Regional deforestation drives the impact of forest cover and matrix quality on primate species richness

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ABSTRACT

Land-use change transforms natural ecosystems, threatening species persistence worldwide. There is increasing evidence that forest loss negatively affects forest-dependent species and matrix quality can favor species maintenance, whereas forest fragmentation has mainly null or positive effects on species. However, the effects of these landscape attributes may depend on the level of regional deforestation. Here, we assess the effects of forest cover, matrix quality, and forest fragmentation (forest patch density) on primate species richness in 92 landscapes in Brazil. We grouped landscapes by their regional deforestation level into low, intermediate, high, and severe deforestation. The effects of landscape attributes varied depending on the level of regional deforestation. Forest loss decreased the proportion of primate species in the four regional deforestation levels, but this association was more important in the low, intermediate and high regional deforestation levels. Matrix quality was positively related to the proportion of primate species in three regional deforestation levels and this association was more important in the high regional deforestation level. Yet, matrix quality decreased the proportion of primate species in the severe regional deforestation level. Forest fragmentation had no clear effects across all deforestation levels. Therefore, different conservation strategies should be prioritized under distinct scenarios. Preventing forest loss is needed in all regions. Increasing matrix quality has positive effects on species richness, especially in highly deforested regions (30–15% remaining forest cover). Finally, as fragmentation had no clear effects on the proportion of primate species, landscape composition should be prioritized in conservation planning over landscape configuration.

1. Introduction

Human activities convert natural ecosystems into anthropogenic landscapes, threatening species persistence (Song et al., 2018; Taubert et al., 2018). This situation is particularly dramatic in the tropics (Taubert et al., 2018), where less than 50% of forests remain (Lewis et al., 2015). Understanding the impact of anthropogenic landscapes on species (e.g., occurrence, abundance, and richness) is key to proposing effective management and conservation strategies, but their effects are still unclear (Arroyo-Rodríguez et al., 2020). This is mainly because most studies are performed at the patch scale or at a single spatial scale when using a landscape perspective without assessing the 'scale of effect' (Galán-Acedo et al., 2019; Jackson and Fahrig, 2015), which can lead to overlooked responses of species to landscape attributes. Additionally, species' ecological responses to anthropogenic landscapes may be modulated by landscape attributes at larger spatial scales, such as the amount of habitat available within a given region (Betts et al., 2019; Pardini et al., 2010; Villard and Metzger, 2014). Unfortunately, most

studies are carried out in a single region, limiting our ability to discern if results can be generalized among regions with similar habitat amounts.

Increasing regional deforestation reduces the dispersal distance of forest-specialist species in regions with less habitat available (Delattre et al., 2013). Landscapes embedded in these regions have lower levels of connectivity, thereby imposing greater risk of dispersal mortality (Delattre et al., 2013) and affecting species-landscape interactions (Galán-Acedo et al., 2021; San-José et al., 2020). For instance, landscape attributes such as matrix openness and edge density have a greater effect on the abundance and richness of wind-dispersed seeds in more deforested (26% remaining forest cover) compared to more conserved (50%) regions (San-José et al., 2020). Additionally, changes in areas with less than 30% of habitat remaining have stronger effects on the abundance of birds and non-volant mammals than in more conserved areas (Andrén, 1994). Therefore, regional habitat amount may be key when examining the effects of landscape attributes on species' ecological responses.

There is strong evidence that deforestation is the main driver of global terrestrial species decline (Fahrig, 2003; Newbold et al., 2016). For forest-dwelling species forest loss limits resource availability and connectivity, increasing the incidence of disease, competition, and stress, thereby decreasing species abundance and richness (Fahrig, 2003; Marsh and Chapman, 2013). Nonetheless, the magnitude of forest loss' effects on species may depend on the regional deforestation level (Galán-Acedo et al., 2019c, 2021). For example, forest loss had a greater effect on howler monkey (*Alouatta palliata* and *A. pigra*) abundance in regions with intermediate and high deforestation (50 and 15% forest cover remaining) compared to severely deforested regions (5%, Galán-Acedo et al., 2021). Yet, given the lack of studies assessing the effect of forest cover in regions with different degrees of deforestation, our understanding on this topic is far from complete.

In human-modified landscapes, forest patches are surrounded by a matrix of anthropogenic land covers (e.g., cattle pastures or crops) that differ in their functionality for different species (Fahrig et al., 2011). Species may use the matrix for resting, travelling, and/or foraging (Ferreira et al., 2018; Galán-Acedo et al., 2019b), influencing a variety of ecological responses, including animal movement or population persistence (Fahrig et al., 2011). How species respond to these matrices may depend on their ecological traits, such as body mass or mode of locomotion (Ferreira et al., 2018; Galán-Acedo et al., 2019b), habitat preferences (Devictor et al., 2008), and the degree of regional deforestation (Galán-Acedo et al., 2021; San-José et al., 2020). For instance, species-matrix interactions may be stronger in more deforested regions than in relatively conserved regions (San-José et al., 2020), because species may be 'forced' to use the distinct matrix types to disperse or find food (Dunning et al., 1992; Galán-Acedo et al., 2019b).

