

# Evaluating the Brazilian system of strictly protected areas using owls as an indicator group

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## Abstract

**AIM** To set or assess conservation and management efforts based on the knowledge of the total biodiversity is unrealistic. For such a reason, the identification of priority areas based on biodiversity hotspots determined through indicator groups has become a common approach. This requires a crystal-clear knowledge of the taxonomy and distribution of such indicator groups, which in the Tropics can be troublesome, especially for rare or secretive taxa. Thus, we assessed the potential distribution of 21 species and 21 subspecies of Brazilian Strigidae through Species Distribution Modelling (SDM) based on a Maximum Entropy approach. **LOCATION** Brazil. **METHODS** We (1) gathered and filtered occurrences data for Brazilian Strigidae, (2) generated SDMs for each species and subspecies, (3) evaluated the niche similarity among subspecies, (4) built up species' richness maps, and (5) contrasted such information to the strict protection areas in Brazil. **RESULTS** With 81% of the Brazilian species recorded, both the Atlantic Forest and the Cerrado have the highest richness, followed by the Amazonia (67%), Pampa (62%), Caatinga (57%) and Pantanal (48%). However, the comparison of the recorded and predicted richness suggests overall incomplete inventories, especially in the Caatinga and Pantanal. On the other hand, subspecies showed marked niches divergencies, suggesting that the recognized Strigidae species richness is underestimated in Brazil. Cerrado and Atlantic forest are the most threatened biomes, with preservation areas relatively small and sparse. **MAIN CONCLUSIONS** We demonstrated that the situation of Brazilian Strigidae involves an underestimated species richness, within an inadequate framework of protected areas, in a megadiverse Country characterized by high rates of habitat transformations. Thus, our study is a hurrying call to explore owl lineage diversification in Brazil to improve biodiversity-related conservation efforts.

## INTRODUCTION

Predicting when and where the species are located gained relevance under the current threats to biodiversity characterizing the Anthropocene. However, despite the means currently available, producing reliable predictions on species distributions is not an easy task, especially in highly biodiverse regions, due to inadequate funding levels (Boakes et al., 2010; Gallo-Cajiao et al., 2018; Waldron et al., 2013), and the bias, low quality and insufficient availability of primary occurrence data (Cayuela et al., 2009; Hortal et al., 2015; Loiselle et al., 2008). Therefore, efforts to generate, gather and standardizing species distribution data, useful to predict the effects of threats to the environment and determining critical areas are crucial in conservation management nowadays (Handley et al., 2021; Ramos et al., 2018; Sánchez de Dios et al., 2017).

These critical areas often correspond to biodiversity 'hotspots', detected by stacking individual species distribution maps. To this end, species distribution modelling (hereafter SDMs) constitutes a reliable alternative to overcome the limitations of more traditional methods such as the widely implemented "Extents of Occurrence" (Elith & Leathwick, 2009; Mainali et al., 2020; Syfert et al., 2014). These modern techniques use

computer algorithms, occurrence data and environmental information to obtain models of the probabilistic distribution of a species in space or environment while reducing both false negatives and false positives errors (Jiménez-Valverde, 2012; Mendes et al., 2020).

Compared to other bird groups, raptors constitute a paradox since they are comparatively under-studied, given their low reproductive rates and abundances, while exercising great appeal for the financial support given their ecological roles as top predators, symbolism and threat levels (Donázar et al., 2016). Among raptors, true owls (family Strigidae) are reliable bioindicators of environmental quality (dal Pizzol et al., 2020; Dayananda et al., 2016; Fröhlich & Ciach, 2018, 2019), suitable conservation areas prioritization given their world diversity (> 220 species; Gill et al. 2021), and interspecific variation in size, distribution ranges, habitat specialization, and responses to habitat structure (Barros & Cintra, 2009; Burgas et al., 2014; Sergio et al., 2005) and alteration (Enríquez, 2017; Rullman & Marzluff, 2014).

However, given their nocturnal habits, owls can be overlooked in fauna inventories (H. G. de Silva & Medellín, 2001), limiting the knowledge on their biology and, probably, the underrepresentation in the official lists of threatened fauna of a megadiverse country such as Brazil (J. C. Motta-Junior et al., 2017; J. C. Motta-Junior & Braga, 2012). Even the information on their distribution is sparse, anecdotal, insufficiently detailed (J. C. Motta-Junior & Braga, 2012) and probably incomplete.

Brazil harbors some 21 recognized species of Strigidae (Gill et al., 2021), with the endemic Pernambuco pygmy owl (*Glaucidium mooreorum*) being critically endangered (BirdLife International, 2019) or even extinct (G. A. Pereira, 2010), while others including the East Brazilian pygmy owl (*Glaucidium minutissimum*), the black-capped screech owl (*Megascops atricapilla*), the long-tufted screech-owl (*M. sanctaecatarinae*), the tawny-browed owl (*Pulsatrix koenigswaldiana*) and the rusty-barred owl (*Strix hylophila*) are "near-endemic" (J. C. Motta-Junior et al., 2017). However, such biodiversity is greatly underestimated, as suggested by the proposition of new owl species for Brazil based on molecular and bioacoustics traits by Dantas et al. (2013).

The need to complete our understanding of the biology, ecology and distribution of owls in Brazil, especially under scenarios of vast and rapid environmental transformations (Escobar, 2020; Sonter et al., 2017), places their SDMs as a challenging and urgent scientific and conservation task. Here, we: (1) generated SDMs for each species and subspecies based on a maximum entropy approach; (2) evaluated niche similarities between conspecific subspecies; (3) created species richness maps for mainland Brazil; (4) determined the biodiversity hotspots; and (5) identified priority conservation areas contrasting them against the existing network of strictly protected areas.

