit forested environments in other biomes (Ribeiro-Júnior & Amaral, 2016). As for the species most tolerant to environmental changes, the species *T. hispidus* and *Hemidactylus mabouia* (Moreau de Jonnès, 1818), found mainly in agricultural areas, more often manage to survive in open environments, and sometimes in ruderal and anthropized environments (Andrade, 2019; Rodrigues, 2003).

In Caatinga areas studied, although no changes in species composition were identified, not all species found in other stages of native vegetation regeneration were present in agricultural areas, such as the arboreal *Lygodactylus klugei* (Smith et al., 1977) and *Hemidactylus brasilianus* (Amaral, 1935; Andrade et al., 2013; Gonçalves-Sousa et al., 2019). Some lizard species from Caatinga are more sensitive to environmental changes, such as increase in temperature and decreasing of tree cover (Gonçalves-Sousa et al., 2022), which may cause restrictions on microhabitat use. Geckonids, such as *L.klugei* and *H.brasilianus*, use trees as their preferred microhabitat (Andrade et al., 2013; Gonçalves-Sousa et al., 2019, 2023; Vitt, 1995). The presence of trees is an essential resource for arboreal species and their loss, associated with changes in environmental conditions, can lead to a significant decline in this group (Scott et al., 2006).

Contrarily to our expectations, we recorded an increase in general abundance of lizards. The increase in general species abundance may reflect the increase in reproductive success of some species tolerant to disturbance (e.g., Flores et al., 2017). Disturbed areas tend to present species that are generalist or more tolerant to new environmental conditions (Sutton et al., 2014) and a reduced abundance of specialist or rare species (e.g., lizards–Nogueira et al., 2009; bees–Flores et al., 2017). Thus, despite a general increase in abundance of lizard in the studied areas, some species showed a reduction in abundance in more anthropized areas (Appendix S3).

Coleodactylus meridionalis, for example, was not found in agricultural areas. This species uses leaf-litter as the main microhabitat to develop its vital activities (Rodrigues, 2003; Silva et al., 2015). The habitat changes associated with changes in conditions and resource loss should influence *C.meridionalis* survival (Sinervo et al., 2010; Sutton et al., 2014). Finally, the increase in abundance of lizards in more anthropized areas has also been identified in other lizard studies (e.g. Berriozabal-Islas et al., 2017–Tropical Dry Forest in Pacific Coast of Mexico; Smart et al., 2005–Savanna in South Africa).

Species evenness was lower in open secondary vegetation and agricultural areas than in conserved vegetation, which may be associated with the fact that more degraded areas may present a higher proportion of species well-adapted to anthropization. *Ameivula pyrrhogularis*, for example, increased its relative abundance from 9% and 10.4% in conserved areas within and without protected areas respectively, to 30.5% in open secondary vegetarion and 49.8% in agricultural areas (Appendix S3). Some teiids, such as *A.ocellifera* (Spix, 1825) and *A.ameiva* are heliophile and generalist lizards that forage in open environments even in the hottest hours of the day (Gonçalves-Sousa et al., 2019; Mesquita & Colli, 2003). The pattern of lower species evenness with higher disturbance was recorded for other animals in other environments, such as ants (Graham et al., 2009–Upland forests in Georgia, EUA), birds (Tu et al., 2020–various types of natural vegetation like broadleaf forest, conifer forest and bamboo forest in Taiwan, China) and fishes (Villéger et al., 2010–estuarine ecosystem in South western part of the Gulf of Mexico, Mexico). Species evenness usually vary earlier than species richness in face of disturbances because changes in the distribution of abundance occurs before local extinctions (Hillebre et al., 2008). This finding is particularly important because ecosystem functioning in communities where few species dominate (low-species evenness) may have low resistance to environmental fluctuations (Wittebolle et al., 2009).