Forest fragmentation is also a consequence of land-use change, but its effects on species remain unclear (Fahrig et al., 2019; Fletcher et al., 2018). A review of forest fragmentation *per se* effects, defining fragmentation as the breaking apart of the remaining habitat (e.g., number or density of patches in the landscape), found mainly positive or null effects on species' responses (Fahrig, 2017). Positive effects of fragmentation are mainly related to decreasing mean inter-patch distance with increasing patch density, potentially increasing dispersal opportunities in the landscape and resource availability through landscape complementation or supplementation (Dunning et al., 1992). Contrastingly, other studies have highlighted additional negative effects of fragmentation (Fletcher et al., 2018). Understanding the effects of landscape attributes is not trivial as it can entail prioritizing landscape composition (i.e., number and quantity of land covers in a landscape) over landscape configuration (i.e., the spatial disposition of land covers in a landscape) for species' maintenance. Increasing our knowledge on the effects of forest cover, matrix quality and forest fragmentation is therefore urgently needed, particularly for species threatened with extinction, such as primates.

Primates are of critical importance in ecosystem functioning, acting as herbivores, seed dispersers, pollinators, predators and prey, and even ecosystem engineers (Andresen et al., 2018; Estrada et al., 2017). However, habitat conversion due to agriculture and resource extraction is the main threat facing primate species (~66% of primate species are threatened with extinction, IUCN, 2021). As most primates are forest-dependent species (Galán-Acedo et al., 2019a), forest conversion restricts their distribution and abundance in anthropogenic landscapes. The loss of primate species will likely have long-term negative consequences on plant diversity, forest regeneration, and ecosystem resilience (Andresen et al., 2018; Culot et al., 2017; Marsh and Chapman, 2013). Unfortunately, our understanding of how anthropogenic landscape changes affect the persistence of primate populations is still not clear (Galán-Acedo et al., 2019).

Here, we assessed the effects of two landscape composition metrics (percentage of forest cover and matrix quality) and one landscape configuration metric (forest patch density) on the proportion of primate species. We assessed 92 forest fragments in Brazil in four regional deforestation levels (low, intermediate, high, and severe deforestation). In addition, we used a multi-scalar approach to identify the 'scale of effect' (i.e., the landscape size that yields the strongest species responses to a particular landscape attribute; Jackson and Fahrig, 2012). We expected that responses of the proportion of primate species to changes in landscape structure would depend on the regional habitat amount (Galán-Acedo et al., 2019; Galán-Acedo et al., 2021; San-José et al., 2020). Forest cover determines the amount of habitat available for these species as all Neotropical primates are arboreal and forest-dependent (Galán-Acedo et al., 2019a). We predicted that the percentage of forest cover would be positively related to species richness, particularly in the higher regional deforestation levels. As primates can use the matrix (e.g., arboreal crops or live fences) for travelling, resting, and/or foraging (Galán-Acedo et al., 2019b), we expected the proportion of primate species to increase with the proportion of matrix types in the landscape that are similar to their original habitat (high matrix quality). This relationship should be higher in regional levels with intense deforestation. Finally, given that habitat fragmentation has been shown to have largely positive or null effects on species (Fahrig, 2017), we predicted positive or null effects of forest fragmentation on species richness across all regional deforestation levels.

2. Methods

2.1. Data compilation

We compiled a database of scientific articles and theses by performing a search and selecting literature that reported primate species richness in forest patches in Brazil (Fig. 1) using SCOPUS (www.scopus.com) and Google Scholar (https://scholar.google.com/). We selected Brazil because this country has the highest primate diversity in the world (131 out of 515 species, https://icmbio.gov.br/) and deforestation rates remain high, particularly in the Atlantic Forest, Cerrado and part of the Amazon Forest (Estrada et al., 2018). We carried out the search on April 22nd 2020 for literature containing the following terms: [(primate* OR monk*) AND ('richness' AND/OR 'diversity' AND/OR 'community' AND/OR 'presence' AND/OR 'occurrence' AND/OR 'fragment' AND/OR 'patch' AND/OR 'fragmentation' AND/OR 'landscape')]. Additionally, we included data on species richness in forest patches from the ATLANTIC-PRIMATES database (Culot et al., 2019).

