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Avian Assemblages in Forest Fragments do not Sum to the Expected Regional Community in the Brazilian Atlantic Forest

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While bird diversity in the Atlantic Forest can be considered well-known, how the communities have been affected by deforestation and habitat fragmentation is not. We studied birds in 10 forest fragments of distinct sizes (all originally within the Atlantic Forest) in southern Bahia. In 5,391 bird encounters, we found 251 species, with 46 endemics and eight considered globally vulnerable or endangered. We also compiled a list of the 380 species that should comprise the expected regional assemblage, and found that only 66% of these species were present in all the fragments combined. Only 9% of all observed species were found in all fragments. The largest fragment (700 ha) had the greatest number of endemic species (40), and seven threatened species. All fragments had some conservation-important species (some were found in one or a few fragments), but no fragment included them all. Fragments shared 10% of endemic species, but overall, the contingent of endemics was unique in each fragment. Finally, most functional traits of bird assemblages decreased with increasing fragment size. Neither species richness nor similarity correlated with fragment size or distance between fragments, and unknown, non-random factors probably influence the likelihood of species survival in each fragment. Thus, to ensure the persistence of threatened species, as well as maintain the most common species, conservation management decisions should include all fragments together because no single fragment is most representative of the local community.

Key words: Habitat modification, Fragment variability, Landscape ecology, Species richness, Conservation.

BACKGROUND

Loss of biodiversity is often attributed to ecosystem decay, which occurs when habitat loss in many small and isolated habitat remnants is associated with greater species loss than when the remaining habitat is not fragmented (Chase et al. 2020). Bird species loss in 10 and 100-ha tropical forest fragments, for example, was demonstrated to be significantly different from random taxonomic loss (Luther et al. 2020). Also, habitat loss can lead to decreasing functional integrity while functional diversity can remain unchanged or increase (De Coster et al. 2015).

Extensive fragmentation has caused interest in the

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drivers of assemblage-level species responses, typically using alpha diversity (Giraudo et al. 2008; Teixido et al. 2020). Previous studies have noted that there is some correlation between biodiversity and fragment size (both decrease together), that forest habitat loss results in local extinctions, that small (< 100 ha) fragments are important habitats, corridors, and stepping stones (in the absence of better options), and that interactions between frugivorous birds and plants decrease as fragment area decreases (Fahrig 2017; Emer et al. 2020; Oliveira et al. 2020; Volenec and Dobson 2020). Also, in a fragmented landscape both large and small fragments can be important for maintaining regional assemblage diversity (Anjos et al. 2011; Bhakti et al. 2018). These observations illustrated the importance of understanding how to maintain diversity in fragmented landscapes at levels comparable to that in continuous forests (Paese et al. 2010; Banks-Leite et al. 2014; Bonfim et al. 2019). Perhaps surprisingly, controlling for the size of habitats, ecological responses to habitat fragmentation may often be positive (Fahrig 2017). However, fragmentation is always accompanied by a reduction in the size of habitat, and species tend to be overdispersed in communities in smaller fragments, resulting in increased functional redundancy (Oliveira et al. 2020).

Forest dependent functional groups seem to be favored by connected landscapes with a higher percentage of forest cover, whereas forest independent groups, on the other hand, are favored by irregularly shaped fragments and negatively impacted by forest cover (Coelho et al. 2016). Landscape composition (variability of the habitat within the fragments) was demonstrated to be more important than landscape configuration (geography of the fragments relative to one another) for taxonomic and functional diversity of frugivorous birds (Bonfim et al. 2021). Decreased forest cover was associated with decreased diversity of forest-specialist birds, and with increased diversity of generalist birds, with an abrupt change when ~50% of the forest area was lost (Morante-Filho et al. 2015).

We wished to examine how fragmentation influences bird assemblages using fragment size and distance between fragments to find an association with the likelihood of finding endemic and threatened species. Because the entire region was once contiguous forest, we predicted that larger remnants have more species and that fragments closer to one another have similar species compositions. We also asked whether fragments sum to the regional species pool, as these species are likely to have been found in all locations prior to fragmentation. Following general predictions of island biogeographic theory, we expected larger fragments to have maintained more—and lost fewer—species (Whittaker and Fernández-Palacios 2006; Losos and Ricklefs 2010). We then carried out functional diversity analysis to evaluate how species diversity might be influenced by fragmentation, and how the actual diversity compares with the expected regional assemblage. Thus, we specifically test the relationship between fragment size and assemblage structure within those fragments, and whether summing species over fragments tends toward recovering the original avian assemblage of this region of Atlantic Forest.

To test our hypotheses, we used the birds of southern Bahia, whose distributions in the Atlantic Forest are well-known. Birds are an ideal taxon for monitoring environmental disturbances as they are sensitive to changes at lower trophic levels (Gregory et al. 2005), and some trophic categories are more susceptible to disappearing due to fragmentation.

MATERIALS AND METHODS

Study area

In Bahia, the Atlantic Forest extends from the coastal plains to the Espinhaço mountain range, with associated variation in topography, climate, and plant diversity. While dense rain forest dominates the coastal plains, deciduous and semideciduous forests become dominant at higher elevations where rainfall is also more seasonal (IBGE 2012). The Atlantic Forest in Bahia is very fragmented, but less so in the south, where the largest, continuous areas remain. Nevertheless, only 17% of the original vegetation remains, with a vegetation debt of 80–100% in southern Bahia (Ribeiro et al. 2009; Rezende et al. 2018).

The Atlantic Forest fragments investigated in this study are located in southeastern Bahia near two municipalities, in northeastern Brazil (Fig. 1): Jaguaquara (13°31'51"S, 39°58'15"W) and Jequié (13°51'27"S, 40°5'1"W). Average annual temperature is ca. 21°C, with an average maximum of 29°C in January, and average minimum of 15°C in August. Average annual rainfall is 816 mm, with November being the rainiest month (121 mm) and September being the driest (44 mm; measurements from 1981–2010) (INMET 2020).

