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REVIEW

A meta-analysis of the effects of fragmentation on the megadiverse herpetofauna of Brazil

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Abstract

Habitat loss and fragmentation are the primary causes of global population decline of amphibians and reptiles. In Brazil, that hosts an extraordinary herpetofaunal richness, amphibians and reptiles are clearly undersampled among vertebrate groups in fragmentation research. This bias may underestimate the effects of fragmentation on herpetofauna in this megadiverse country. Here, we conducted an exhaustive literature review to evaluate the effects and patterns of fragmentation on amphibians and reptiles in Brazil. We analyzed 55 papers between 1994 and 2020, comprising 350 cases of the effect (positive, negative, or neutral) of a given fragmentation metric on a particular biological response. Forest biomes (Amazon and Atlantic Forest) were largely overrepresented in relation to non-forest biomes, comprising 82% of studies. We also found a disproportional prevalence of fragmentation articles on amphibians (75%). Among lower taxonomic groups, Anura and Testudines were significantly overrepresented, whereas Caudata and Crocodylia were neglected. Fragment size reduction, habitat degradation, habitat loss, and matrix contrast were the most studied metrics (70% of studies), while single-species abundance was the most considered response (59%). The effects of fragmentation were not statistically different between amphibians and reptiles. In general, the impacts were predominantly negative or neutral, while positive effects were infrequent or even non-existent. Our findings suggest that amphibians and reptiles respond similarly and may not be as vulnerable to fragmentation. We call future research to consider non-forest biomes and less-studied taxonomic groups (e.g., Squamata) to fully understand the effects of fragmentation on the megadiverse Brazilian herpetofauna and to take well-informed conservation actions.

KEYWORDS
amphibians, biogeographic bias, biological responses, forest biomes, fragmentation metrics, non-forest biomes, reptiles, taxonomic bias

1 | INTRODUCTION

Habitat loss and fragmentation are two major and increasing perturbations of landscape associated with human-induced global change. Both processes lie among the most important threats to biodiversity, affecting distribution and persistence of populations and species, biotic interactions, and genetic variation of individuals (e.g., Chase et al., 2020; Haddad et al., 2015; Hanski, 2005; Harrison & Bruna, 1999). However, while habitat loss (i.e., reduction of natural habitat amount in the landscape over time) has long been considered to reduce biodiversity, the negative effects of fragmentation *per se* (i.e., alteration in the continuity of habitat into small and isolated patches independent of habitat loss) remain a contentious topic (Fahrig, 2003, 2013, 2017; Fletcher et al., 2018; Hanski, 2015). Fahrig (2003, 2017) proposed several methodological approaches to distinguish between the effects of habitat loss and fragmentation. For example, studies between multiple landscapes (landscape-scale studies) may precisely provide a rigorous statistical control of habitat amount effects (refer also Fahrig et al., 2019). Likewise, landscape-scale studies are required to estimate reliable effects of fragmentation *per se* (as the proportion of habitat comprised in the larger patch, i.e., habitat continuity) on biodiversity regardless of habitat loss (Almeida-Gomes et al., 2016; Martini et al., 2011; Watling et al., 2020).

Today, fragmentation is the primary cause of population decline of amphibians and reptiles, with a large number of studies linking it to extinctions for both groups (e.g., Böhm et al., 2013; Falaschi et al., 2019; Gibbons et al., 2000; Wake & Vredenburg, 2008). Over the last decade, substantial research evaluating the effects of fragmentation across the globe has also provided evidence that amphibian and reptiles are the vertebrate groups most sensitive to human-induced landscape changes (Keinath et al., 2017; Mantyka-Pringle et al., 2012; Powers & Jetz, 2019). This vulnerability is principally associated with complex and particular life-history traits among amphibian and reptilian fauna, including dispersal limitations, habitat requirements, and physiological responses, with desiccation proneness and thermal tolerance playing a key role (Böhm et al., 2013; Cushman, 2006; Pfeifer et al., 2017; Watling & Braga, 2015). While forest specialist reptiles are markedly affected by habitat loss and fragmentation (Keinath et al., 2017), amphibians, mainly those with aquatic larvae, seem to be particularly vulnerable to habitat split (i.e., disconnection between suitable aquatic and terrestrial habitats: Becker et al., 2007; Becker et al., 2010; Lion et al., 2014). Despite the growing body of studies stressing the remarkable sensitivity of herpetofauna communities to human-induced habitat modification, amphibians and reptiles are still clearly undersampled among vertebrate groups in fragmentation-related research (Deikumah et al., 2014; Keinath et al., 2017; Teixido et al., 2020).