## METHODS

### Study area

Brazil is a continent-sized country of contrasting topographic features (plain landscapes in the Amazon basin, or mass of ridges and mountain ranges in the southeast) and a latitudinal extent exceeding the Equator to the North and the Tropic of Capricorn to the South. Concomitantly, according to the Köppen classification system, there are three major climatic types (Alvares et al., 2013): humid subtropical, tropical rainy and tropical dry. Also, six major terrestrial biomes: Amazonia, Atlantic Forest, Caatinga, Cerrado, Pampa and Pantanal (IBGE, 2019).

Despite the aforementioned contrasts, and acknowledging the importance of areas accessibility via dispersal in SDMs (Barve et al., 2011), we considered Brazil as an orographic continuum for flying species based on two facts. First, Brazil lacks massive and steeply orographic barriers. Second, the Brazilian system of rivers includes wide ones, but their course and level underwent dramatic changes throughout their recent geological history, limiting their influence in shaping bird species distributions (Fluck et al., 2020; Santorelli et al., 2018).

### Species and subspecies account

We followed the International Ornithological Committee v. 11.1 (Gill et al., 2021), which considers 21 valid

species and 21 conspecific subspecies. To model the distributions of the subspecies separately, and given the lack of more comprehensive sources, we split the occurrences based on Gill et al. (2021), and the maps from [www.xeno-canto.org](http://www.xeno-canto.org) (Table 1).

### Environmental covariates

Bioclimatic covariates are successfully used in SMDs since their beginning (Booth et al., 2014), and perhaps reflect physiological constraints. Soil type and geology have been used in SDMs for Neotropical flying vertebrates (Ramoni-Perazzi et al., 2012, 2017, 2020) likely echoing deeper ecological and historical constraints. Soil characteristics modulate aspects of vegetation as functional traits, biodiversity, and speciation, among others (Hulshof & Spasojevic, 2020; Le Stradic et al., 2015; Mori et al., 2021; Nunes et al., 2015; Rajakaruna, 2018). Besides, plant species distributions can shape primary (Freeman & Mason, 2015) and secondary (Sanín & Anderson, 2018) consumers distributions. Furthermore, geology underpins several soil characteristics (Bockheim et al., 2014), as well as topography and geological events that can influence biological diversification processes over short timespans and over regional or local scales (Antonelli et al., 2018; Gillespie & Roderick, 2014; S. L. Pereira & Baker, 2004).

We used an *ad hoc* database of bioclimatic covariates for Brazilian mainland (Ramoni-Perazzi et al., in press), information on elevation (GMTED2010; Danielson and Gesch 2011), geological substrate (hereafter geology; Gómez Tapias et al. 2019), and soil type (Hengl et al. 2017). All variables were used at (or resampled to) 30 arc seconds resolution.

We performed all the analyses using R 3.6.3 (R Core Team, 2020). To remove collinearity, we reduced the number of continuous (bioclimatic + elevation) covariables through a principal component analysis using ‘RStoolbox’ (Leutner et al., 2018), keeping the first four components, whose eigenvalues were higher than one and explained 90.4% of the variance (Supplementary material A, Appendix 1, Fig. A). The first component (PC1) can be interpreted as a contrast between the temperature during the most extreme conditions and its seasonality/variability (Supplementary material A, Appendix 1, Fig. B1). Similarly, the second component (PC2) contrasts the precipitation during extreme conditions and its seasonality. The third component (PC3) involves the effect of water availability, since involves temperatures under extreme conditions/seasonality and precipitation during the warmest quarter. Finally, the fourth component (PC4) has a weak negative association between Mean Diurnal Temperature Range (Bio 02) and elevation.

### Spatial distribution models

We gathered information on the distribution (= occurrences) of the Strigidae in Brazil from: (1) skin specimens deposited in several museums according to the Global Biodiversity Information Facility (GBIF.org, 2019); (2) more than 164 publications in peer-reviewed literature regarding taxonomic assessments, fauna inventories or owl biology; and (3) field records from the bioacoustics database [www.xeno-canto.org](http://www.xeno-canto.org). We provide the citations of these sources in Supplementary material A, Appendix 2. The quality of the geographic coordinates varied from GPS recordings until those of the nearest town listed on the specimens’ labels. We corroborated the localities through an ornithological gazetteer specific for Brazil (Paynter & Traylor, 1991) and online ([www.geonames.org](http://www.geonames.org)).

There are no records for the buff-fronted owl (*Aegolius harrisii*) in Northern Brazil, but in the nearby Northern border at both Cerro de la Neblina (Willard et al., 1991) and Roraima Tepui (Braun et al., 2003). Similarly, most of the records for the foothill screech owl (*Megascops roraimae*) come from outside Brazil in Cerro Urutaní (Dickerman & Phelps, 1982), Cerro de la Neblina (Willard et al., 1991), Acary Mountains (Robbins et al., 2007), and Roraima Tepui (Milensky et al., 2016). In both cases, we included these records in our analyzes by reassigning coordinates within their respective closest Brazilian territory. The Pernambuco pygmy-owl is known from two localities (J. M. C. da Silva et al., 2002), to which we added eight random points located within a polygon resulting from two merged circles, each centered in one of the known localities and radius equaling the distance between both, clipped by the neighbor coastline. We excluded a record of the short-eared owl (*Asio flammeus*) in the Roraima State ([wikiaves.com.br](http://wikiaves.com.br); consulted on April 10, 2021), likely belonging to the subspecies *A. f. pallidicaudus* from “Venezuela, Guyana and Suriname” (Gill et al.,

2021).