Originally the entire region was covered by dense Atlantic Rainforest (300–900 m in elevation), but today it is very fragmented into many small fragments < 1,000 ha. Thus, all fragments under study were originally very similar. Fragmentation of this region is contemporaneous and most fragments are at least 35 (1985–2020) years old (Project MapBiomas 2020).

During this study they had similar vegetation structure, with a relatively open understory, trees

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up to 15 m tall, and a few, taller, emergent trees. One fragment was being extensively logged, and all fragments had signs of poachers. The matrix between the fragments comprises mostly pasture with many smaller, rural, properties of coffee and cocoa farms and subsistence gardens.

Sampling design

We selected 10 forest fragments that varied in size (from 9 to 703 ha, median area – 94.5 ha, mean area – 196 ha) and measured pairwise distances between all studied fragments (0.4–12 km, median 4.6 km, Fig. 1).

Sampling Methods – the list method

Rapid assessment requires gathering a lot of information in little time, and we used the 10-species list method (MacKinnon and Phillipps 1993) because it is efficient for the purposes of estimating: 1) species richness, 2) relative abundance of species, 3) diversity indices, and 4) species accumulation curves. Additionally, the use of lists with statistics to estimate species is more easily standardized and repeatable than other sampling effort-based methodologies (Poulsen et al. 1997; Herzog et al. 2002; Ribon 2010; Cavarzere et al. 2012).

Using the list method begins with placing the species in chronological order as they are encountered in the field, by fragment. Next, the species are counted sequentially until reaching a total of 10 species (regardless of numbers of sightings) which must not be repeated, to form the 10-species lists (with often varying numbers of individuals), in each fragment. Every time 10 different species compose one list, another one is initiated. The total number of lists accumulated are then used as the sampling units (Ribon 2010).

In November and December 2012, we divided into two teams of two experienced observers and noted all birds encountered (by sight or sound) while walking trails between the hours of 04:00–11:00 h over three-day intervals. Each team counted birds in two

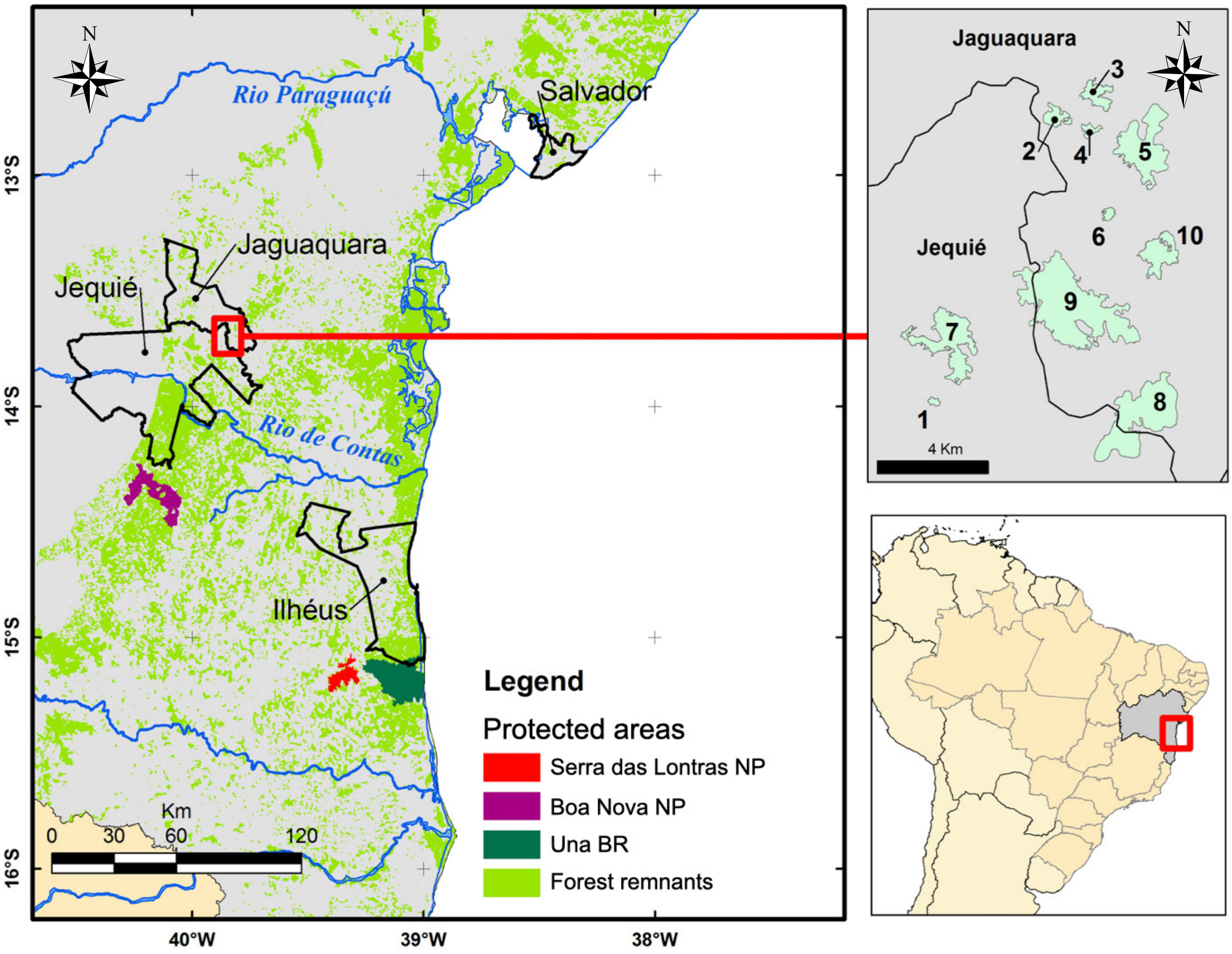

Fig. 1. Map of Bahia within Brazil, and the location of the fragments under study.