We selected studies performed in forests immersed in fragmented landscapes to adequately assess the effects of landscape attributes on the proportion of primate species. We only included studies that reported precise geographic coordinates (<500 m error) and that disclosed sampling effort (km walked). In total, we selected 32 studies reporting primate richness in forest patches. We did not find studies in Central Brazil and thus, the geographic distribution of the studies across Brazil is not well balanced.
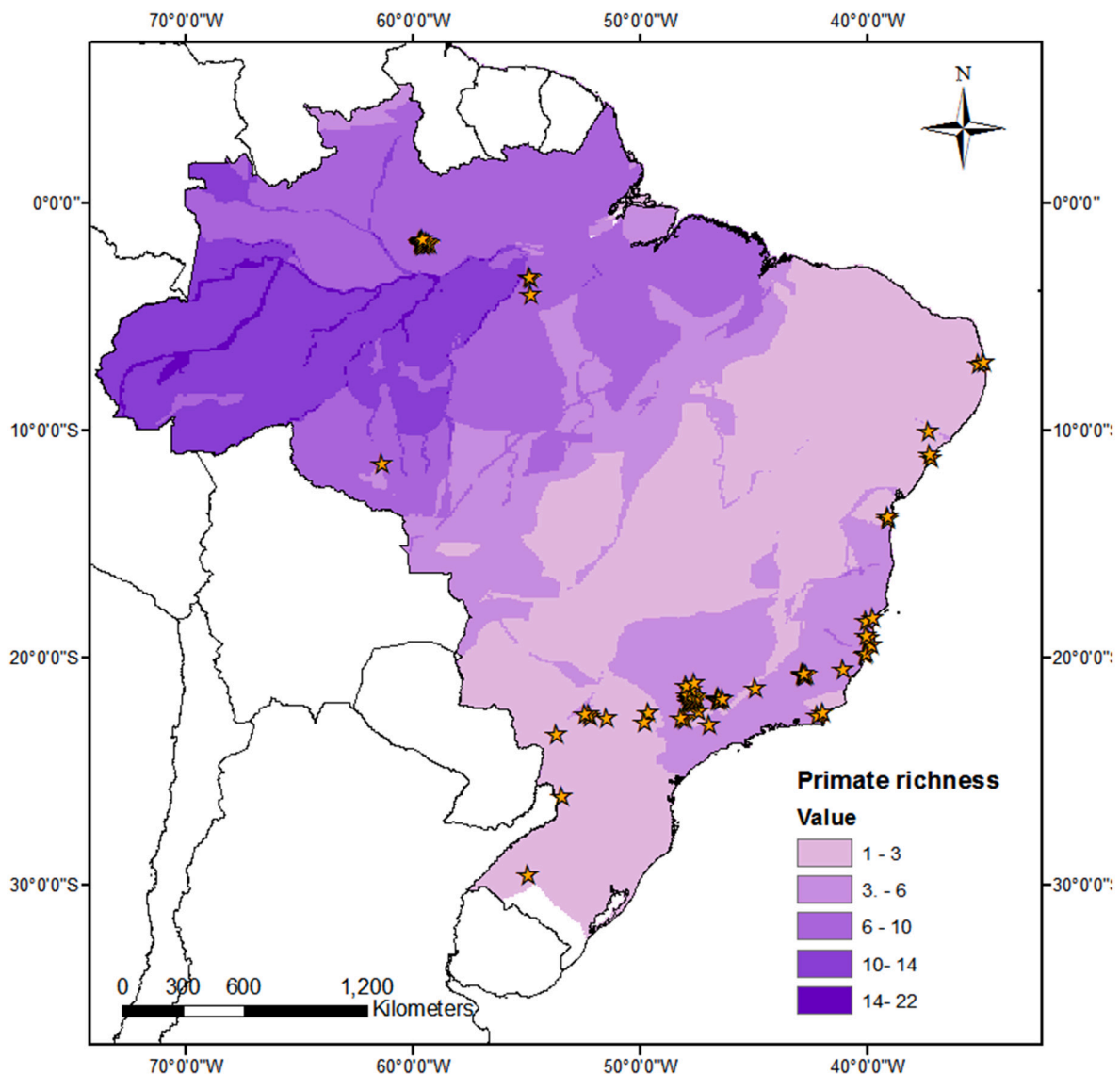
Fig. 1. Location of the study regions in Brazil. The location of each study patch is marked by a yellow star. The pattern of primate richness based on Pimm et al. (2014) is illustrated in purple. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.2. Response variable: proportion of species richness

We defined our response variable as the proportion of species of the local assemblage present in a patch relative to its respective regional species richness to control for differences in regional species richness across the selected forest patches (range = 2–9). This proportion ranges from 0, where the forest patch is devoid of all primates, to 1, where all species expected to occur in the region are present in the local assemblage. We extracted regional species richness from the original publications, when available, or directly requested this information from the original authors of the studies. Additionally, we revised the regional primate richness based on the record of each taxon prepared by experts during the national workshop for the assessment of the risk of extinction of Brazilian primates (https://www.icmbio.gov.br/cpb/index.php/primatas-brasileiros) and Luna et al. (2018). We did not include nocturnal primates because studies did not perform nocturnal surveys. Finally, whenever hybrids were reported, we recorded the presence of both parental species.