In neotropics, amphibians and reptiles can reach high densities and biomass, playing key roles in all types of ecosystem services (e.g., food sources, seed dispersal, biological pest control: Miranda, 2017; Valencia-Aguilar et al., 2013). Specifically, Brazil hosts an extraordinary herpetofaunal richness, being the world leader in amphibian diversity (1136 species: Segalla et al., 2019) and the third country for reptiles (830 species: Uetz et al., 2020). This megadiversity of amphibians and reptiles shows contrasting patterns of species endemism and phylogenetic endemism across the country (Fenker et al., 2020; Vasconcelos et al., 2019). The vast Brazilian territory encompasses different types of highly biodiverse forest and non-forest biomes, including the world's largest rainforest and two biodiversity hotspots (Myers et al., 2000). These ecosystems have been dramatically altered by anthropogenic actions, with increased agribusiness expansion in the last 30 years (Lapola et al., 2014; Overbeck et al., 2015; Strassburg et al., 2017). Such expansion of agricultural frontiers jeopardizes the future herpetofaunal communities in Brazil, with many known examples of short- and long-term negative effects associated with fragmentation following land conversion (Almeida-Gomes & Rocha, 2014; Dixo & Martins, 2008; Moreira et al., 2020; Ribeiro et al., 2017). However, geographic and taxonomic biases are prevalent issues in fragmentation research in Brazil, an unevenly sampled country (Teixido et al., 2020). Coupled with regional challenges of conservation in a megadiverse region (Rodrigues, 2005; Silvano & Segalla, 2005), these biases may underestimate the effects of fragmentation on herpetofauna inhabiting forest and non-forest biomes of Brazil.

In this study, we determine patterns of fragmentation-related research on herpetofauna in Brazil. To do this, we conducted an exhaustive literature review including all publications about this topic. For simplicity, we consider the term “fragmentation” in its broadest sense, thereby encompassing both habitat loss and fragmentation *per se*. Each fragmentation metric (i.e., metrics reporting fragmentation-related patterns that have implications for biodiversity conservation: Didham et al., 2012; Fahrig, 2003, 2017; Hanski, 2015; Watling et al., 2020) may differentially affect biotic communities and biological responses of species, even when species' composition and distribution are unaltered (Chase et al., 2020; Fahrig, 2003; Hanski, 2015). Consequently, the identification of gaps in both fragmentation metrics and biological responses across biomes and herpetofaunal groups is also crucial to provide useful information to better support conservation decisions. Our specific objectives were to: (1) estimate biogeographic (across biomes) and taxonomic (among taxa) biases; (2) determine which fragmentation metrics and biological responses have been studied best and which worst; and (3) compare the effects of these metrics on these responses between amphibians and reptiles.

2 | METHODS

2.1 | Data collection

We conducted our survey on 31 May 2020 using both the Web of Science (WOS: www.webofkowledge.com) and the Scielo platform (www.scielo.br), this last database to include also the articles published in Brazil's local journals. We searched for topics related to herpetofauna diversity, fragmentation metrics, and Brazilian biomes in the title, abstract, and keywords of papers. Specifically, we included the following keywords in both English and Portuguese: "herpeto*" or "reptil*" or "amphibia*" or "anfibio*" or "squamat*" or "escamados" or "crocod*" or "lizard*" or "lagart*" or "snake*" or "serpent*" or "cobra*" or "testudin*" or "cheloni*" or "turtle*" or "tortoise*" or "anur*" or "caudata" or "caudados" or "urodel*" or "gymnophiona" or "gimnofionos" or "apoda", and "connectivity" or "conectividade" or "deforest*" or "desmatamento" or "edge effect*" or "efeito* de borda" or "forest area" or "forest cover" or "forest edge" or "forest loss" or "fragment*" or "habitat amount" or "quantidade de habitat" or "habitat area" or "área de habitat" or "habitat degradation" or "degradação de habitat" or "habitat loss" or "perda de habitat" or "habitat perturbation" or "perturbação do habitat" or "habitat quality" or "qualidade do habitat" or "habitat split" or "separação de habitat" or "isolation" or "isolamento" or "land cover" or "cobertura da terra" or "land use*" or "uso* do solo" or "matrix quality" or "qualidade da matriz" or "patch area" or "área de mancha*" or "patch size" or "tamanho de mancha*" or "split distance" or "split matrix" or "vegetation cover" or "cobertura vegetal", and "Bra?il*" or "amaz?n*" or "atlantic forest*" or "mata atl?ntica" or "caatinga" or "cerrado" or "pampa*" or "pantanal".

We exclusively focused on human-induced fragmentation research on native herpetofauna from Brazil. Thus, we excluded articles on naturally fragmented landscapes (e.g., land-bridge island systems), studies reporting effects of human-induced fragmentation on a set of diverse animal groups pooled in the analyses, although including herpetofauna, and data from non-Brazilian Amazon and all other biomes outside the country (e.g., Argentinian Pampas). We also omitted marine (i.e., sea turtles) and urban ecosystems, as well as studies specifically focused on naturalized and/or invasive exotic species. Finally, we excluded articles reporting species checklists or any biological response (e.g., abundance) in a single fragment at only one time (i.e., descriptive studies without analyzing any fragmentation metric). Reviews and book chapters including our sampling criteria were also checked to complete our database.