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fragments, and the teams alternated fragments such that one team visited each fragment twice and the other team once during each sampling period (Table 1). We used trails that were already available in some fragments as sample transects. When necessary, we cleared trails the day prior to the first sampling period.

Analysis

Alpha diversity

We first tested the predictions that species richness increases with fragment size and that species similarity decreases with increasing distance between fragments for both overall and strictly forest species using linear regressions (with $\log_{10}$ transformations if needed to meet the assumptions) after testing for statistical premises. Using G-tests, we compared the proportions of all observed species that were of the regional expected assemblage of the Atlantic Forest fragment size. We also used G-test to ask whether the number of fragments in which a species was found was associated with it being in the regional expected assemblage of the Atlantic Forest. Forest species were those thus classified for Neotropical birds (Stotz et al. 1996).

From the 10-species lists we generated species accumulation curves and estimated asymptotic species richness using the non-parametric estimator Chao1 in BiodiversityR (Kindt 2020).

Beta diversity

The list method provides encounter frequencies (an estimate of relative abundance) for which we used Principal Coordinate Analysis (PCoA) with Bray distances to compare and illustrate fragments by similarity (testing that similarity was associated with either fragment size or distance between fragments). We also compared the alpha diversity of fragments based on the species found in each fragment using Jaccard dissimilarity. This index does not need to be normally distributed, but the residuals do. In the regression of shared species, we found no relationship nor any other evidence that might suggest one and, thus, felt that the regression served its purpose. Species analysis and PCoA were carried out using the BiodiversityR, lm, and vegan packages in R (R Core Team 2020).

Gamma diversity

We compared the assemblages of birds in each fragment with that of the expected regional assemblage – that is, birds that should have been found within the previously contiguous Atlantic Forest of the region (Gonzaga et al. 1995; Gonzaga and Pacheco 1995; Pacheco et al. 1996; Pacheco and Gonzaga 1995; Silveira et al. 2005; Souza and Borges 2008; Vasconcelos et al. 2013; Maurício et al. 2014; Cavarzere et al. 2019). This list was compiled using all forest species whose range maps showed that their geographic distribution encompassed the entire study area. This analysis used alpha diversity due to the nature of the expected regional assemblage. We generated random assemblages by fragment using the expected regional assemblage, assuming that all species were possible in all fragments. We then selected subsets of the total list. For example, if a fragment had 100 total sightings (independent of the number of species) we selected

Table 1. Fragments, by area, number of bird lists generated (List), total number of species observed (N), predicted number of species (Chao1), evenness (*J'* Pielou's index), the number and percentage of endemics (End), the number of threatened species (Th), and dates that the fragments were visited (dates in 2012 were all in December unless otherwise noted)

Area (ha)	List	N	Chao1	*J'*	End (%)	Th	Dates
9	32	106	150	0.92	10 (9)	0	2, 3, 4
15	39	114	155	0.89	18 (15)	2	29, 30 Nov., 1 Dec.
19	40	126	148	0.94	21 (15)	3	11, 12, 13
47	36	111	158	0.92	27 (22)	2	11, 12, 13
65	42	120	141	0.92	30 (23)	4	5, 6, 7
124	48	150	213	0.91	32 (19)	4	29, 30 Nov., 1 Dec.
259	30	125	161	0.92	27 (20)	4	8, 9, 10
281	42	120	176	0.92	37 (24)	3	8, 9, 10
441	58	117	138	0.87	19 (15)	2	5, 6, 7
703	49	131	151	0.91	40 (24)	7	2, 3, 4
Total	428	251	271	0.88	46 (18)	18	

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100 random sightings from the total list of all birds observed in all fragments. Also, we estimated the distribution of the number of fragments in which any species should be found under the null hypothesis (that all fragments should have the same species) based on 1) the expected regional Atlantic Forest assemblage, 2) the total observed Atlantic Forest assemblage, and 3) the observed distribution of species among fragments. If forest birds were found in or had disappeared from fragments for random reasons, then the observed assemblages would be similar to the expected assemblages. We estimated the number of species lost using the difference between the number of species in the observed and randomized assemblages and the expected regional assemblage (because their maximum possible values must be equal). Randomizations were carried out using the "sample" (with replacement) function in R. Because we were interested in the general expected trend rather than a statistical test to determine exactly how different the randomized assemblages would be, we used one randomization per context for these comparisons.

Functional diversity

Functional diversity indices address the ecological parameters of diet and foraging strata (similar to a niche concept), and thus represent ecological tendencies of the species groups rather than the species themselves. We carried out a functional diversity analysis to ask three questions about how functional diversity might be influenced by fragmentation. We assumed that all fragments were part of the contiguous Atlantic Forest, so the list we compiled of Atlantic Forest birds from southern Bahia should include species found in the area of the current fragments prior to fragmentation. We tested whether: 1) fragments are similar in measures of functional diversity (that is, are the functional traits of the species that remain after fragmentation essentially interchangeable among fragments, or are they associated with fragment size or distance between fragments; 2) fragments differ in functional diversity measures from the original Atlantic Forest and the differences are associated with fragment size or distance; and 3) the species lost from fragments are functionally similar in all fragments (that is, is functional diversity among the absent species similar among fragments or associated with fragment size or distance? We used functional evenness (FEve), functional dispersion (FDis) and functional divergence (FDiv), because these variables are good, previously used indicators of functional diversity (Oliveira et al. 2020).