The geographical and environmental clustering of field surveys, known as spatial autocorrelation (Araújo & Guisan, 2006; Loiselle et al., 2008), can negatively affect the performance of the SDMs (Veloz, 2009). Consequently, some authors remove those records under the same environmental conditions within an arbitrary distance (Delgado-Jaramillo et al., 2020). Thus, we created two datasets for each species, one including all the records and another excluding those closer than 25 km, and computed empirical entrograms for both using “elsa” (B. Naimi et al., 2019), comparing the entropy-based local indicators of spatial association for both categorical or continuous environmental covariates. Entrograms are variogram-like graphs quantifying the spatial association of geographical covariates based on information entropy concepts (B. Naimi, 2015).

We used “ENMeval” (Muscarella et al., 2014), a package based on Maxent (Phillips et al., 2006, 2017, 2004), that automatically splits data into training/test subsets, performs SDMs across a range of settings, and calculates diverse evaluation metrics. For each taxon, we ran 10 models, each one after partitioning occurrences in testing and training bins using a 10-fold cross-validation scheme (Fielding & Bell, 1997). For each run, we created 10 000 pseudoabsence points distributed randomly throughout Brazil and selected the model with the lowest Akaike information criterion corrected for small samples sizes ( $\Delta AIC_c = 0$ ) as the best one, since it reflects both model goodness-of-fit and complexity (Burnham & Anderson, 2002; Warren & Seifert, 2011) and less overfitting (Muscarella et al., 2014).

Different habitat suitability thresholds may disagree in terms of suitable areas and omission errors (Bean et al., 2012; Liu et al., 2016; Nenzén & Araújo, 2011). Thus, for each taxon, we plotted the extension of the predicted area (in number of pixels) against the number of omissions and compared across taxa the performance of the different thresholds, keeping the one that consistently provided the lowest values for both measurements. The final binary models combined the best models ( $\Delta AIC_c = 0$ ) and the threshold with the lower number of omissions within the smallest predicted area. We stacked these binary distributions to create two maps of taxa richness for (A) the 21 species evaluated (hereafter *sensu stricto* map), (B) the 12 monotypic species (including polytypic ones represented by only one subspecies in Brazil) and 21 subspecies (henceforth *sensu lato* map). We overlapped the protected areas distributions corresponding to IUCN’s categories I to IV (according to Protected Planet 2021) on each richness map.

### Subspecies niche analysis

We used ‘phyloclim’ (Heibl & Calenge, 2018) to quantify the niche overlap measurements for each pair of conspecific subspecies based on predictions (Warren et al., 2008):  $D$  (Schoener, 1968) and  $I$  (van der Vaart, 1998). Both report whether the average agreement of environmental requirements calculated between subspecies pairs is greater or smaller than expected if such subspecies were independent of each other, ranging from zero (no overlap) to one (identical niches). Then, we assessed the null hypothesis of niche identity, evaluating the equivalency between pairs of predictions, comparing the respective observed values of  $D$  and  $I$  against those generated through 100 pseudoreplicates, assigning the occurrence points for both subspecies to one lineage or the other at random to simulate the potential overlap of a group of points occurring across a given geographic space (Warren et al. 2008).

Moreover, we used background randomization tests to contrast the observed niche overlap values against a null distribution of 100 overlap values resulting from contrasting the predictions of one subspecies against those created from points taken at random from the geographic space of the another subspecies (Warren et al., 2008). We considered that: (1) there was niche conservation when the backgrounds overlapped and niche distance was not significantly different from zero; (2) there was niche divergence when the distance between both subspecies was significantly different from zero, independently of backgrounds’ overlap.

## RESULTS

### The occurrences

We gathered 2600 occurrence localities, after removing redundant ones (Supplementary Material B). Most occurrences were from the Atlantic Forest (48%), followed by the Amazonia (21%), Cerrado (17%), Caatinga

(8%), Pampa (4%), and Pantanal (3%; Fig. 1; Table 2). The Southeastern Region, ~11% of the Brazilian territory, was represented the best with 34% of the records, while the Northern region, 45% of the Brazilian territory, only provided 25% of the records. Both the Atlantic Forest and Cerrado were the most diverse biomes harboring records for ~81% of the species each, followed by the Amazonia (67%), Pampa (76%), Caatinga (57%), and Pantanal (48%).

For several species, we found records far outside the geographical or ecological limits traditionally reported in the literature. For example, the spectacled owl (*Pulsatrix perspicillata*) is frequently split into an Amazonian population and another from the Atlantic Forest, but there are records for all the remnant biomes except the Pampa.

### Spatial distribution models

Excluding the case of the striped owl (*Asio clamator*), the empirical entrograms showed no substantial variations when excluding those localities closer than 25 km (Supplementary Material A, Appendix 1, Fig. C). Thus, we performed the SDMs including all the occurrences, except for the aforementioned species.

We provide detailed information of the models in Supplementary material A, Appendix 3, Table A. In concordance with Liu et al. (2005, 2016), we found that thresholds based on sensitivity-specificity outperformed the remnant ones (Supplementary material Appendix 1, Fig. D). For such a reason, we used the sensitivity-specificity equality threshold to create the binary maps.

The climatic variables were usually the most important predictors of suitability (Table 3). Temperature-based PC1 and, especially, PC4 ranked highest for percentage contribution for 27 of the taxa studied, followed by precipitation-based PC3 (nine taxa), geology (four), and both soil and PC2 (one each).