The database ultimately included the following items: (1) year of study; (2) geographic coordinates of the study location(s); (3) studied biome(s) (following the Brazilian Institute of Geography and Statistics: IBGE, 2004): Amazon, Atlantic Forest, Caatinga, Cerrado, Pampa and Pantanal; (4) group(s) of study: amphibians and reptiles; (5) subgroup(s) (at the order level) of study (following the Tree of Life Web Project –http://tolweb.org/tree, accessed on September 2020–; Maddison & Schulz, 2007): Anura, Caudata, Gymnophiona, Testudines, Squamata and Crocodylia; (6) number and identification of studied species; (7) spatial scale of study (i.e., patch or landscape; Fahrig, 2017); (8) fragmentation metrics reported (compiled from specialized reviews: Didham et al., 2012; Fahrig, 2003, 2017; Hanski, 2015; Watling et al., 2020): edge effects, fragment size reduction, fragmentation *per se*, habitat degradation, habitat loss, habitat split, isolation and matrix contrast; (9) biological responses investigated (following Teixido et al., 2020): diversity, functional traits, genetics, multispecies abundance, mutualistic interactions, protection against parasites, reproduction, richness, and single-species abundance; and (10) effects of the fragmentation metrics reported on the biological responses investigated: positive, negative, and neutral (i.e., non-significant differences).

Brazilian biomes have the following equivalence in the classification of Olson et al., (2001): Amazon and Atlantic Forest =Tropical and Subtropical Moist Broadleaf Forests; Caatinga =Deserts and Xeric Shrublands; Cerrado and Pampa =Tropical and Subtropical Srasslands, Savannas, and Shrublands; and Pantanal =Flooded Srasslands and Savannas. We asked the authors for a list of studied species when the article (including supplementary material) lacked it. Taxa identified only at the genus level were deleted, and all species were checked following Frost (2020) for amphibians and Uetz et al., (2020) for reptiles. Patch-level studies included observational or experimental studies in a single landscape with one or several fragments (e.g., fragments differing in size, which was considered as "fragment size reduction"), whereas landscape-level studies included multilandscape differences with statistical control of habitat amount effects and/or fragmentation *per se* (Fahrig, 2017; Fahrig et al., 2019; Watling et al., 2020). We only collected the effects based on statistical tests (e.g., generalized linear models) or ordination methods (e.g., correspondence analysis). Most articles conducted statistical analyses for an assemblage of species (e.g., richness) and only a few reported specific effects, either for one particular species or for each of the species included in the study. Several studies reported data from multiple species with several fragmentation metrics and biological responses. Therefore, each relationship studied between a particular metric and a specific response for a given species or assemblage of species within an article was termed as a case, the sample unit in our database. Following our criteria, our database ultimately comprised 55 articles including 350 cases studied between 1994 and 2020 (Teixido et al., 2021).

2.2 | Data analysis

We elaborated a map comprising all the geographic coordinates of the study areas from each article in ArcGIS version 10.5 (ESRI, Redlands, California, USA). To calculate biogeographic bias in the number of studies, we regressed the number of articles in each biome against its human population (data from IBGE, 2015). Both variables were square-root transformed to standardize their variances and improve normality (Zar, 2010). We subsequently tested significant departures of the slope from 1 (i.e., the expected relationship: $\beta \pm SE = 1 \pm 0$) in the observed relationships by means of *t*-tests (Barros et al., 2020). When the observed slope is significantly >1, the bias is positive (i.e., the number of articles is disproportionately high in the most populated biomes) and when <1, the bias is negative (i.e., the number of articles is disproportionately low in the most populated biomes). These analyses were conducted in software R version 4.0.2 (R Development Core Team, 2020).

We assessed the interrelations between categorical variables with the Fisher exact test, performed with R software, as follows. To study taxonomic bias, we analyzed a contingency table (number of rows and columns, respectively, in brackets) considering orders of amphibians and reptiles (6) × studied/non-studied species of each herpetofauna order (2). We calculated these numbers of non-studied species by subtracting studied species from total species of each order in Brazil (amphibians: Segalla et al., 2019; reptiles, excluding the five species of sea turtles: Costa & Bérnils, 2018). To explore biogeographic bias in number of species studied, we analyzed amphibians and reptiles separately in two tables: biomes (6) × studied/non-studied amphibian species in each biome (2), and biomes (6) × studied/non-studied reptile species in each biome (2). We obtained the numbers of species per biome from IBGE (2020).

To test whether the effects of fragmentation differ between taxonomic classes, we analyzed contingency tables considering amphibians/reptiles (2) × negative/neutral/positive effects (3) of fragmentation metrics on biological responses. Although our initial objective was to study the effects of each fragmentation metric on each biological response, the total sample sizes (i.e., grand total of the tables) were low. Thus, we performed a power analysis with G*Power software version 3.1.9.6 (Faul et al., 2009), setting a large effect size (w = 0.5), standard alpha error probability (α = 0.05) and low power ($1-\beta$ = 0.8) in the goodness-of-fit tests option. The resulting minimum sample size for those 2 × 3 tables (df = 2) was 39. Given that no single metric-single response combination reached this minimum, we pooled the frequencies of metrics or responses and only analyzed the resulting tables with a grand total greater than 39.

We analyzed significant departures from expected frequencies for each table cell with the Fisher exact approach post-hoc test proposed by Shan & Gerstenberger (2017). We used the web-based program provided in this reference (https://gshan.i2.unlv.edu/ZPostHoc/; accessed in September 2020) and set a significance level of 5%, adjusted with Simes' (1986) method.