Variables chosen for the functional diversity analysis are those in Oliveira et al. (2020) and associated with feeding patterns (overall diet and foraging strata). As in Oliveira et al. (2020), we accessed the data in EltonTraits 1.0 (Wilman et al. 2014). To more precisely divide the Atlantic Forest species into regionally meaningful groups and to reduce redundancy (Petchey and Gaston 2006), we modified the diet groups in Wilman et al. (2014), from five to eight categories based on our own information and observations, supplemented with the Handbook of Birds of the World (https://birdsoftheworld.org/bow/home, Table 2). By doing so, we distributed the categories in such a way as to increase the numbers of species in the smallest category and reduce the number in the largest, thereby improving the distribution for the analysis. We also included five variables that describe predominant foraging strata (in percentages of observations) (Wilman et al. 2014). We combined the ground and low understory categories to generate a single variable (LOW), which improved the distribution of the variable among species. With one diet variable and four foraging strata variables, we weighted them such that the four foraging strata variables together (w = 1 each) had the same weight as the single diet variable (w = 4). Average species weight was also weighted (w = 4) to have the same importance as diet. We weighted species abundance by fragment (w.abund = T), and standardized the numeric variables (stand.x = T). When the expected regional assemblage was used, functional analysis was based on presence-absence rather than abundance. For these analyses and figures, we assumed the area of the source (with the entire expected regional assemblage) was 10,000 ha, another order of magnitude larger than the fragments, because the range of observed fragment areas varied by roughly two orders of magnitude (from ~10 to ~1,000 ha).

We compiled lists of the expected regional assemblage that were absent from each fragment to test our prediction that the lost diversity included a functional component that may increase with fragment size. We predicted an increase in FEve because of the added redundancy of more species in a larger area. Similarly, an increase in FDis because, as fragment size increases, the forest should become more variable and allow the addition of species, typical of patterns associated with species-area curves (Whittaker and Fernández-Palacios 2006). FDiv, on the other hand, was less easily predicted and so we simply posit a potential association with fragment size. We then estimated FEve, FDis and FDiv of the absent birds in the fragments using presence-absences rather than abundances, which cannot be estimated (Oliveira et al. 2020). Functional diversity indices were calculated and compared using the R package FD, function dbFD (Laliberté and Legendre 2010). Our null model predicted that all birds in all fragments should be subsets of the same larger

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species pool, the expected regional assemblage.

Atlantic Forest endemic species follow Vale et al. (2018) and Caatinga endemic species follow Pacheco (2004). Threatened species follow the IUCN (IUCN 2021), the Brazilian (ICMBio/MMA 2018) or the state (Bahia 2017) Red Lists. Nomenclature, taxonomy, and phylogenetic sequences follow Pacheco et al. (2021).

RESULTS

Alpha diversity

A total of 251 species (Table S1) in 5,391 individuals were encountered during the 15 field days (30 transects walked during a total of 105 h observer^{-1}), which comprised a total of 428 10-species lists. Fragments had 106 to 150 species, 10 to 40 endemic species, and 0 to 7 threatened species (Table 1). Of the observed 251 species, only 165 (66%) were in the expected regional assemblage (of 380 Atlantic Forest species, 44%), and the other 86 species (34%) were from adjacent habitats (the matrix formed during anthropic fragmentation).

The number of species observed in each fragment was independent of fragment size ($\log_{10}$ transformed in the regression, $F_{1,8} = 2.18$, $p = 0.178$). Species accumulation curves did not reach an asymptote in any of the fragments, and the number of species predicted (Chao1), was also independent of fragment size (observed: $r = 0.275$, $p = 0.442$, Chao1: $r = -0.108$, $p = 0.767$, both N = 10). Each fragment had only 52–79% of the predicted value of all 271 species (Chao1) for all fragments combined (Fig. 2A). The number of predicted species (271) rather than observed (251) was 109 fewer than the known number of species (380).

Only 23 species (9% of the total observed) were found in all fragments, 46 species (18%) were found in a single fragment, and 148 (59%) species were found in five or fewer fragments. Thus, species composition of fragments was quite variable.

Beta diversity

Fragments tended to be very dissimilar and varied 0.56–0.83 (mean = 0.67). Distance between fragments did not influence their likelihood of sharing species (as measured by Jaccard and minimum linear distance between fragments, $r = 0.17$, $p = 0.265$, $N = 45$ pairs of dissimilarity and linear distance measures, Fig. 2B).

All fragments had between one and six species that were in only one list, and the number of species on a single list was independent of fragment size ($r = -0.22$, $N = 10$, $p = 0.538$). The species found in half or

Table 2. Diet classifications used in the functional analyses, derived from Wilman et al. (2014). Briefly, their Diet* and Description below which is our modified classification. The column N Species indicates how many of the 251 species in this study are in each group

Diet following Wilman et al. (2014)			
Diet*	Description	Justification	N Species
FruiNect	Fruit, Nectar	Globally, many species along with Meliphagidae (Old World) and Trochilidae (New World)	44
Invertebrate	Animals, not vertebrates	Many species	142
Omnivore	Anything	Many species	35
PlantSeed	Granivores and folivores	No folivores	14
VertFishScav	Vertebrates, both alive and dead	Includes many taxa not found in South America	16
Modified from the above for the Atlantic Forest			
Fruit	Primarily frugivores	Mostly Cotingidae, Pipridae, Fringillidae, (all unique to the Americas)	15
Nectar	Primarily nectar	In AF, essentially hummingbirds	15
Insect/Invert	Insectivores	Carnivorous, but smaller, eat invertebrates, small Tyrannidae, Furnariidae	111
IF	Insects and fruits	Tyrannidae, Tityridae, Turdidae	54
Granivore	Seeds	Seed dependent, many Cardinalidae	8
GF	Seeds and fruit	Columbidae, Passerelidae, some Psittacidae	11
Omnivore	Anything	Tinamidae, Rallidae, Cracidae; some Psittacidae (because they eat seeds, fruits, flowers, stems)	16
Carnivore	Typically vertebrates	Accipitridae, Falconidae, Cathartidae, one Alcedinidae	21

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more of the lists were uniformly distributed among the fragments, which had from 24–29 of those species, and these species were found in 8–10 of the fragments. Of those species, 10 are endemic, 19 are not, and only one (*Thripophaga macroura*) is threatened (vulnerable). Of the 48 endemic species, only five (10%) were encountered in all fragments, while eight (17%) were found in only one among five fragments. Twenty-seven endemics were found in five or fewer fragments. Thus, all fragments share 10% of endemics, while many fragments have unique combinations of endemics that are not found in any other fragment.