2.3. Landscape attributes

We measured landscape attributes based on a 30-m resolution map of Brazil provided by MapBIOMAS (collection 5.0, Souza et al., 2020). For each study site, we used the map corresponding to the year when fieldwork was conducted (from 1995 to 2017). We extracted all metrics using ArcGIS 10.5 software with the Patch Analyst extension (Rempel et al., 2012).

We measured two landscape composition metrics (percentage of forest cover and matrix quality) and one landscape configuration metric (forest patch density). We calculated the amount of forest as the percentage of forest cover in a landscape. Forest cover was based on the following MapBIOMAS categories: forest, natural forest, forest formation, forest plantation and mangroves (Souza et al., 2020). To estimate matrix quality, we ranked the quality of all non-forest land-cover types and calculated a matrix quality index (Galán-Acedo et al., 2019c; Garmendia et al., 2013). Following other studies (da Silva et al., 2015; Galán-Acedo et al., 2019b, 2021; Kempf, 2009), we ranked the quality of different land covers in the matrix based on our understanding of the ability of Neotropical primates to use them for feeding and/or travelling: 0.5 (water bodies), 1 (open areas), 2 (human settlements), 3 (annual

crops), and 4 (arboreal crops). We included water bodies because primates may use them for drinking or even swimming to move between habitat patches (Kempf, 2009). Open areas refer to pastures, grassland formations, rocky outcrops, other non-forest natural formations, beaches and dunes, mining, and other non-vegetated land categories (Souza et al., 2020). Human settlements were given a higher score than open areas as infrastructure associated with settlements (e.g., buildings and powerlines) may facilitate travel for arboreal primates and home-gardens can provide food sources in urban areas (Chaves and Bicca-Marques, 2017; Corrêa et al., 2018). We calculated the matrix quality index as follows: [(0.5 × % water bodies) + (1 × % open areas) + (2 × % human settlements) + (3 × % annual crops) + (4 × % arboreal crops)]. This index varies between 50 (100% of the matrix is composed of water, lowest quality matrix) and 400 (100% composed of arboreal crops, highest quality) and is therefore positively related to resource availability in the matrix (Galán-Acedo et al., 2019c, 2021; Garmendia et al., 2013). Finally, we measured fragmentation as forest patch density, i.e., the number of isolated forest patches ($\geq$ 1 ha) within the landscape divided by the total landscape area (n/ha). This metric of forest fragmentation is widely used (Fahrig, 2017).

2.4. Selection of the appropriate spatial scale

We identified the scale of effect, which is the landscape size that yields the strongest species' responses to a particular landscape attribute (Jackson and Fahrig, 2012) to assess the effect of landscape attributes on the proportion of primate species (Appendix S1). Using regression analyses, we tested 11 spatial scales, increasing the radius of the circular landscapes (measured from the center of the studied area or from the study patch coordinate reported by the authors) in 200-m increments. The smallest radius was 500 m and the largest was 2500 m (with no overlap between the radii of adjacent landscapes). To avoid overlap between landscapes, we excluded those study patches in which the biggest landscape (2500-m radii buffer) overlapped with another study landscape. When landscapes overlapped, we included the landscapes that lead to the highest number of non-overlapping landscapes in our analyses (from 1 landscape to 16 non-overlapping landscapes in each study). Following Jackson and Fahrig (2015), we chose the largest landscape to measure ~2000-ha, which is >140% larger than the home range of *Sapajus xanthosternos* (~846 ha; Galán-Acedo et al., 2019a), the species with the largest home range of all our studied primates.

2.5. Regional deforestation level

We created a 10,000-ha buffer from the center of each study site as a proxy of 'regional' deforestation. We chose this buffer size as it is >1100% larger than the maximum home range of *Sapajus xanthosternos* and has been used in other publications (Pardini et al., 2010). We then extracted the percentage of forest cover of each buffer and grouped landscapes depending on their regional deforestation level. Similar to Galán-Acedo et al. (2021), we classified the regional deforestation levels into low deforestation (from 100 to 60% remaining forest cover), intermediate deforestation (60–30%), high deforestation (30–15%), and severe deforestation (15 > 0%).

2.6. Statistical analyses

We used the software R 3.0.1 for all analyses (R Core Team, 2013). Before entering predictor variables into the models, we used the variance inflation factor (VIF) to assess collinearity among them using the 'car' package (Fox et al., 2012). We found significant collinearity among landscape attributes in the intermediate deforestation region at the best scale (scale of effect). Therefore, we used the value of matrix quality at the second-best scale (Table S1). In general, a VIF < 4 indicates no collinearity, a VIF > 4 indicates possible collinearity, and a VIF > 10 indicates severe collinearity (Neter et al., 1996). Accordingly, there was

no collinearity between our predictor variables (VIF < 3.2). In the low deforested region the scale of effect was too small to assess fragmentation (500-m radii) and most landscapes did not present fragmentation. We therefore used the second-best scale (700-m radii) in our analyses.