3 | RESULTS

3.1 | Biogeographic and taxonomic bias

Research analyzing the effects of fragmentation on herpetofauna in Brazil is biogeographically biased. Overall, forest biomes (Amazon and Atlantic Forest) comprised most of the articles (82% out of 55

FIGURE 1 Location of the study areas based on the geographic coordinates reported in each article analyzing the effects of fragmentation on herpetofauna in the biomes of Brazil

articles) and no studies were conducted in the Caatinga (Figure 1; Table S1). Although the Atlantic Forest, the most populated biome, included the highest number of articles (*ca*. 56%), the Amazon, the third most populated biome, comprised about 26% of articles, being largely oversampled. Thus, the increase in the number of articles was disproportionately lower than the increase of population across biomes (Figure 2).

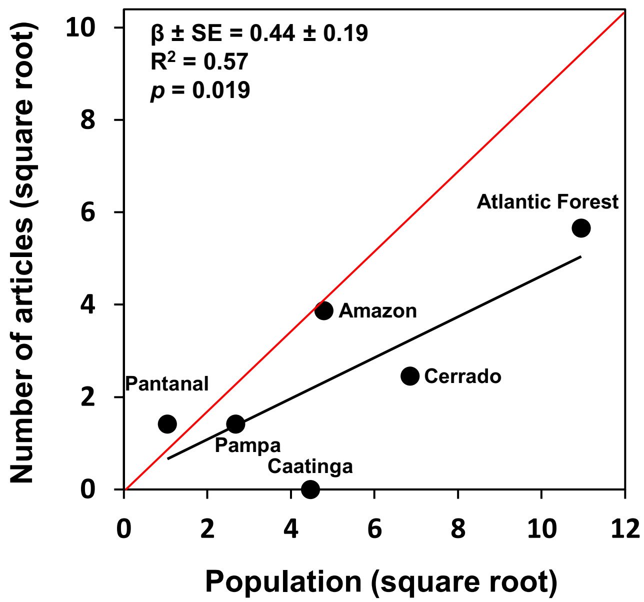

FIGURE 2 Graphical representation of the expected versus observed relationship of the number of articles depending on the human population in the biomes of Brazil. The red line represents the expected slope (i.e., β = 1) and the black line represents the observed slope

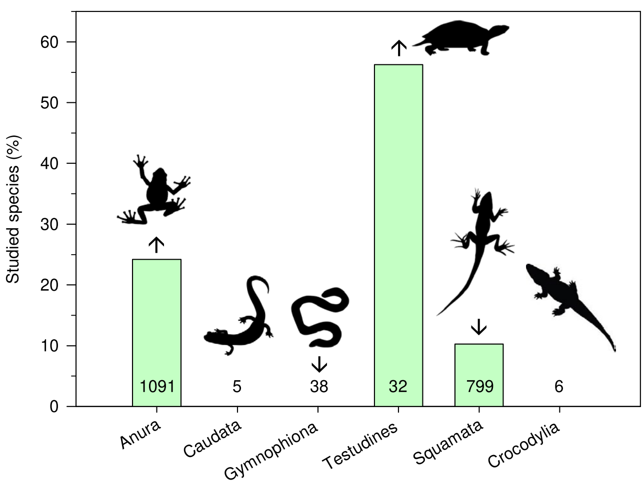

FIGURE 3 Species of each herpetofauna order included in fragmentation studies in Brazil. Percentages are calculated in relation to the total number of species known in the country, which is shown above each order. In Caudata, Gymnophiona and Crocodylia, no species were studied. Arrow up or down above the bars indicate significant excess or deficit, respectively, compared to the expected frequencies (Fisher exact approach, $p < 0.05$)

We found a disproportional prevalence of fragmentation articles on amphibians ($n = 41$) over those on reptiles ($n = 11$), with a few studies ($n = 3$) considering both classes. The proportion of studied species also differed significantly between orders (Fisher exact test, $p < 0.001$). Anura and, above all, Testudines were overrepresented, while Squamata and Gymnophiona were underrepresented (Figure 3). The absence of studies on Caudata and Crocodylia was not statistically significant in post-hoc tests (Fisher exact approach, $p > 0.05$) because the numbers of species known in Brazil for both orders are low (Figure 3). The proportion of amphibian and reptile studied species also varied significantly across biomes (Fisher exact test, $p < 0.001$ for both classes). Amphibians from the Amazon were significantly overrepresented (Fisher exact approach, $p < 0.05$), whereas none of the 79 species in the Caatinga was studied (Figure 4). In the other four biomes, the numbers of studied species did not differ significantly from the expected values. The Pantanal did not have a significant excess of species studied, despite having the maximum value (53%), because the total number of known species in this biome is low ($n = 47$). Reptile species from the Atlantic Forest and, especially, from the Pampa (29%) were significantly overrepresented. Reptiles from the Amazon, the richest biome ($n = 550$ species), were barely studied, and none of the species from the other three biomes were included in fragmentation studies (Figure 4).