The predictions of the monotypic species fitted the best their traditionally reported distributions and had lower omission percentages (median 13%, ranging between 0% for *G. mooreorum*, to 31%, for *Lophotrix cristata*; Supplementary material A, Appendix 1, Fig. E) compared to the polytypic ones (median 34%, from 24% for *Strix virgata* to 42% for *Megascops choliba*). These omissions usually felt outside the corresponding most represented biome (often, outside the Atlantic Forest). Besides, we found a general tendency towards fitting improvements after running models based on occurrences of their respective subspecies (median 15% of omissions, from 4% in *Athene cunicularia cunicularia* and, exceptionally, 66% for *Strix huhula huhula*). For the endemic and probably extinct Pernambuco pygmy-owl, our models predicted a very restricted range around both known localities, but also two additional separated spots, one located in the protected area of Manguezais da Foz do Rio Mamanguape, and the other in the mouth of the Sergipe river: unassessed areas from the ornithological point of view.

According to the *sensu stricto* map (Fig. 2A), the Atlantic Forest hosts the highest potential richness (ca. 15 species), especially within the Dense Ombrophylous Forest range (around the littoral and mountainous areas of the Southeastern region). Scattered areas along the Amazonas river lowlands, notably in the belt of siliclastic sedimentary rocks north of the river and around its mouth are also highly diverse. Conversely, wide coldspots (around zero predicted species) characterize more open environments such as Cerrado, Caatinga or Pampa, as well as broad areas in the Amazonia. Moreover, the *sensu lato* map (Fig. 2B) keeps the same areas of high biodiversity (over 15 taxa) but reducing the extension of the coldspots in the Amazonia, keeping only some areas in the Rondônia State. Thus, both approaches indicate that the Atlantic Forest, which harbors the highest richness, is poorly covered by strictly protected areas since these become substantially smaller and sparser within a gradient from Northwest to Southeast Brazil. However, by comparing the number of species (*sensu stricto*) recorded against those predicted, we found that all biomes are under-sampled (Table 2), especially the Pantanal and the Caatinga.

### Subspecies' niche analysis

The results of the similarity tests between conspecific subspecies are summarized in Supplementary material A, Appendix 1, Fig. F. We found niche overlap values significantly lower than expected from a null model

distribution for all the pairwise comparisons. Consequently, we reject the null hypothesis of niche identity for all pairs, suggesting that in all cases niches are not identical to one another.

Our background tests yielded a more complex scenario (Supplementary material A, Appendix, 1 Fig. G). The observed values of  $D$  and  $I$  usually lied below the corresponding null distributions; hence, differences are bigger than expected by chance. However, we were failed to reject the null hypotheses of the background similarity tests when contrasting *A. c. cunicularia* - *A. c. grallaria* , *B. v. nacurutu* - *B. v. deserti* , *M. c. choliba* - *M. c. decussatus* , *M. c. choliba* - *M. c. uruguayi* , and *M. w. watsonii* - *M. w. usta* , with arrows indicating the directionality of the comparison: the first subspecies against a randomized background derived from the second one. However, the  $D$  and  $I$  metrics of the respective complementary comparisons fell below their corresponding null distributions, indicating that these were more different than expected by chance, hence leading us to reject the null hypothesis that their niches are similar.

## DISCUSSION

In general, our results show that the situation of Brazilian Strigidae is complicated, involving an underestimated richness, within an inadequate framework of protected areas, in a megadiverse Country characterized by high rates of habitat transformations.

### Sampling biases, distribution patterns and taxonomic knowledge

Brazil harbors a rich owl diversity, distributed unequally throughout its territory. Indeed, our models suggest a markedly variable richness across the Country, ranging between zero and 16, averaging three, species per 30 arcsec \* 30 arcsec pixel. Since 69% of the occurrences are from Atlantic Forest and Amazonia, their higher predicted richness can partially respond to sampling biases. The Atlantic Forest exemplifies those situations where sampling efforts are favored by neighboring established research centers and major urban areas (Brito et al., 2009; Moerman & Estabrook, 2006; G. V. T. Ribeiro et al., 2016). The Amazonia replicates the pattern already described for botanical and ornithological records (Vale & Jenkins, 2012), probably prompted by local facilities or recurrent bird-oriented inventories.

However, all biomes are under-sampled, as suggested by the difference between the number of recorded and predicted species, especially in the Caatinga and Pantanal. Hence, our results agree with Silva (1995) and Fernandez-Arellano et al. (2021) regarding the need for research efforts addressed to unexplored areas and periods, less detectable species, in neglected biomes. It is reasonable to expect that such efforts oriented to nocturnal birds would increase the respective species lists for all biomes, especially in Caatinga and Pantanal.

Excluding the possibility of factors shaping the distributions of the Brazilian Strigidae, not considered in the present study, several not mutually exclusive possibilities can explain the overall elevated number of omissions for the models. First, misidentifications. For example, (Rocha & Lopez-Baucells, 2014b) reported a young *Lophostrix cristata* that was indeed a *Strix virgata* (Rocha & Lopez-Baucells, 2014a). Thus, similar unnoticed mistakes, especially those involving species more alike, can result in false occurrences reported far from the actual range.