We assessed the effects of landscape attributes (predictor variables) on the response variable (proportion of primate species) for each regional deforestation level via generalized linear models with a binomial error distribution and a logit link function using the package 'glmulti' (Calcagno and de Mazancourt, 2010). We controlled for sampling effort (km walked in each study patch) in the models (see Appendix S2).

We used an information-theoretic approach and multi-model inference to assess the relative effect of each predictor on each response variable (Burnham and Anderson, 2002). We constructed 16 models representing all combinations of the four explanatory variables (three landscape attributes and sampling effort) plus the null model. We computed Akaike's information criterion corrected for small samples (AICc) for each model, and we ranked the models from best to worst. We used Akaike weights (w_i) to evaluate the importance of each predictor and produce model-averaged parameter estimates (Anderson, 2007). We summed w_i of ranked models until the total was >0.95 (Whittingham et al., 2005). The set of models for which Σw_i is 0.95 represents a set that has 95% probability of containing the true best-fitting model (Whittingham et al., 2005). Following Crawley (2007), we estimated the goodness-of-fit of the models as: (deviance explained by the complete model/deviance explained by the null model) x 100.

3. Results

A total of 40 primate species inhabited 87 (95%) of the 92 studied forest patches in the four regional deforestation levels (Table 1, Appendix S3). Our study included more landscapes in the high regional deforestation level (n = 33) compared to the other regional deforestation levels. All regional deforestation levels included landscapes where all primate species of the region were found (i.e., richness = 1). Mean (proportional to the expected) primate richness ranged from 0.47 in the high regional deforestation level to 0.76 in the low regional deforestation level (Table 1).

Considering all landscape sizes, the percentage of forest cover in the landscape was higher in the low regional deforestation level (mean = 82.9%, range = 0.3–100%), followed by the intermediate regional deforestation level (mean = 63.1%, range = 9.3–100%), the high regional deforestation level (mean 44.4%, range = 3.8–100%), and the severe regional deforestation level (mean = 26.5, range = 0.4–100%) (Appendix S4). In all regional deforestation levels (low, intermediate, high and severe), the mean percentage of forest cover was higher in the smallest landscape size (500-m radius) and gradually decreased because of the decreasing influence of focal patch area on landscape forest cover. Mean matrix quality was highest in the high regional deforestation (mean = 123, range = 50–400), and lowest in the intermediate regional deforestation level (mean = 100, range = 50–400). Forest patch density remained relatively constant in the four regional levels. The high

Table 1
Characteristics of the four regional deforestation levels. Total and range values (in parentheses) per patch are indicated.

	Low deforestation	Intermediate deforestation	High deforestation	Severe deforestation
Number of patches	*19*	*20*	*33*	*20*
Occupied patches	19	19	29	20
Mean patch proportion of primate species	0.76 (0.43–1)	0.62 (0–1)	0.47 (0–1)	0.65 (0.13–1)

regional deforestation level was the regional level with the highest patch density (mean = 0.02 n ha^{-1} range = 0.007–0.07 n ha^{-1}) and the low regional deforestation level showed the lowest forest patch density (mean = 0.01 n ha^{-1}, range = 0.006–0.05 n ha^{-1}).

The complete models (those including the three landscape attributes) explained between 33% and 48% of the variance in the proportion of primate species due to the effects of forest cover, matrix quality and/or forest fragmentation (Figs. 2, 3). In the low regional deforestation level, the proportion of primate species was mainly and positively associated with forest cover ($\Sigma w_i = 0.5$, Figs. 2a, 3a). In the intermediate regional deforestation, the proportion of primate species was positively related to forest cover ($\Sigma w_i = 0.4$, Fig. 2b) and was associated with forest fragmentation ($\Sigma w_i = 0.4$, Figs. 2b, 3b). However, in the case of forest fragmentation, the unconditional variance of this variable was greater than the model-averaged parameter estimate; that is, parameter estimates were widely spread out around the mean. This means that forest fragmentation effects on the proportion of primate species are highly variable and cannot be interpreted as purely positive, negative or null, thereby preventing interpretation of the variable's effects as positive, negative, or null. This association between fragmentation and the proportion of primate species was constant in all regional deforestation levels. In the high regional deforestation level, the proportion of primate species was mainly and positively related to matrix quality ($\Sigma w_i = 0.9$, Figs. 2c, 3c) but also to forest cover ($\Sigma w_i = 0.4$). Finally, in the severe regional deforestation level, the proportion of primate species was mainly and negatively related to matrix quality ($\Sigma w_i = 0.7$, Figs. 2d, 3d) and positively associated with forest cover ($\Sigma w_i = 0.3$).