3.2 | Effects of fragmentation

Fragment size reduction (20% out of 350 cases), habitat degradation (18%), habitat loss (17%), and matrix contrast (15%) were the most studied metrics, followed by edge effect (11%), isolation (9%), habitat split (7%), fragmentation *per se* (2%), and fragment number (1%) (Table S2). Single-species abundance was the most considered response in the articles (59% of cases), followed by richness (16%), multi-species abundance (10%), diversity (6%), genetics (4%), and functional traits (3%). Otherwise, mutualistic interactions were considered in three cases and protection against parasites and reproduction only in two (Table S2). Overall, 13 articles (23.6%) included a landscape-scale statistical control, discerning between the effects of habitat loss and fragmentation *per se*, but only one article considered both metrics.

The effects of all single fragmentation metrics on biological responses pooled were not statistically different between amphibians and reptiles (Fisher exact tests: $p \gg 0.05$, Table 1). Total negative effects outweighed total neutral effects in response to fragment size reduction and, above all, habitat degradation (Figure 5). In contrast, total neutral effects were predominant in response to habitat loss and matrix contrast, although negative effects were also frequent. In both metrics, the large differences between these total frequencies and the frequencies for reptiles are due to the scarcity of data on this class (Figure 5; Teixido et al., 2021). Positive effects of all these metrics were few or even non-existent in the case of matrix contrast. The effects of fragmentation metrics pooled on single biological

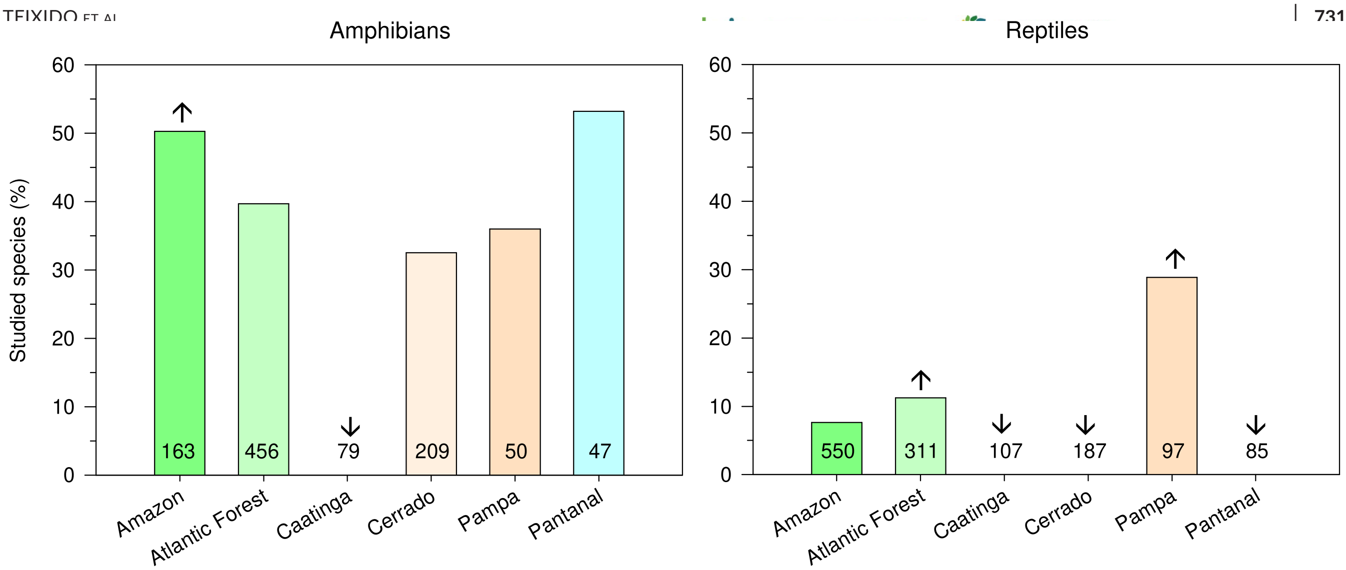

FIGURE 4 Amphibian and reptile species included in fragmentation studies of each Brazilian biome. Percentages are calculated in relation to the total number of species known in each biome, which is shown above it. No amphibian was studied in Caatinga, nor any reptile in Caatinga, Cerrado, and Pantanal. Arrow up or down above the bars indicate significant excess or deficit, respectively, compared to the expected frequencies (Fisher exact approach, $p < 0.05$)

TABLE 1 Fisher exact tests for differences between classes in the effects of fragmentation metrics on biological responses. In the contingency tables analyzed, class had two categories (amphibians, reptiles) and effects had three categories (negative, neutral, positive). Frequencies of all responses or all metrics were pooled to have sufficient cases

	p-value	Number of cases (*n*)
Single metric on responses pooled		
Habitat loss	0.1899	59
Fragment size reduction	0.3487	70
Habitat degradation	0.5484	68
Matrix contrast	0.1742	52
Metrics pooled on single response		
Richness	0.3514	57
Single-species abundance	0.7287	206

responses did not differ between amphibians and reptiles either (Fisher tests: $p \gg 0.05$, Table 1). Richness showed mostly negative effects, while single-species abundance had more neutral than negative effects (Figure 5). Positive effects on both biological responses were infrequent. The small sample sizes for other responses or other metrics did not allow their statistical analyses (refer Methods).