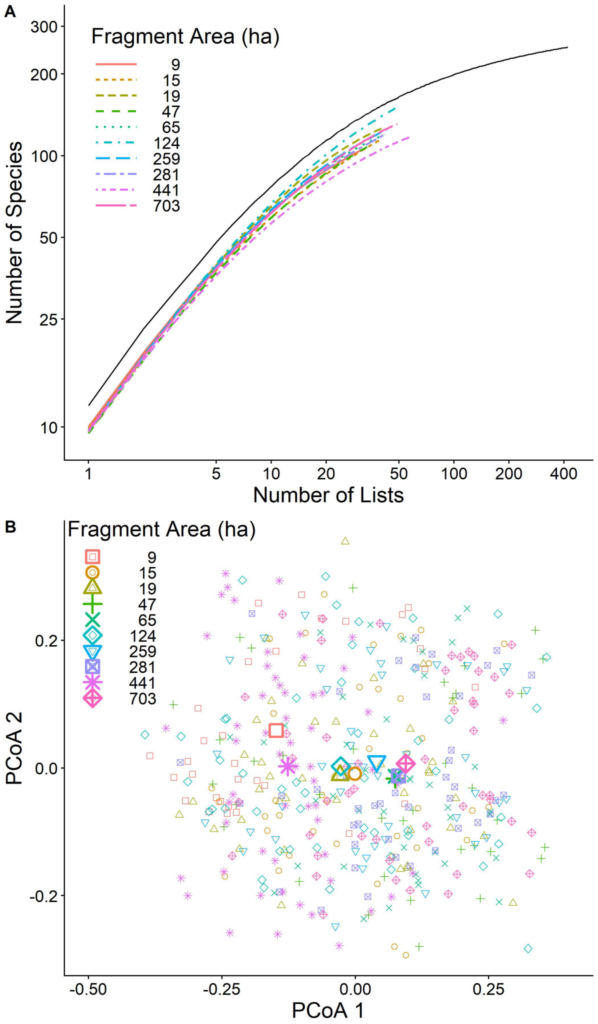

Fig. 2. Numbers of species and similarities (PCoA) among the 10 Atlantic Forest fragments in southern Bahia, Brazil. A) Species accumulation curves, illustrating that with over 5000 sightings, the predicted total number of species had not been reached in any fragment, or in all fragments combined. Also, the similarity of the curves and their lack of a relationship with fragment size suggests that all fragments are similar with respect to accumulation of species. Note that both axes are $\log_{10}$ scaled. B) Principal Coordinate Analysis, using Bray similarities, illustrating that similarity among fragments was always low. Larger symbols indicate fragment centroids, and each smaller point indicates a sample list of species (see text). No particular pattern is evident, and all fragments are variable and do not form groups based on fragment size.

In the list of 251 species, seven are globally vulnerable and one is endangered (*Phylloscartes beckeri*). In Brazil, six are vulnerable and three are endangered (*Cichlopsis leucogenys*, *Dysithamnus plumbeus*, *Phylloscartes beckeri*), the latter two of which are endemic. These threatened species were found in nine of the ten fragments, being absent from only the smallest 9-ha fragment (Table 1). Three species were found in only one fragment (2 in the 703-ha, 1 in the 441-ha fragment), and one species was found in 2, 5, 7, and 8 fragments. Again, we can see that no single fragment contained most or all of the endemic or threatened species.

Gamma diversity

We compiled a list of 380 expected species of birds (Table S2). Of the observed 251 species, only 165 (66%) were in the expected regional assemblage (44%), and the other 86 species (34%) were from adjacent habitats (the matrix formed during anthropic fragmentation).

Of the 165 forest species observed, fragments had 56 (15% of the total in the expected regional assemblage, 34% of the total observed) to 101 (27% and 61%) species. The number of observed species of the expected regional assemblage increased with fragment size ($\log_{10}$Number of species = 1.76 + 0.089 * $\log_{10}$Fragment size, $F_{1,8} = 13.4$, $r^2 = 0.625$, $p = 0.0065$). The distribution of points in that regression suggests that there is a cutoff at around 50 ha, above which all fragments have more or less the same number of species (90–101) and below which fragments have fewer than 90 species (56–83, Fig. 3). The number of the remaining, non-forest species in each fragment was independent of fragment size ($F_{1,8} = 3.17$, $p = 0.113$). Another way of expressing this result is that larger fragments tended to have more forest species, and fewer non-forest species than expected (and smaller fragments the converse, $G = 30.0$, $d.f. = 9$, $p < 0.001$). That trend was not exceedingly strong, however, because two fragments (47, 65 ha) had 5–7 more forest species than expected, and the 124 ha fragment had 5 fewer than expected. Thus, the three fragments in the middle of the range were exceptions, while both extremes (9, 15, 19, 281, 441, 703 ha) followed the pattern. From the perspective of the species, whether it was or was not a forest species was independent of the number of fragments in which it was found ($G = 12.9$, $d.f. = 9$, $p = 0.170$).

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The number of species in the expected regional assemblage of Atlantic Forest was much greater than the observed number of species in each fragment (Random versus Observed in Fig. S1). The expected number of the subset of 165 species of the Atlantic Forest was also greater than observed, if the species were randomly distributed among fragments (Observed randomized versus Observed, Fig. S1A). The distribution of those species among fragments was very different than expected under random processes (Fig. S1B). In the fragments, more species than expected were seen in only 1–3 fragments. On the other hand, more species were expected in 5–8 fragments (Random 380), 8–10 fragments (random 165), or 9–10 fragments (Observed randomized). Thus, the observed distribution of species among fragments is very different from that expected if that distribution were random.