Second, vagrancy, a phenomenon frequently reported in the ornithological literature at least since Grinnell (1922), including cases of owls impacting native fauna in remote islands (Bried, 2003), and prompted by factors as diverse as expanding populations, weather conditions, geography, age, and genetics (Kalwij et al., 2019; Ralph & Wolfe, 2018; Veit, 2000). According to the 'Exodus Hypothesis' (Flade & Lachmann, 2008), vagrancy can be triggered by severe habitat loss, and individuals occasionally can settle in available but less adequate habitats affecting their fitness and population permanence (Part et al., 2007; Robertson & Hutto, 2006). Here, most omissions corresponded to taxa from the Atlantic Forest recorded in open areas such as the Cerrado. Currently, the Atlantic Forest covers less than 16% of the original extent, and more than 80% of the fragments are smaller than 50 ha (Ribeiro et al. 2009; but see Rezende et al. 2018), a dramatic situation that could have triggered the translocation of owls toward the comparatively less impacted Cerrado areas in the past.

Third, range expansions, as frequently reported for Strigiformes in well-monitored areas in North America

(Livezey, 2009a), Europe (Bashta, 2009; Mysterud, 2016), and Oceania (Hyde et al., 2009), occasionally mediated by human activities. For example, Livezey (2009b) postulated that the forest expansions after the arrival of European settlers (who excluded fires set by Native Americans, planted trees, and overhunted bison, elks, deers and beavers) allowed barred owls (*Strix varia*) to overcome the historical lack of trees in the Great Plains of North America granting their expansion westward. According Haywood (2010), the plantations of Tasmanian Blue Gum (*Eucalyptus globulus*) facilitated the range expansion of the powerful owl (*Ninox strenua*) in South Australia. Similar situations could be shaping the distributions of some Brazilian owl species, such as the tree-nester *A. harrissi*, whose omissions mostly correspond to records from the last two decades in open biomes such as Cerrado and Caatinga (A. F. T. da Silva et al., 2021) or Pampa (Muller Rebelato et al., 2011). That is, these new records correspond to biomes anthropized the most during the recent decades according to MAPBIOMAS (<https://plataforma.brasil.mapbiomas.org/>, consulted April 14, 2021), with steady increases in planted tree surfaces (<http://atlasagropecuario.imaflo.org/>, consulted April 16, 2021), perhaps offering new more suitable areas for these owls.

Notwithstanding, a more likely option is that the taxonomy of the Brazilian owls is far from being completely understood, with local populations/morphs representing in many cases valid species, as recently demonstrated by Dantas et al. (2021). In these cases, it is reasonable to expect SDMs biased toward the best-represented subspecies, failing to predict regions suitable for the remnant ones. Our models for the con-specific subspecies and our results on niche equivalency, even if assigning the occurrences in an approximative way, reinforced this possibility.

Our analyses agree with Peterson et al. (1999) that the speciation process involves geographic dimensions first and then ecological aspects. Environmental parameter variations may result in niche divergences (Pyrón et al., 2015; Ramoni-Perazzi et al., 2020), which may explain to some extent most of the speciation patterns within the Brazilian Strigidae since our results imply that the niches of the subspecies under comparison can be more dissimilar than expected, in most cases obligated by dissimilarities of their respective backgrounds. This situation may also involve species considered as monotypic. For example, the high omission rates of over 26% in the case of the Amazonian pygmy owl (*Glaucidium hardyi*) may suggest a species complex since the central portion of the Amazon River basin is a secondary contact zone for taxa isolated in the main Amazonian sub-basins during the Mid- and Late Pleistocene (Thom et al., 2020).

All the aforementioned options deserve further evaluations, especially involving morphological, molecular and bioacoustics approaches.

### Conservation-related issues

The combination of sampling biases, plus ecologic and taxonomic knowledge gaps, can lead to misguided conservation decisions. For example, similarly to what had already reported for bats (Delgado-Jaramillo et al., 2020), most of the coldspots in our *sensu stricto* map (Fig. 2A) are placed along areas severely deforested during the last decades, particularly along the contact zone between Amazonia and Cerrado in the so-called “arch of deforestation” (Becker, 2005). Such coldspots could erroneously be interpreted as regions of lower conservation interest, instead of originated by the absence of information after local extinctions prompted by anthropic impacts (Delgado-Jaramillo et al., 2020).

The greater diversity of Strigidae within the Atlantic forest corresponds to an extensively degraded biome with small-sized and sparse protected areas, whose efficiency is lower than other regions, such as the Amazonia (Sobral-Souza et al., 2018). Worse yet, the buffer zones around these protected areas in the economically prosperous Brazilian regions tend to be as degraded as the surrounding unprotected ones (Almeida-Rocha & Peres, 2021). Bird species were already extinct and others were extirpated, from large parts of the Atlantic Forest, especially the Pernambuco Centre of Endemism in northeast Brazil (Develey & Phalan, 2021). Besides the probably extinct Pernambuco pygmy-owl (*G. mooreorum*), the spectacled owl (*Pulsatrix perspicillata pulsatrix*) may be extinct in most of its range (Leal & Assis, 1993). Thus, we agree with Oliveira et al. (2017) who highlighted the deficiencies of the Brazilian network of protected areas given the combination of the scarce knowledge on their biodiversity and an inadequate spatial disposition which

offers limited or no protection to most species and even evolutionary lineages. We also agree with Jenkins et al. (2015), regarding the need to substantially improve the network of protected areas in Brazil, with an emphasis in the Atlantic forest.

### Final remarks

The frequently adopted biological concept has been criticized (Hauser, 1987) since many biological species and subspecies seems to be unsuitable for practical or theoretical purposes. Thus, it is likely that differentiation processes reported across several groups of Neotropical birds (Harvey et al., 2017; McGuire et al., 2014) are being overlooked. The Anthropocene, with its widely recognized adverse impacts on biodiversity, driven by the current trends of wide and quick habitat conversion (Gaston et al., 2003), and climatic change (Devictor et al., 2008; Urban, 2015) worsens this scenario. In consequence, as indicated by Mishler (2021), the adoption of less restrictive concepts, as the phylogenetic one, will allow abandoning the biases and restrictions imposed by the use of the species rank, improving the evolutive and ecological research, and ultimately influencing positively areas of public interest such as conservation.