4 | DISCUSSION

4.1 | Biogeographic and taxonomic bias

Our review demonstrates the existence of marked biogeographic and taxonomic biases in research related to the effects of fragmentation on the megadiverse Brazilian herpetofauna. More than 80% of the studies were conducted in forest biomes (Amazon and Atlantic Forest). This predominance is consistent with the trends reported in fragmentation reviews at both global scale (exclusively focused on forest ecosystems, e.g., Deikumah et al., 2014) and the Brazilian territory (Teixido et al., 2020). The Atlantic Forest is the most densely populated and industrialized biome in Brazil, which has resulted in a historical forest conversion with the highest rates of habitat loss and fragmentation in the country (Rezende et al., 2018). In the Amazon, the overrepresentation of articles is partially explained by the logistics provided by the Biological Dynamics of Forest Fragments Project (BDFFP), the world's largest and longest-running project of habitat fragmentation (Laurance et al., 2011), within which half of the studies in this biome have been carried out.

In non-forest biomes, the low number of studies and consequential flawed knowledge about the effects of fragmentation on herpetofauna may hamper appropriate conservation practices. This is particularly relevant for the Caatinga, a neglected biome (Figure 4). This semiarid region comprises a heterogeneous mosaic of dry woodlands, sand dunes, and mountain isolated forests with notable endemicity levels of amphibians and reptiles (Camardelli & Napoli, 2012; Rodrigues, 2005). However, about 50% of native vegetation has been transformed into agricultural and urban areas and, in such a scenario, further research about the ecology and responses of herpetofauna to fragmentation is needed to better support conservation actions in this biome (Garda et al., 2017). Likewise, more sampling effort should be made in the Cerrado, a priority conservation hotspot with concerning increases of human-induced perturbations such as agriculture and mining, which negatively affects amphibian species assemblage (e.g., Ribeiro et al., 2017; Signorelli et al., 2016). Non-forest biomes are differently affected by fragmentation worldwide when compared to forest biomes (Bond & Parr, 2010). Ultimately, this requires particular conservation frameworks and management strategies for biodiversity (Overbeck et al., 2015).