Effects of changes in stage of native vegetation regeneration and agricultural land use on on functional diversity

Functional evenness was lower in agricultural areas than in conserved areas. Reduction in FEve reflects that species are more irregularly distributed in terms of abundance in relation to their functional characteristics (Villéger et al., 2008). This pattern may result from the simplification of environmental heterogeneity (Sitters et al., 2016). The reduction in FEve is also associated to the reduction of stability and an increase in the invasion opportunity for species more adapted to degraded environments (Ding et al., 2013; Mason et al., 2005). We recorded the invasion of an exotic species, *H.mabouia*, only in agricultural areas. This species benefits from anthropization, and is predominantly associated with perianthropic habitats in Brazil (Rodrigues, 2003; Sousa et al., 2017). Overall, it is expected that there is a negative relationship between FEve and the intensity of land use by humans, where increasing disturbance may led to reduced FEve (Braschler et al., 2021; Mouillot et al., 2013; Present study), although this is not a general pattern (e.g., Berriozabal-Islas et al., 2017; Pakeman, 2011).

We did not detected any variation in FRic. Changes in FRic is expected when occurs extinction or colonization of species with functionally distinct traits (Mouillot et al., 2013). When functional homogenization occurs with the increase of disturbance intensity (Devictor et al., 2008), species present in high-disturbance areas may present more redundant traits, resulting in similar or lower FRic even after environment changes. We also did not recorded significant variation in the FDiv. This index reflects how abundance is

associated with more extreme functional traits, that is, distinctive features of those present at the center of the functional space (Villéger et al., 2008). This metric is influenced by resource competition and niche partitioning (Mason et al., 2005). Thus, it is expected that more heterogeneous environments present higher FDiv values. It is noteworthy, however, that the results found for functional diversity at different land use intensities may vary across taxa (Arnold et al., 2021; Flynn et al., 2009), physiognomies (Biswas & Mallik, 2010) functional traits, and selected indexes (Petchey & Gaston, 2006).

CONCLUDING REMARKS

This study dicovered that variations in the regeneration stage of native vegetation and agricultura land use in the Caatinga domain can mediate lizard diversity. Although species richness have not varied, it is possible that anthropogenic changes can operate as an environmental filter, selecting species that are better adapted to the new environment (Smart et al., 2006; Zhang et al., 2012). This is supported by the presence of *A.pyrrhogularis*, a heliophile species that survives well in environments with high-radiation conditions, and by the occurrence of the invasive species *H.mabouia*, which can influenced the species composition. More refined analyzes that consider each species separately can help to clarify this suggestion. We found variation mainly in indexes that include the abundance of species, which underscores the relevance of this type of metric to assess the effects of environmental changes. The reduction in (i) species evenness, indicates that fewer species can quantitatively dominate more disturbed environments; (ii) in FEve, that there is a higher frequency of some functional traits and (iii) in abundance, suggests a possible increase in the reproductive success of species well adapted to anthropized areas. Most of the changes in diversity occurred between conserved and agricultural areas. The reduction in diversity showed by some of the metrics used in open secondary vegetation areas demonstrates that, in some cases, even less severe changes than transformed areas in agricultural fields may change biodiversity patterns.

The low or moderate correlation between the response variables and the importance of investigating multiple facets of biodiversity (taxonomic and functional, for example) highlights the importance of using joint metrics to infer the effect of environmental disturbances. Finally, it should be noted that the agricultural areas investigated here are small-scale production areas; therefore, it is vital to assess the effect of agricultural land use in large-scale agricultural areas, since the response of the diversity of lizards can differ depending on the size of the degraded area (Biaggini & Corti, 2015, 2021).

AUTHOR CONTRIBUTIONS
Ana Carolina Brasileiro: Conceptualization (equal); formal analysis (lead); funding acquisition (lead); investigation (equal); methodology (equal); writing–original draft (lead). **Ronildo Alves Benício:** Writing – original draft (equal); writing – review and editing (equal). **José Guilherme Gonçalves-Sousa:** Formal analysis (equal); writing – original draft (equal); writing – review and editing (equal). **Robson Waldemar Ávila:** Conceptualization (equal); investigation (equal); methodology (equal); resources (lead); supervision (lead); writing – review and editing (lead).

CONFLICT OF INTEREST STATEMENT

The authors declare no the conflict of interest.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in Figshare online repository (https://doi.org/10.6084/m9.figshare.21941486.v2) and in the supplementary material of this article.

ETHICS APPROVAL

Collection permission for animals released for Instituto Chico Mendes de Conservação da Biodiversidade – ICMBio (n° 68031–1 and 72762).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.