Functional evenness decreased with increasing fragment size, in the Atlantic Forest expected regional assemblage (ERA, $F_{1,9} = 19.9$, $p = 0.002$), and the observed assemblage minus the non-Atlantic Forest species (Frags – F, $F_{1,8} = 6.05$, $p = 0.039$, Fig. 4A). Functional dispersion decreased with fragment size for the total observed assemblage (Frags + F, $F_{1,8} = 17.6$, $p = 0.003$), but not the expected regional assemblage ($F_{1,9} = 0.169$, $p = 0.691$), nor the observed assemblage minus the non-Atlantic Forest species (Frags – F, $F_{1,8} = 1.40$, $p = 0.270$, Fig. 4B). Functional divergence decreased with fragment size for the expected regional assemblage (ERA, $F_{1,9} = 6.89$, $p = 0.028$), the total observed assemblage (Frags + F, $F_{1,8} = 8.70$, $p = 0.018$), and the observed assemblage minus the non-Atlantic Forest species (Frags – F, $F_{1,8} = 6.12$, $p = 0.039$, Fig. 4C, Table 3). In the assemblage of species missing from the fragments, only FEve increased with fragment size (FEve: $F_{1,8} = 10.58$, $p = 0.012$), while FDis ($F_{1,8} = 0.90$, $p = 0.372$) and FDiv ($F_{1,8} = 1.63$, $p = 0.238$) were independent of fragment size (Fig. 4D–F, Table 3). The range of the functional diversity values for the missing assemblage was much narrower than for the observed assemblages.

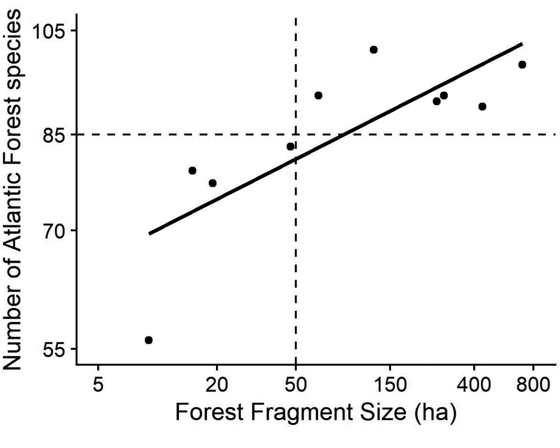

Fig. 3. The number of local Atlantic Forest species by forest fragment size ($\log_{10}$ scales), showing that the number increases with fragment size ($F_{1,8} = 13.4$, $r^2 = 0.625$, $p = 0.0065$).

DISCUSSION

Atlantic Forest fragments in southern Bahia have a diverse, but depauperate bird community, with a somewhat unique assemblage in each fragment, and with species richness and composition that are both unrelated to fragment size or distance to other fragments. Each fragment has several species of birds not found in any other fragment, often including endemic or threatened species. Also, each fragment comprises a small part (18–26%) of the expected regional assemblage of the 380 species of southern Bahia and comprise less than half when they are summed together (43%). These results are surprising and counter many observed and theoretical relationships between fragment size, distance, and species richness and composition (Anjos 2004; Ferraz et al. 2007; Stouffer et al. 2011; MacArthur and Wilson 2016).

As was the case in a fragment study in the Amazon (Bierregaard Jr et al. 2001), the surrounding matrix was originally uniformly forested, and all fragments should have had all species in the expected regional assemblage. We can only conclude that differential, local extinctions caused the losses of species in each fragment. Because we do not have repeated measurements of these fragments, we cannot examine how species disappeared, or returned, over time. How do we explain that no fragment include more than 30% of the expected species, and all fragments together had only 44% (165) of the expected species?

Our surveys were not exhaustive, but the evidence does not imply that patterns were due to incomplete sampling. For example, because the number of fragments in which a species was found was independent of the origins of that species (of the expected regional assemblage, or not), there is no obvious rhyme nor reason as to why any species became extinct in some fragments and not others (Faria et al. 2007; Boscolo and Metzger 2009). While the assemblages in larger fragments tended to have a larger proportion of forest species, that proportion only varied from around 53 to 77%. Considering both the fact that the largest fragment was > 70 times larger than the smallest fragment and results of other studies (Ferraz et al. 2003 2007; Stouffer et al. 2006), we expected a much larger effect. Also, fragment size and edge effects associated with nest predation or adult survival,

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differential survival among different sized fragments (and consequently, with proportionately different sized edges), should have generated some species-area relationships (Stouffer et al. 2011; Wolfe et al. 2020).

The relative paucity of forest species in fragments might explain part of the lack of a general relationship with fragment size. The total of 251 species in all fragments was only 66% of the expected number of species, and no fragment had more than 60% of the total number of species among all fragments. The remaining 34–40% of the birds were from the anthropic matrix, and those species should be more or less equally likely to be found among fragments. While the total number of species in each fragment was unrelated to fragment size, the Atlantic Forest fraction did increase with fragment size. These observations suggest that biotic homogenization of the avifauna in the region is likely to become more important over time. Biotic homogenization will happen because species that use the anthropic matrix will become more abundant and will be common in all fragments. At the same time, if the species of forest birds decline over time, as they tend to do in fragments, then homogenization will be the result (Woodruff 2001; Sodhi et al. 2008; MacGregor-