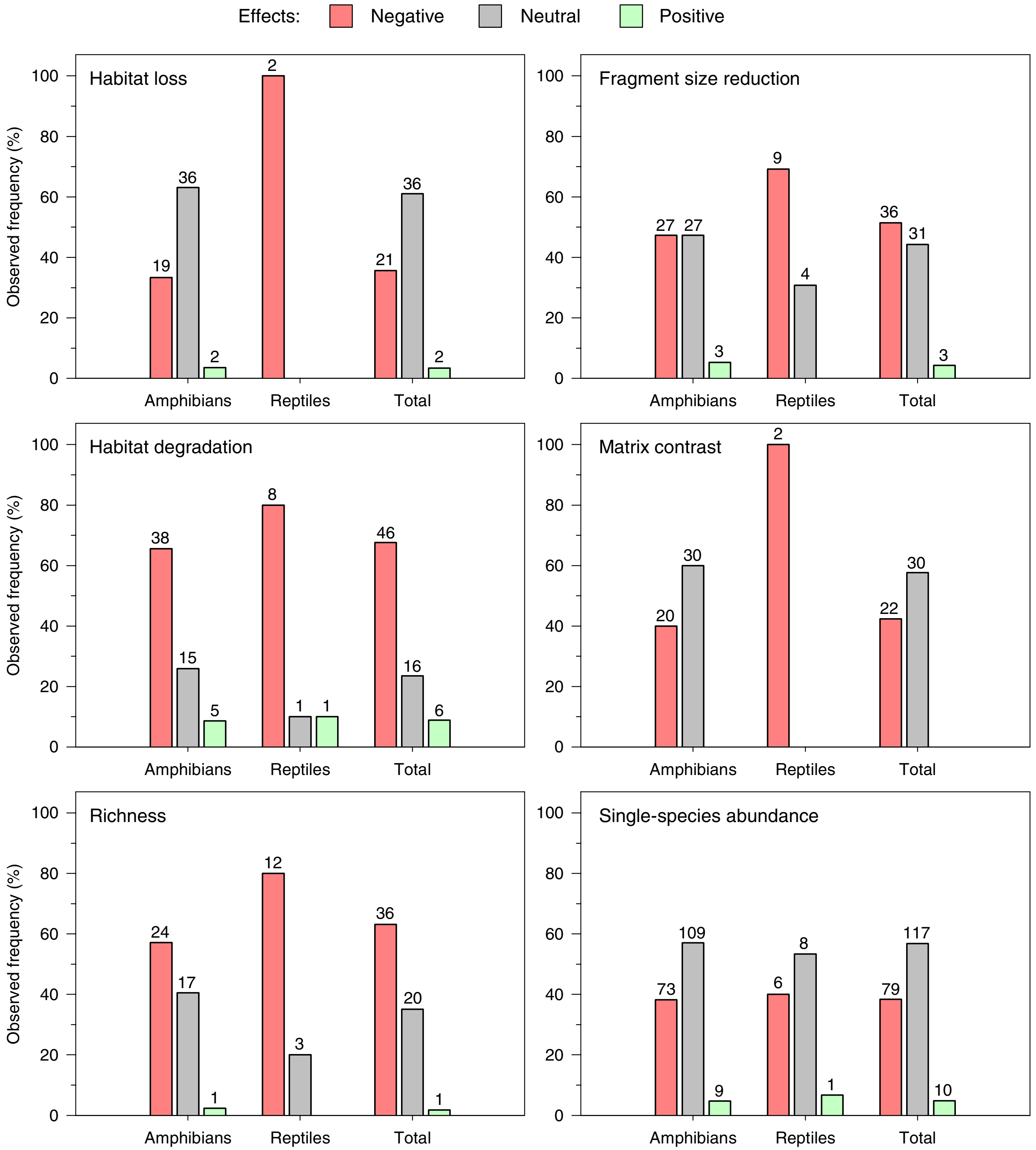

FIGURE 5 Relative frequencies of negative, neutral and positive effects of fragmentation metrics on amphibians and reptiles in Brazil. Total is the sum of frequencies of amphibians and reptiles, which is also shown since there were no significant differences between both taxonomic classes (refer Table 1 for Fisher exact tests). The absolute frequencies are also shown above the bars

We recommend considering the impacts of fragmentation on herpetofauna in non-forest Brazilian biomes.

Reptiles were underrepresented in relation to amphibians, mainly across non-forest biomes. This is mainly due to undersampling of species of Squamata, the largest order of reptiles, and overrepresentation of anuran species. Testudines, however, were disproportionately considered when compared to the other groups. This result actually reflects the fact that 17 out of 32 testudine species were considered in a large-scale single study (Fagundes et al., 2018). Continental testudines, which include land-dwelling tortoises and freshwater turtles, are broadly distributed in Brazil (Fagundes et al., 2018; Rodrigues, 2005). We suggest that similar studies at landscape-level and/or with multiple species of lizards and snakes occupying large distribution areas should be considered to fill information gaps regarding fragmentation-related research on these taxa, at least for multispecies responses in a community context (e.g., Faria et al., 2007; Palmeirim et al., 2017).

The disproportional prevalence of studies with amphibians, especially anurans, may be accounted for the interest aroused by their worldwide decline and the widespread evidence of their vulnerability to human-altered landscapes associated with low dispersal abilities, high disease risks or ontogenetic niche shifts (e.g., Arntzen et al., 2017; Becker et al., 2007; Cushman, 2006; Watling & Braga, 2015). Although anuran species comprise >95% of amphibians in Brazil (Segalla et al., 2019), studies on salamanders (Caudata) and especially the more diverse caecilian group (Gymnophiona) should be recommended. In fact, taxonomy and distribution of some Gymnophiona species are relatively well-studied and these are more abundant than previously assumed, but the threats and conservation status are still poorly known (Maciel & Hoogmoed, 2011). Taken together, our results show that studies quantifying the impacts of fragmentation on herpetofauna in Brazil are biased toward anuran species and were mostly conducted in forest biomes.

4.2 | Effects of fragmentation

An important gap revealed by our review is that few fragmentation metrics and biological responses have been investigated. Firstly, we found a relatively low number of articles considering multilandscape analyses, that are essential to disentangle the effects of habitat loss from fragmentation *per se* (refer Almeida-Gomes et al., 2016 for amphibians in Brazil). Secondly, habitat split was poorly studied, although it is a determinant negative process on richness, abundance, and reproduction of forest-associated amphibians with aquatic larvae (e.g., Becker et al., 2007; Fonseca et al., 2013; Lion et al., 2014). Finally, we detected a predominance of assemblage-level species responses (i.e., abundance and richness). By contrast, many relevant responses associated with ecological processes (e.g., protection against parasites) and individual conditions (e.g., reproduction) were practically overlooked. For example, fragmentation increased the emergence of the fungal parasite *Batrachochytrium dendrobatidis* in amphibian communities of the Atlantic Forest, an infectious pathogen implicated in the global decline of this group (Becker et al., 2016).

Our data for the relationships between metrics and responses revealed two main findings: amphibians and reptiles responded similarly to fragmentation, and the impacts were predominantly negative or neutral. In agreement with our results, studies considering the effects of fragmentation on amphibian and reptile species separately reported similar responses of both groups in Atlantic Forest fragments (Dixo & Martin, 2008; Faria et al., 2007). However, reptiles showed a higher frequency of negative effects than amphibians in a Pampa grassland (Saccol et al., 2017). A recent meta-analysis of global impacts of fragmentation on terrestrial vertebrates has pointed that forest-core reptiles are significantly more sensitive to fragmentation than amphibians (Keinath et al., 2017). Indeed, despite the vulnerability of amphibians to habitat fragmentation and their decline crisis worldwide (Grant et al., 2019), empirical evidence suggests that they are more capable of persisting to anthropogenic changes in landscape than reptile species (Larson, 2014; Mantyka-Pringle et al., 2012; Russildi et al., 2016). In fact, reptiles are increasingly undergoing a pronounced sensitivity to fragmentation across the globe, which may be associated with dispersal constraints, functional and morphological specialization, and limited thermoregulatory responses (Böhm et al., 2013; Keinath et al., 2017; Mantyka-Pringle et al., 2012). However, the gaps in data collection for this class preclude us from taking solid conclusions and further studies would be advisable to provide more reliable estimates of the effects of fragmentation on Brazilian reptiles.