4. Discussion

In this study, we assessed the effects of forest cover, matrix quality, and forest fragmentation on primate species richness in four regional deforestation levels. As expected, forest cover was positively related to the proportion of primate species across all regional deforestation levels, but this association was of greater relative importance in the low, intermediate, and high regional deforestation levels. Matrix quality was positively related to the proportion of primate species in the first three regional deforestation levels but was particularly important in the high regional deforestation level. Yet, contrary to our expectations, matrix quality was negatively related to the proportion of primate species in the severe regional deforestation level. Finally, forest fragmentation had undefined effects on the proportion of primate species in all regional deforestation levels. Therefore, we found support for the hypothesis that the responses of primate assemblages to changes in landscape structure depend on the regional context, particularly the regional deforestation level. In addition, our results suggest that conservation actions should focus on managing landscape composition (e.g., through forest preservation and restoration) over landscape configuration (e.g., through increasing landscape connectivity).

Forest cover determines the amount of habitat available for arboreal species and is positively related to landscape connectivity and resource availability (Fahrig, 2013, 2003; Marsh and Chapman, 2013). We found that forest loss decreased primate species richness regardless of the regional deforestation level. This finding supports the idea that forest loss, instead of forest fragmentation, is the major driver of species decline in anthropogenic landscapes (Fahrig, 2003). Similarly, other studies have found that forest loss decreases primate richness (Rabelo et al., 2017; Urquiza-Haas et al., 2011). In particular, forest cover was the most important landscape attribute explaining the proportion of primate species in the more conserved regional levels (low and intermediate deforestation). Other studies have found similar results with other response variables (Galán-Acedo et al., 2021; San-José et al., 2020). For instance, Galán-Acedo et al. (2021) found that forest cover was strongly and positively associated with howler monkey abundance in the most conserved region (50% forest cover remaining). Likewise, San-José et al. (2020) found that forest cover was more positively related to seed abundance and richness in more conserved regions. In regions with greater amounts of remaining habitat, resources can be found in the prevailing forest. Arboreal and forest-dependent species' responses (e.g., species richness) may therefore depend largely on the amount of habitat available as species may not need to use other forest fragments or the matrix to meet their needs (Dunning et al., 1992).

As expected, matrix quality was positively related to the proportion of primate species at all levels of regional deforestation, except in the most severe level. Primate persistence in anthropogenic landscapes may benefit from some degree of supplemental use of the matrix for resting, travelling, feeding and/or drinking (Ferreira et al., 2018; Galán-Acedo et al., 2019b) (Dunning et al., 1992). Landscape supplementation may also contribute to the shallower species-area relationships (less extinction driven) associated with higher matrix quality, as found by Reider et al. (2018). Interestingly, we found that the effect of matrix quality was relatively more important in the high deforestation level (30–15% forest cover remaining), suggesting that matrix composition plays important roles in highly deforested regions. In these regions primates may rely
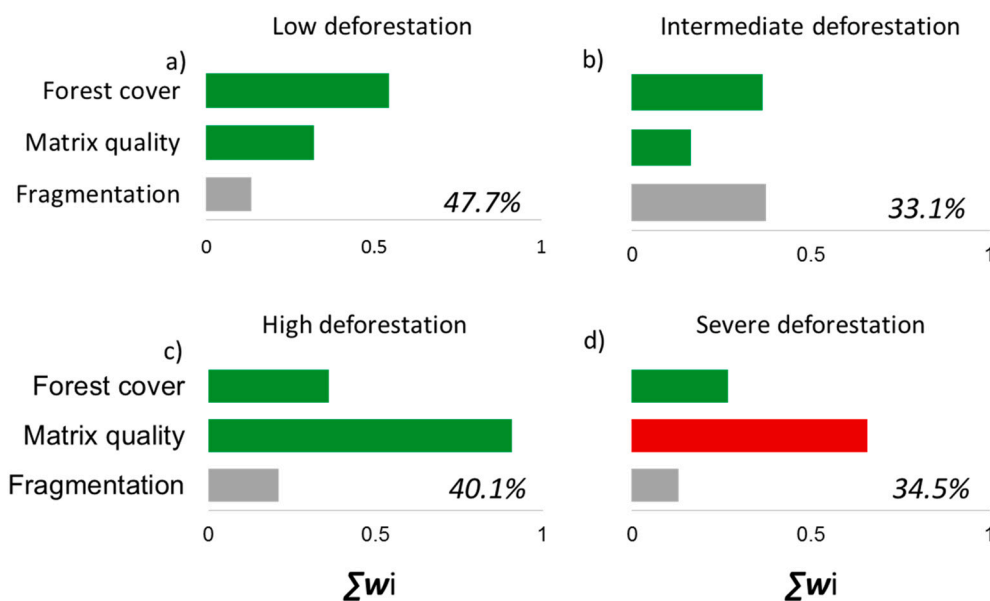