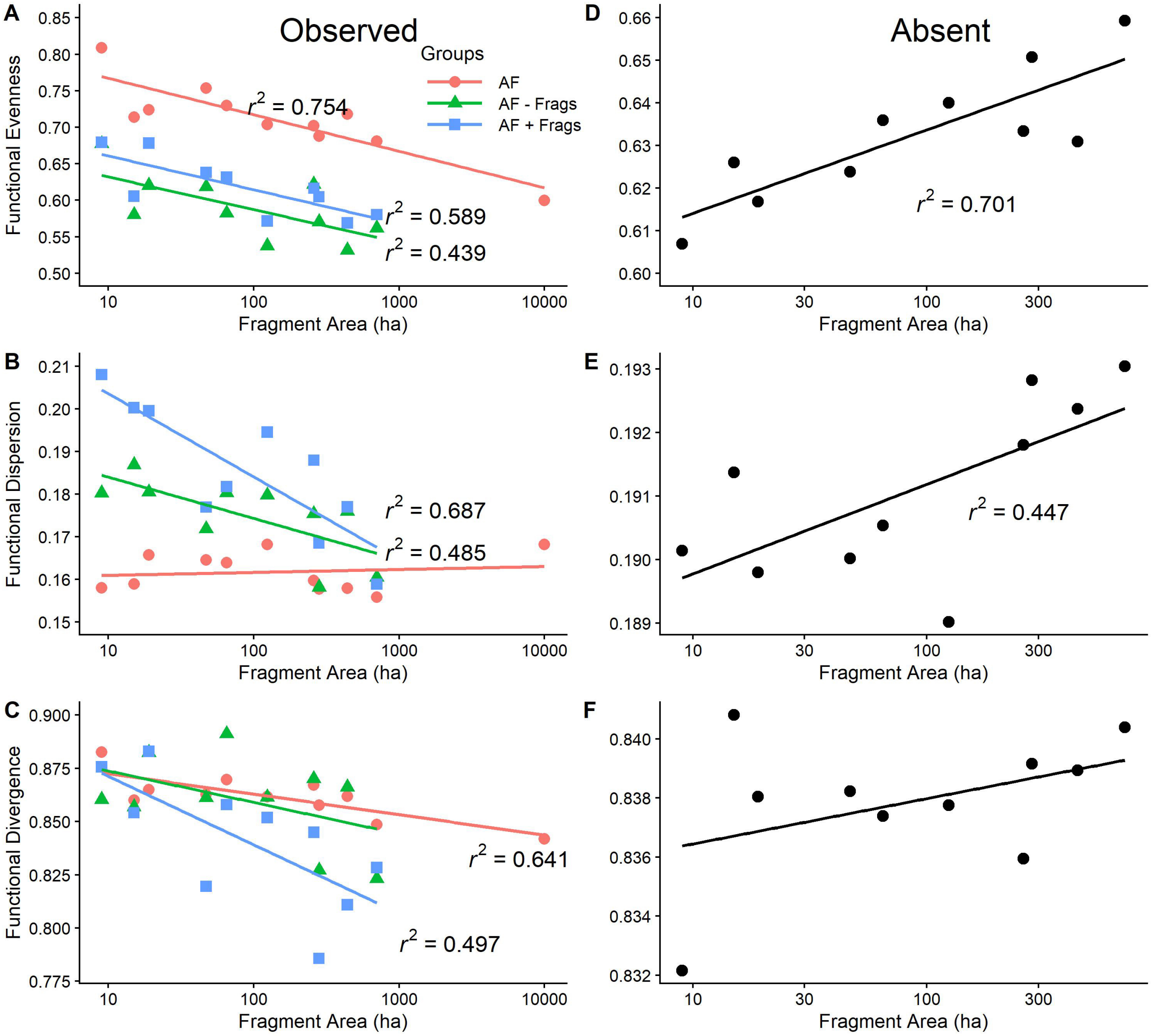

Fig. 4. Functional diversity analysis comparing different-sized fragments and functional evenness, dispersion, and divergence. A–C: Black squares and lines indicate the Atlantic Forest expected regional assemblage, circles and lines indicate the observed assemblages, with blue indicated only the Atlantic Forest species, and the open circle indicates all observed species (all based on presence-absence). D–F: estimated from presence-absence data of the expected local assemblage that were absent from the fragment. Regression results are presented in table 3.

Fors et al. 2010; McDonald et al. 2012).

More forest species were found in larger fragments and the six largest fragments all had similar species richness. This may indicate a threshold of fragment size that supports these birds. Larger fragments may support more species simply because, with a smaller edge effect, birds have more successful nests (Lloyd et al. 2006; Young et al. 2008; Vergara and Hahn 2009; Vetter et al. 2013; Roper et al. 2018). Also, the threshold may be due to competition with a less diverse but more abundant non-forest assemblage of birds (references in Pizo and Tonetti 2020). Finally, the threshold may be a consequence of the Allee effect, in that for each species, the relationship between home range size and fragment size may be such that, depending on the species, the fragment may not support enough pairs, and nest predation may be too high for the populations to persist because reproductive success is too low to maintain the population (Allee and Bowen 1932; Roper et al. 2018; Fadai et al. 2020).

Compared to nearby, but better-preserved forests (Silveira et al. 2005; Cavarzere et al. 2019), these fragments were depauperate. Small fragments tend to not support parrot diversity, nor large frugivores, such as guans and currassows, or large birds of prey (Willis 1979; Cordeiro 2003), all of which were absent from all fragments. Additional sampling efforts may find these species, but they would have to be much greater, as suggested by the accumulation curves. While unobserved presences are always an issue for rare species (MacKenzie et al. 2002), their rarity remains a problem due to fragmentation that will have repercussions on their population dynamics.

Isolation, as well as fragmentation, should be important in community dynamics (Ferraz et al. 2007). However, distance among fragments was independent of species richness, and of similarities of the assemblages. A variety of habitat characteristics may contribute to fragment dynamics (Uezu et al. 2008; Boesing et al. 2018), but here, these appear to be unimportant because all fragments are relatively near one another and of similar age and characteristics, so it is difficult to attribute local extinctions to any particular cause. A long-term study would be required to find causes for idiosyncrasies, extinctions, recolonizations, Allee effects, and invasion to explain patterns in these forests (Laurance et al. 2011; Stouffer et al. 2011; Willrich et al. 2019).