The traditional use of single umbrella species for conservation purposes received critics since a single species can hardly encapsulate the environmental requirements and geographical distribution of the remaining species to be protected (Fourcade et al., 2013). Consequently, alternative multi-species approaches appeared, balancing the number of taxa involved and their sensitivity to area/resources requirements (including connectivity and natural processes) to establish realistic, concrete and quantitative landscape design criteria (Lambeck, 1997; Roberge & Angelstam, 2004). As top predators with variable size, and differential environmental sensitivity and requirements, owls are good candidates to be considered for a multi-taxa approach, for which our study serves as a hurrying call to explore in-depth owl lineage diversification in Brazil to improve biodiversity-related efforts.

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### Data availability statement

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Table 1. Account of the species and subspecies occurring in Brazil, according to the International Ornithological Committee v. 11.1 (Gill et al. 2021). “Distribution” refers to the range described in the aforementioned source, used jointly to biomes, major hydrographic basins and reinforced by other sources such [www.xeno-canto.org](http://www.xeno-canto.org), to proximately assign the occurrences to the different subspecies (our “interpretation”), to create the occurrences databases used to model the subspecies distributions.

English name	Scientific name	Distribution
Buff-fronted Owl	<i>Aegolius harrisii</i>	“Paraguay, SE Brazil, Uruguay and NE Argentina”
	<i>A. h. iheringi</i>	
Striped Owl	<i>Asio clamator</i>	“Colombia and Venezuela to E Peru and C, NE Brazil” “E Bolivia to Paraguay, S Brazil, Uruguay and N Argentina”
	<i>A. c. clamator</i>	
	<i>A. c. midas</i>	
Short-eared Owl	<i>Asio flammeus</i>	“S Peru and S Brazil to Tierra del Fuego”
	<i>A. f. suinda</i>	
Stygian Owl	<i>Asio stygius</i>	
Burrowing Owl	<i>Athene cunicularia</i>	“C, SE Venezuela, S Guyana and N Brazil” “S Bolivia, Paraguay and S Brazil to Tierra del Fuego” “E and C Brazil”
	<i>A. c. minor</i>	
	<i>A. c. cunicularia</i>	
	<i>A. c. grallaria</i>	
Great Horned Owl	<i>Bubo virginianus</i>	“NE Brazil (NC Bahia)” “E Colombia through the Guianas to N, E Brazil, Argentina, B
	<i>B. v. deserti</i>	
	<i>B. v. nacurutu</i>	
Ferruginous Pygmy Owl	<i>Glaucidium brasilianum</i>	“Amazonia” “E Brazil to NE Argentina”
	<i>G. b. ucayalae</i>	
	<i>G. b. brasilianum</i>	
Amazonian Pygmy Owl	<i>Glaucidium hardyi</i>	
East Brazilian Pygmy Owl	<i>Glaucidium minutissimum</i>	
Pernambuco Pygmy Owl	<i>Glaucidium mooreorum</i>	
Crested Owl	<i>Lophotrix cristata</i>	
Black-capped Screech Owl	<i>Megascops atricapilla</i>	
Tropical Screech Owl	<i>Megascops choliba</i>	“S Brazil and E Paraguay” “E Colombia and E Peru through Venezuela, the Guianas to N “SE Brazil, Uruguay and NE Argentina” “C, E Brazil”
	<i>M. c. choliba</i>	
	<i>M. c. cruciger</i>	
	<i>M. c. uruguaii</i>	
	<i>M. c. decussatus</i>	
Foothill Screech Owl	<i>Megascops roraimae</i>	
Long-tufted Screech Owl	<i>Megascops sanctaecatarinae</i>	
Tawny-bellied Screech Owl	<i>Megascops watsonii</i>	“N of the Amazon” “S of the Amazon”
	<i>M. w. watsonii</i>	
	<i>M. w. usta</i>	
Tawny-browed Owl	<i>Pulsatrix koeniswaldiana</i>	
Spectacled Owl	<i>Pulsatrix perspicillata</i>	“E Colombia through the Guianas and Amazonia” “Paraguay, E Brazil and NE Argentina”
	<i>P. p. perspicillata</i>	
	<i>P. p. pulsatrix</i>	

English name	Scientific name	Distribution
Black-banded Owl	<i>Strix huhula</i>	“Colombia, Venezuela and the Guianas S to E Peru, E Bolivia, “SE Brazil, Paraguay and NE Argentina”
	<i>S. h. huhula</i>	
	<i>S. h. albomarginata</i>	
Mottled Owl	<i>Strix virgata</i>	“NC, NE Brazil” “S Brazil, Paraguay and NE Argentina”
	<i>S. v. superciliaris</i>	
	<i>S. v. borelliana</i>	

Table 2. Numbers of records, omissions, number of species (*sensu stricto*) recorded and predicted and their differences for the different Brazilian biomes. Numbers in parentheses represent percentages based on the total of 2608 occurrences (2600 from collections/literature + eight generated for *Glaucidium mooreorum*) or the 21 species.