Interestingly, we found that total neutral effects outweighed total negative effects in response to both habitat loss and matrix contrast. This is consistent with a global review by Thompson et al., (2016), who reported a substantial proportion of neutral effects of land-use changes such as agriculture and grazing on amphibians and reptiles, especially due to the presence of species less sensitive to fragmentation. However, habitat loss, along with habitat degradation, have been broadly recognized as the major threats to amphibian and reptile populations (Falaschi et al., 2019; Grant et al., 2019). Moreover, the metrics we analyzed apart from habitat loss (i.e., habitat degradation, fragment size reduction, and matrix contrast) may have confounding and exacerbated effects of fragmentation *per se* (e.g., Chase et al., 2020).

We also found some noteworthy positive effects, especially for fragment size reduction and habitat degradation on amphibians, and when considering single-species abundance. Specific traits of individual anuran species such as dietary behavior and habitat preference may account for these results. For example, some generalist species inhabiting grasslands and open areas respond positively to habitat degradation associated with the introduction of alien plant species in the Pantanal (Moreira et al., 2016). Likewise, smaller fragments in the Atlantic Forest may provide higher availability of leaf-litter invertebrates for amphibian species less sensitive to fragmentation (Steinicke et al., 2018). The reduction in the number and diversity of predators following fragmentation can similarly increase the abundance and survival probability of Neotropical anuran species (Poulin et al., 2001). Finally, some patterns related to fragment size reduction and subsequent edge effects may potentially offer plausible explanations to the positive effects. In this regard, the higher edge length by increasing the number of smaller patches subsequently enables colonization by individuals interspersed in the matrix (Fahrig, 2020; refer also Dixo & Martin, 2008 for the lizard species *Tropidurus torquatus* included in this review).

An important caveat is that our meta-analysis lacks robustness to disentangle the effects of fragmentation between generalist and specialist species. Mounting evidence shows that forest-associated, more habitat-specialist, species of amphibians and reptiles are mostly unable to adapt to perturbations associated with fragmentation of their habitats, while these disturbances could even lead to positive effects on generalist species (e.g., Becker et al., 2007; Falaschi et al., 2019; Keinath et al., 2017; Thompson et al., 2016). These patterns have also been reported among diverse species of the Brazilian herpetofauna, in both forest and non-forest biomes (Almeida-Gomes et al., 2019; Moreira et al., 2016; Palmeirim et al., 2017). Another limitation of our analysis is the possible existence of spatial autocorrelation in the responses of the species included in the same study, which can bias the significance rates of statistical tests (Dale & Fortin, 2009). These biases can be important because single-species abundance was the most considered response and the abundance of the species at the same study site may have spatial dependence. More fine-grained analyses are required to take more solid conclusions about the effects of fragmentation on amphibians and reptiles in Brazil.

In conclusion, the effects of fragmentation on the megadiverse amphibian and reptilian fauna in Brazil are based on major biases of studies mostly conducted in forest biomes and anuran species. Current knowledge about the impacts of fragmentation on these vulnerable groups is insufficient to take well-informed conservation actions. On the bright side, the existence of abundant neutral effects could indicate that some species are not as vulnerable to fragmentation, but more in-depth analyses are required to differentiate the effects between generalist and specialist species. Our findings should stimulate researchers to guide future sampling efforts toward less-studied biomes (i.e., non-forests) and taxonomic groups (e.g., Squamata). Beyond these biogeographic and taxonomic general topics, investigations should be directed toward landscape-scale approaches and responses alternative to occurrence patterns (e.g., ecological interactions, genetics, reproduction), to disentangle and fully understand the effects of habitat loss and fragmentation *per se* on the megadiverse Brazilian herpetofauna.

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AUTHOR CONTRIBUTIONS

Alberto L. Teixido: Conceptualization, Methodology, Validation, Formal Analysis, Investigation, Data Curation, Writing – Original Draft, Writing – Review and Editing, Visualization, Supervision, and Project Administration. **Heivanice Sehn:** Data Curation, Writing – Review and Editing, and Visualization. **Luis G. Quintanilla:** Conceptualization, Methodology, Formal Analysis, Data Curation, Writing – Original Draft, and Writing – Review and Editing. **Stela R. A. Gonçalves:** Methodology, Data Curation, and Writing – Review and Editing. **Gilberto J. Fernández-Arellano:** Data Curation and Writing – Review and Editing. **Wesley Dáttilo:** Conceptualization, Data Curation, and Writing – Review and Editing. **Thiago J. Izzo:** Data Curation, and Writing – Review and Editing. **Viviane M. G. Layme:** Data Curation, and Writing – Review and Editing. **Leonardo F. B. Moreira:** Conceptualization, Methodology, Data Curation, Writing – Original Draft, and Writing – Review and Editing.

DATA AVAILABILITY STATEMENT

Data are available from the Figshare Digital Repository https://doi.org/10.6084/m9.figshare.14110415.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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