The measures of functional diversity were different for forest species than for the entire assemblage. FEve decreased with fragment size rather than increased as predicted, but only with the expected regional assemblage and the observed assemblage minus the non-forest species (Fig. 4A). FDis, on the other hand, only decreased with fragment size in fragments when including those non-forest species. FDiv decreased with fragment size under all conditions. With the assemblage of species of the expected regional assemblage that were apparently missing from the fragments, FEve of those species increased with fragment size. Thus,

Table 3. Linear regressions of three measures of functional diversity (based on presence-absence) by forest fragment area (FA). FEve – functional evenness, FDis – functional dispersion, FDiv – functional divergence. Data subsets are: Atlantic Forest – with species of the expected regional assemblage only, AF + Frag – the Atlantic Forest (the preceding include the 10,000 ha of the expected regional assemblage) plus the species observed in the fragments but not of the Atlantic Forest domain, Fragments (AF) – only species of the Atlantic Forest domain observed in the fragments, Fragments (all) – all species observed during this study in the fragments. r^2 values are only included with the statistically significant models. In parentheses below the data subset name are the codes used in figure 4A–C and for missing species figure 4D–F

Data subset	Equation	r^2	p
Atlantic Forest (ERA)	$\text{FEve} = 0.822 - 0.011(\log_{10} \text{FA})$	0.654	0.002
	$\text{FDis} = 0.270 + 0.001(\log_{10} \text{FA})$		0.691
	$\text{FDiv} = 0.856 - 0.019\ (\log_{10} \text{FA})$	0.371	0.028
Fragments (AF) (Frags - F)	$\text{FEve} = 0.817 - 0.008\ (\log_{10} \text{FA})$	0.359	0.039
	$\text{FDis} = 0.281 - 0.004\ (\log_{10} \text{FA})$		0.270
	$\text{FDiv} = 0.818 - 0.018\ (\log_{10} \text{FA})$	0.362	0.039
Fragments (all) (Frags + F)	$\text{FEve} = 0.778 - 0.003\ (\log_{10} \text{FA})$		0.420
	$\text{FDis} = 0.396 - 0.039\ (\log_{10} \text{FA})$	0.512	0.012
	$\text{FDiv} = 0.920 - 0.066\ (\log_{10} \text{FA})$	0.461	0.018
Atlantic Forest (missing)	$\text{FEve} = 0.782 + 0.006\ (\log_{10} \text{FA})$	0.516	0.012
	$\text{FDis} = 0.306 + 0.001\ (\log_{10} \text{FA})$		0.372
	$\text{FDiv} = 0.835 + 0.005\ (\log_{10} \text{FA})$		0.238

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decreasing evenness with increasing fragment size seems to suggest that the species composition of larger fragments tends to clump into fewer functional groups with a variable number of species (Schleuter et al. 2010). The increase in FEve of the missing species suggests the complementary viewpoint that those absent species are in fewer, more evenly distributed, functional groups. FDis only decreased with increasing fragment size for the assemblage that included non-forest species, and FDiv declined for all groups, but most steeply for the assemblage containing non-forest species. For conservation concerns, we must consider the species or habitat type that we are trying to conserve when carrying out functional diversity analyses. We cannot simply collect the data as if all species were of equal interest (Anjos et al. 2019; Oliveira et al. 2020). Perhaps some, but not all, of the species that were absent from all fragments have some underlying commonality and so they disappeared for similar reasons, a topic for future study.

More importantly for understanding the consequences of fragmentation are the implications for the use of functional diversity indices, which are typically calculated based on the observed assemblage of species within the parameters of the study design (Mason et al. 2005; Schleuter et al. 2010; Mammola et al. 2020). Studies of this nature tend to include the observed species in the region of interest, rather than the species that are expected to be in that region. Consequently, studies may include species with origins outside of the domain of interest – that is, the observed species (regardless of origin) are all included in the community matrix. As we demonstrated here, the observed species may be comprised of many species from different biomes (as a consequence of fragmentation and a changing matrix) and exclude many that should be in the region. We found that fewer than a third of all the species of the expected regional assemblage were found in any fragment. A similar pattern is likely to have occurred in other, species-rich areas of South America (Anjos et al. 2019; Oliveira et al. 2020). One must ask of what are we estimating the functional attributes? If it is not the community of interest that we wish to conserve, then the usefulness of functional diversity indices comes into question for these kinds of conservation questions.

CONCLUSIONS

Our goal was not to understand exactly how these forest assemblages acquired their characteristics, but rather to help conservation efforts in the future. The lack of distance relationships implies that the stepping-stone model does not apply, and the only way to increase the likelihood that species occur in all fragments is by connecting them. Next, at least some of the fragments should be allowed to increase in size. Fragments smaller than 50 ha tend to have fewer species, and so increasing the size of small fragments may be especially helpful in maintaining diversity, especially if those fragments are connected by corridors and restored environments.

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Supplementary materials

Fig. S1. Simulation results showing that the distribution of species among fragments is neither explained by fragment size, nor does it appear to be random. A) The number of species per fragment based on a random selection of species by the number of individual birds observed in each fragment. The observed curve is the number of birds observed in the field. Observed randomized is based on 165 Atlantic Forest species observed but chosen randomly from the list of all observations. Random is based on the 380 expected local Atlantic Forest species. The number of species seems more determined by the sample size than fragment size. Both axes are log10 scaled. B) The number of species observed from 1–10 fragments. Observed indicates the actual number of species reported in this study. Observed randomized was randomized over all observations, but then randomly selected in each fragment based on the number of individuals observed in each fragment. Random 165 is from choosing from the list of the 165 Atlantic Forest species noted in this study, using the number of individuals observed in each fragment. Random 380 is the expected curve if all species were randomly distributed among all fragments, such as when the forest was continuous, using the number of individuals observed in each fragment. The observed curve tends to have more species in fewer fragments and fewer species in more fragments than all the other curves. (download)

Table S1. List of species encountered in the fragments during this study in southern Bahia, Brazil. The species list is followed by columns indicating the fragment size (x indicates presence in that fragment), followed by endangered ratings in the state of Bahia (Bahia 2017), Brazil (ICMBio/MMA 2018) and IUCN (IUCN 2021), and their endemic status (AF = Atlantic Forest, CA = Caatinga). (download)

Table S2. List of all species in the expected regional assemblage (Atlantic Forest birds of southern Bahia). (download)

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