Biome	Records	Omissions	Richness <sub>rec</sub>	Richness <sub>pred</sub>	Difference
Amazonia	540 (21)	284	14 (67)	16 (76)	2
Atlantic Forest	1249 (48)	84	17 (81)	21 (100)	4
Caatinga	209 (8)	129	12 (57)	19 (90)	7
Cerrado	438 (17)	210	17 (81)	20 (95)	3
Pampa	104 (4)	14	13 (62)	16 (76)	3
Pantanal	68 (3)	9	10 (48)	15 (71)	5

Table 3. The mean  $\pm$  standard deviation of the percent of contribution and permutation importance of the explanatory variables to the SDMs of each species and subspecies. The percent of contribution is the gain of the model by including a given environmental covariate at each step of the Maxent algorithm. The permutation importance is the influence of each environmental covariate on the final model, measured through the random permutation of the values of such covariate among the training points and measuring the resulting decrease in the training area under the curve.

	Percent of contribution	Percent of contribution	Percent of contribution	Percent
Species/subspecies	PC1	PC2	PC3	PC4
<i>Athene cunicularia</i>	6.4 $\pm$ 3.2	3.2 $\pm$ 1	6.2 $\pm$ 8.6	64 $\pm$ 9
<i>Athene cunicularia cunicularia</i>	14.1 $\pm$ 4	0.5 $\pm$ 0.4	2.9 $\pm$ 1.7	51.7 $\pm$
<i>Athene cunicularia grallaria</i>	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	100 $\pm$ 0
<i>Bubo virginianus</i>	3.2 $\pm$ 4.2	0.6 $\pm$ 0.4	1.4 $\pm$ 2.6	59.4 $\pm$
<i>Bubo virginianus nacurutu</i>	2.9 $\pm$ 2.5	0.4 $\pm$ 0.7	3.9 $\pm$ 3.1	61.3 $\pm$
<i>Glaucidium brasilianum</i>	1.9 $\pm$ 2	1.9 $\pm$ 0.9	10.1 $\pm$ 12	54.7 $\pm$
<i>Glaucidium brasilianum brasilianum</i>	2.9 $\pm$ 1.8	1.7 $\pm$ 0.7	12.7 $\pm$ 12.8	51.7 $\pm$
<i>Glaucidium hardyi</i>	2 $\pm$ 2.1	33.9 $\pm$ 3.2	5.6 $\pm$ 0.5	34.8 $\pm$
<i>Lophotrix cristata</i>	1.2 $\pm$ 1.1	48.5 $\pm$ 0.9	2.2 $\pm$ 0.6	42.9 $\pm$
<i>Megascops atricapilla</i>	10 $\pm$ 5.8	17.4 $\pm$ 1	10 $\pm$ 5.8	33.8 $\pm$
<i>Megascops choliba</i>	16.4 $\pm$ 4.7	16.1 $\pm$ 1.1	17.5 $\pm$ 2.6	21.3 $\pm$
<i>Megascops choliba choliba</i>	24.1 $\pm$ 17.7	1.1 $\pm$ 0.8	15.3 $\pm$ 16.2	37.4 $\pm$
<i>Megascops choliba cruciger</i>	7.4 $\pm$ 2.7	47.7 $\pm$ 3.9	4.2 $\pm$ 1.4	26.1 $\pm$
<i>Megascops choliba decussatus</i>	13 $\pm$ 2.5	17.2 $\pm$ 1.2	5.7 $\pm$ 0.7	22.9 $\pm$
<i>Megascops roraimae</i>	23 $\pm$ 1.3	0 $\pm$ 0	36.2 $\pm$ 3	31.8 $\pm$
<i>Megascops watsonii</i>	5 $\pm$ 6	3.5 $\pm$ 4.4	1.3 $\pm$ 2.8	41.4 $\pm$
<i>Megascops watsonii usta</i>	4.5 $\pm$ 2.6	3.7 $\pm$ 2	11.8 $\pm$ 4.2	28 $\pm$ 4
<i>Pulsatrix koeniswaldiana</i>	36.4 $\pm$ 5.3	7.9 $\pm$ 0.9	10.3 $\pm$ 4.6	17.1 $\pm$

	Percent of contribution	Percent of contribution	Percent of contribution	Percent
<i>Pulsatrix perspicillata perspicillata</i>	0.3 ± 0.6	44.4 ± 5.1	1.7 ± 0.9	34 ± 3
<i>Pulsatrix perspicillata pulsatrix</i>	4.9 ± 3.2	58.3 ± 4.7	9.4 ± 2.7	14.6 ±
<i>Strix virgata borelliana</i>	37.9 ± 4.8	19.7 ± 0.7	5.6 ± 1.5	13.8 ±
<i>Strix virgata superciliaris</i>	0 ± 0	15.2 ± 1.3	0 ± 0	84.8 ±
<i>Asio clamator</i>	21.3 ± 3.9	12.6 ± 0.8	18.5 ± 3.7	34.1 ±
<i>Asio clamator midas</i>	48.1 ± 5.4	8.7 ± 0.8	16.1 ± 5.4	14.3 ±
<i>Athene cunicularia midas</i>	0.7 ± 1.5	4.4 ± 1.7	13.3 ± 4.2	74.4 ±
<i>Glaucidium minutissimum</i>	10.2 ± 3.6	18.2 ± 1.6	17.1 ± 3.7	15.5 ±
<i>Megascops choliba uruguaei</i>	8.3 ± 2.3	3.6 ± 0.8	13.5 ± 4.8	71.9 ±
<i>Megascops sanctaecatarinae</i>	41.9 ± 7	5 ± 1	5 ± 2.7	40.2 ±
<i>Megascops watsonii watsonii</i>	0 ± 0	46.5 ± 2.7	36.7 ± 3.1	0 ± 0
<i>Strix huhula</i>	2.3 ± 0.4	12.7 ± 1.9	15.2 ± 1.5	10.8 ±
<i>Strix huhula albomarginata</i>	17.3 ± 7.5	16.4 ± 1.5	12.6 ± 4.8	14.1 ±
<i>Aegolius harrisii</i>	30.8 ± 4.1	0 ± 0.1	1 ± 0.3	8.1 ± 0
<i>Asio flammeus</i>	85.3 ± 4.7	0 ± 0	0 ± 0	0.9 ± 0
<i>Asio stygius</i>	47.1 ± 5.9	5.9 ± 1.3	0.5 ± 0.3	1.9 ± 2
<i>Strix hylophila</i>	69.7 ± 2.6	0.2 ± 0.2	0.8 ± 1.3	4.3 ± 2
<i>Strix virgata</i>	31.7 ± 5	31.2 ± 3.3	4.4 ± 0.6	7.5 ± 0
<i>Asio clamator clamator</i>	0 ± 0	0 ± 0	0 ± 0	29.4 ±
<i>Glaucidium brasilianum ucayalae</i>	0.1 ± 0.2	0.2 ± 0.3	0 ± 0	26.1 ±
<i>Pulsatrix perspicillata</i>	2.8 ± 1.4	37.3 ± 2.2	3.4 ± 1.8	18.3 ±
<i>Strix huhula huhula</i>	7.2 ± 11.4	0 ± 0	0.3 ± 0.5	14.3 ±
<i>Bubo virginianus deserti</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Glaucidium mooreorum</i>	0.2 ± 0.1	73.0 ± 4.5	0 ± 0	0.2 ± 0