Fig. 2. Predictor variables included in the set of models for which Σw_i was 0.95, for primate richness. We assessed four regional deforestation levels: low (from $100 > 60\%$ remaining forest cover), intermediate ($60 > 30\%$), high ($30 > 15\%$) and severe ($15 > 0\%$). The importance of predictor variables is represented by bar length, which corresponds to the sum of Akaike weights (Σw_i). The percentage of deviance explained by each complete model is indicated in each panel. A green bar represents a positive response to the predictor, the red bar represents a negative response, and the gray bar show that the unconditional variance was higher than the model-averaged parameter estimate, indicating that the parameter can have positive, negative or null effects. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
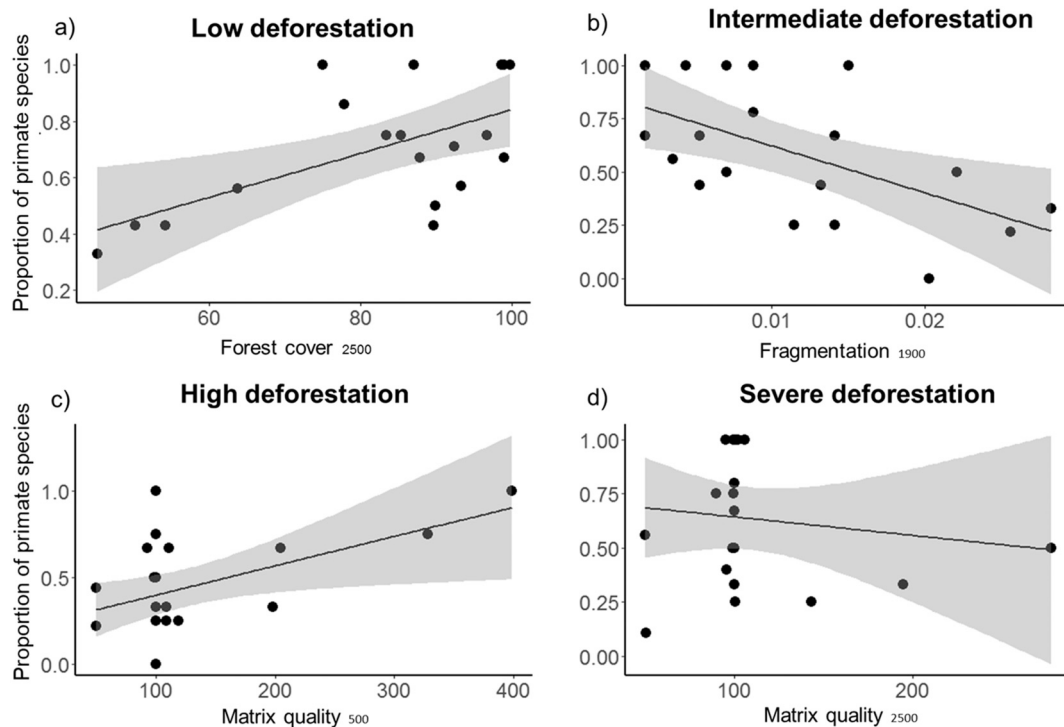
Fig. 3. The most important relationship between the proportion of primate species and landscape predictors in each deforestation level. Only the best models are included. Points represent the study sites in each deforestation level. The black line indicates the predicted estimates from the binomial regression using a generalized linear model and gray areas show 95% confidence intervals. Numbers on the x-axis shows the scale of effect detected for each landscape variable (See Appendix S1).

more on elements available in the matrix (Anderson et al., 2007; Galán-Acedo et al., 2019b).

Surprisingly, matrix quality was negatively related to the proportion of primate species in the severe regional deforestation level (15 > 0% forest cover remaining). This is consistent with the findings of Galán-Acedo et al. (2021), where matrix quality was negatively associated with howler monkey abundance in high deforested regions (17% forest remaining). As high-quality matrices (e.g., crops, urban areas) are associated with high human presence (Corsini et al., 2019), primates in severely deforested regions may be more exposed to hunting, dog predation, road accidents, or electrocutions (Corrêa et al., 2018; Petrucci et al., 2009), thereby decreasing the proportion of primate species. Alternatively, high-quality matrices have higher availability of arboreal covers, such as arboreal crops, which can increase landscape connectivity and offer dispersal opportunities across the landscape for arboreal species, particularly when the amount of forest is severely diminished (Anderson et al., 2007; Galán-Acedo et al., 2019b). Therefore, some primate species (particularly *Callithrix* sp. and *Sapajus* sp.) may leave forest patches to use resources in the matrix. This may also explain why we found the second highest mean patch proportion of primate species in the severe regional deforestation level but a lower number of species in patches surrounded by higher quality matrices. Still, given the scarce information on the effects of matrix quality on primate species' responses in severely deforested regions, more studies are required to understand the mechanisms behind these negative effects and to propose adequate management strategies.