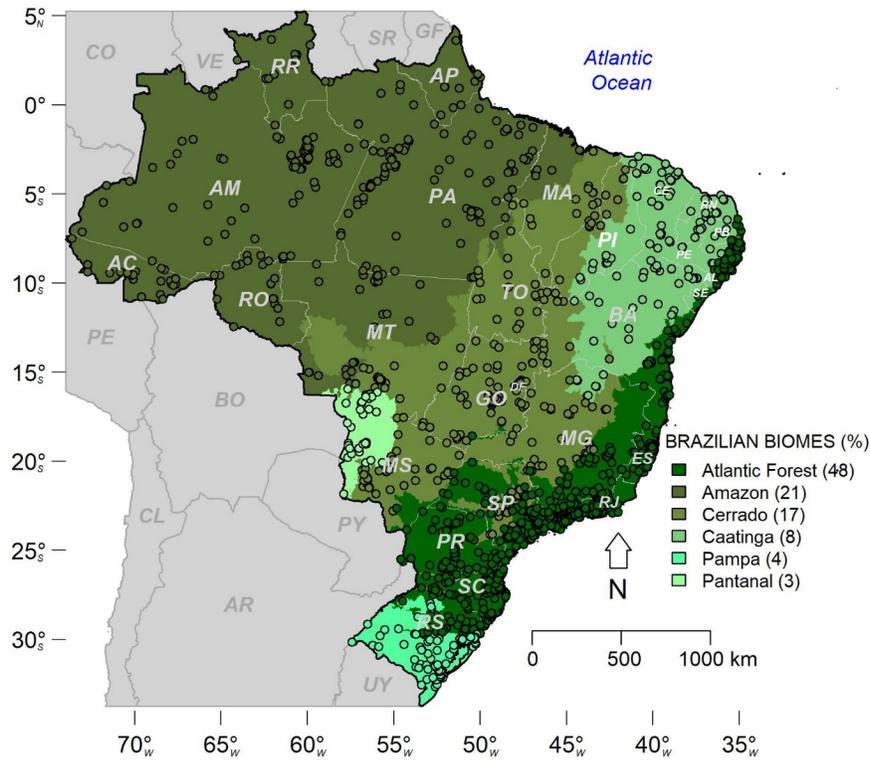


Figure 1. Records of Brazilian Strigidae used in the modeling process. Biome colors correlates with the abundance of records (the darkest the most abundant). State and countries acronyms follow ISO 3166-2 and ISO 3166-1 alpha-2, respectively.

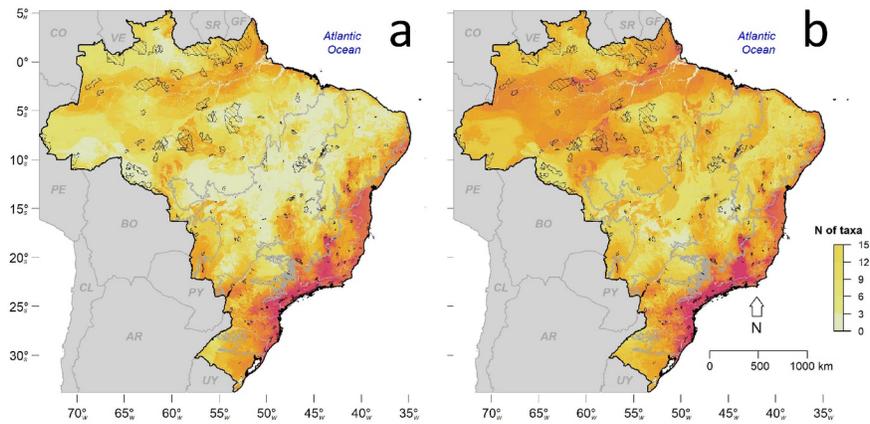


Figure 2. Predicted Strigidae species richness patterns in Brazil based on (A) species *sensu stricto* ; and (B) *sensu lato*(including subspecies). Dashed polygons represent the strict protected areas. Biome limits in dark gray lines.