The relatively high proportion of primate species in the severe regional deforestation level was also surprising. This finding does not support the extinction threshold hypothesis, which predicts that species richness can decrease sharply in areas with <30% of remaining habitat (Andrén, 1994; Swift and Hannon, 2010). Persistence of primate populations in severely deforested regions may be attributed to the high degree of behavioral flexibility exhibited by some Neotropical primates (e.g., marmosets, howler and capuchin monkeys; McKinney, 2015). For instance, these species can reduce their dispersal rates, alter the timing

of their activities, or change their diets (Arroyo-Rodríguez and Dias, 2010; Bicca-Marques, 2003; Gaynor et al., 2018), enabling them to persist in anthropogenic landscapes in the short-term. However, individuals may accumulate in forest patches leading to over-crowding (Laurance, 1994; Link et al., 2010), which can have negative consequences on the long-term maintenance of their populations (Bicca-Marques et al., 2020). High population densities are related to reductions in resource availability, changes or increments in inter- and intra-specific food competition (Arroyo-Rodríguez and Dias, 2010; Rose et al., 2003), and even inbreeding (Caperos et al., 2011). Alternatively, the relatively high proportion of primate species in the severe regional deforestation level could suggest an extinction debt (Tilman et al., 1994), as primates have long lifespans (~10 to 50 years) and slow life-histories (Jones et al., 2009). However, we did not account for the time since deforestation in this study. Studies exploring extinction debt in different regional contexts are therefore needed.

Unlike forest cover and matrix quality, forest fragmentation (i.e., density of patches in the landscape) had no clear effects on the proportion of primate species in all regional deforestation levels. Given that we could not determine if forest fragmentation had a positive, negative, or null effect, interpretation requires caution (Burnham and Anderson, 2002). Similar results of no clear effects of fragmentation on species' responses have been found in landscape studies of spider monkey encounter rates (Galán-Acedo et al., 2019), sapling assemblages (Arasa-Gisbert et al., 2021) and tree seed dispersal (San-José et al., 2020). On the other hand, Fahrig (2017, 2003) found that the effects of habitat fragmentation *per se* on species are mainly positive. Positive effects of habitat fragmentation have been associated with increased landscape connectivity, which facilitates species dispersal across the landscape as well as providing opportunity for landscape complementation and supplementation (Dunning et al., 1992). In contrast, other authors consider habitat fragmentation as having mainly negative effects on species (Fletcher et al., 2018; Haddad et al., 2015). However, this argument is largely based on extrapolations from studies assessing the effects of patch attributes such as patch size, isolation, or edge effects on

species. Given that habitat fragmentation is a landscape process, it needs to be evaluated at the landscape scale (Fahrig, 2003, 2017; Fahrig et al., 2019). At the landscape scale, negative effects of habitat fragmentation have mainly been related to greater exposure to threats such as hunting or illegal trade (Fahrig, 2017). Our study supports the idea that the effects of fragmentation *per se* (a landscape configuration metric) on species are relatively weak (Fahrig, 2003, 2017; Fahrig et al., 2019) whereas forest loss has pervasive negative impacts (Fahrig, 2003; Newbold et al., 2016; Watling et al., 2020). However, assessing the effect of other landscape configuration variables (e.g., mean patch isolation) is needed to draw stronger conclusions about the effects of landscape configuration on primate richness.

Finally, we note that our study has some limitations. First, the geographic distribution of the study sites across Brazil is unbalanced. For example, we did not find study sites in Central Brazil. However, if the regional deforestation level influence the effects of landscape structure on species we would expect to find similar results in Central Brazil. Still, such geographic unbalance could imply additional biases as some Brazilian primate species were not included in this study. Second, we grouped landscapes from different geographical regions together and, as a result, we did not consider the effect of local and regional variables such as hunting pressure, forest patch age, land-use history, or time since forest loss. These variables can have important effects on primate richness. Nonetheless, our study offers key insights into how the remaining regional forest amount influences primate richness. We call for caution when generalizing landscape-scale results to different regional contexts but highlight that these results could be extrapolated to regions with similar habitat amounts.

5. Conservation implications

We highlight that species responses to changes in forest cover and matrix quality depend on the remaining regional forest amount. As forest fragmentation showed no clear effects across all regional deforestation levels, we suggest that conservation management plans should focus on landscape composition strategies, such as preventing forest loss and increasing forest cover (restoration; Chapman et al., 2020). The spatial configuration of the remaining forest cover is relatively less important, but other metrics should be explored. Improving matrix quality with arboreal elements can be highly valuable for arboreal mammals, especially in highly deforested regions. Although forest preservation and restoration should be implemented in all regions, it should be prioritized in severely deforested regions. However, given our limited knowledge on the influence of the regional context on the effects of landscape structure on species, future research comparing more regions with different levels of deforestation is needed. This information is important to develop targeted conservation and scientific actions that can help to stop the decline of primates and other ecologically relevant species in anthropogenic landscapes.

Author statements

CGA developed the idea of the study and collected the data. CGA and DS analyzed the data. All authors made substantial contributions to the intellectual content, interpretation of results and editing of the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2021.109338.

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