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Ecological traits modulate bird species responses to forest fragmentation in an Amazonian anthropogenic archipelago

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Abstract

Aim: We assessed patterns of avian species loss and the role of morpho-ecological traits in explaining species vulnerability to forest fragmentation in an anthropogenic island system. We also contrasted observed and detectability-corrected estimates of island occupancy, which are often used to infer species vulnerability.

Location: Tucuruí Hydroelectric Reservoir, eastern Brazilian Amazonia.

Methods: We surveyed forest birds within 36 islands (3.4–2,551.5 ha) after 22 years of post-isolation history. We applied species–area relationships to assess differential patterns of species loss among three data sets: all species, forest specialists and habitat generalists. After controlling for phylogenetic non-independence, we used observed and detectability-corrected estimates of island occupancy separately to build competing models as a function of species traits. The magnitude of the difference between these estimates of island occupancy was contrasted against species detectability.

Results: The rate of species loss as a function of island area reduction was higher for forest specialists than for habitat generalists. Accounting for the area effect, forest fragmentation did not affect the overall number of species regardless of the data set. Only the interactive model including natural abundance, habitat breadth and geographic range size was strongly supported for both estimates of island occupancy. For 30 species with detection probabilities below 30%, detectability-corrected estimates were at least tenfold higher than those observed. Conversely, differences between estimates were negligible or non-existent for all 31 species with detection probabilities exceeding 45.5%.

Main conclusions: Predicted decay of avian species richness induced by forest loss is affected by the degree of habitat specialisation of the species under consideration, and may be unrelated to forest fragmentation per se. Natural abundance was the main predictor of species island occupancy, although habitat breadth and geographic range size also played a role. We caution against using occupancy models for low-detectability species, because overestimates of island occupancy reduce the power of species-level predictions of vulnerability.

KEYWORDS
detectability, insularization, island biogeography, occupancy, rarity, species-area relationships

1 | INTRODUCTION

Amazonian forests have been extensively converted to cattle pasture and cropland inducing widespread loss and fragmentation of formerly continuous forests, especially in the eastern and southern portions of the basin (Laurance et al., 2001; Peres et al., 2010). This scenario is further exacerbated by a massive growth in hydroelectric dams, which invariably inundate large tracts of forest, creating archipelagic landscapes (Lees, Peres, Fearnside, Schneider, & Zuanon, 2016). Forest fragmentation is widely recognised as a pervasive and lasting threat to biodiversity and ecosystem functioning as forest fragments are subject to the combined detrimental effects of core area reduction, edge proliferation, and isolation (Haddad et al., 2015). Nevertheless, the quality of the matrix surrounding forest fragments plays a major role in determining the severity of fragmentation (Kennedy, Marra, Fagan, & Neel, 2010). Old-growth forest fragments surrounded by secondary forests favour species that exploit matrix resources (Blake & Loiselle, 2001), are less affected by edge effects (Laurance et al., 2011), and are more permeable, ensuring species movements among forest fragments (Powell, Stouffer, & Johnson, 2013). Conversely, forest islands within hydroelectric reservoirs exhibit lower functional connectivity, are expected to be dominated by edge-mediated decay in forest structure (Benchimol & Peres, 2015), and harbour depauperate extinction-driven species assemblages (Wolfe, Stouffer, Mokross, Powell, & Anciães, 2015). The detrimental consequences of forest fragmentation are therefore amplified by a water matrix (Mendenhall, Karp, Meyer, Hadly, & Daily, 2014), rendering hydroelectric dams a more severe threat to forest biotas.

Habitat loss and fragmentation are the twin processes associated with land-use change. From a species perspective, the former is defined as the conversion of a "habitat" into a "non-habitat" (i.e., habitat amount shrinkage), and the latter as the subdivision of a single large "habitat" into several smaller "habitat patches" separated from one another by an intervening "non-habitat" matrix (Lindenmayer & Fischer, 2007). While habitat loss has pervasive negative effects on native biodiversity, fragmentation affects species differently (Fahrig, 2003). For instance, habitat specialists are more consistently impaired by fragmentation than habitat generalists (Devictor, Julliard, & Jiguet, 2008). Predictions of species loss based on species–area relationships are therefore expected to be underestimated for habitat specialists if habitat generalists are included in the species pool (Matthews, Cottee-Jones, & Whittaker, 2014). Moreover, habitat fragmentation per se (i.e., accounting for habitat loss) may either decrease or increase the number of species that would be predicted by habitat loss alone (Yaacobi, Ziv, & Rosenzweig, 2007). Therefore, a proper assessment of species loss in variable-sized habitat patches should focus on groups of target species (Matthews et al., 2014) and disentangle the effects of habitat loss from fragmentation (Fahrig, 2003; Yaacobi et al., 2007).

Species-level studies on responses to habitat fragmentation can further enhance our understanding of vulnerability-prone traits at both landscape (Feeley, Gillespie, Lebbin, & Walter, 2007) and global scales (Bregman, Sekercioglu, & Tobias, 2014), complementing assemblage-wide studies (Moura et al., 2016). Accordingly,

low-density, large-bodied species at high trophic levels (Ewers & Didham, 2006), and those with restrict habitat breadth (Henle, Davies, Kleyer, Margules, & Settele, 2004) and wide geographic range (Newbold et al., 2014) are expected to be at higher risk of extinction. The same holds true for bird species inhabiting the lower strata of closed-canopy forests (Sekercioglu et al., 2002), following ant-swarms and foraging in mixed-species flocks (Stouffer & Bierregaard, 1995). Understanding trait-based patterns of extinction proneness is therefore invaluable to anticipate species losses and tailor conservation programmes to vulnerable species. However, idiosyncratic species responses across different regions (Gage, Brooke, Symonds, & Wege, 2004; Moura et al., 2016), and the co-occurrence of confounding factors in human-modified landscapes, such as matrix type, may limit the extent to which clear patterns can be uncovered (Ewers & Didham, 2006), reinforcing the need for landscape-scale studies.

In fragmented landscapes, the area of remaining patches is the main driver of species patch occupancy (Keinath et al., 2017). Area-sensitive species can no longer occur in patches below a minimum spatial requirement, and are consequently relegated to fewer patches than species requiring smaller areas (Dardanelli, Nores, & Nores, 2006). Thus, the proportion of patches occupied in a landscape has often been used as a measure of species vulnerability to habitat fragmentation (e.g., Meyer, Fründ, Lizano, & Kalko, 2008; Thornton, Branch, & Sunquist, 2011; Wang, Thornton, Ge, Wang, & Ding, 2015). Due to inherent differences in species detectability and the fact that non-detections do not necessarily imply absences, observed estimates of patch occupancy can be underestimated. To overcome this bias, occupancy modelling has often been uncritically used as it can estimate patch occupancy while accounting for imperfect detectability (Banks-Leite et al., 2014). Unlike observed estimates, this analytical approach can overestimate patch occupancy for species with low detection probability (< 30%; MacKenzie et al., 2002), which may degrade inferential power about species vulnerability.

Habitat fragmentation research has largely focused on terrestrial landscapes (Fahrig, 2017), where the remaining habitat (i.e., area of native vegetation) is typically termed as "remnant," "fragment," or "patch." Nonetheless, the term "island" best describes remaining habitats in archipelagic landscapes. To avoid misleading terminology (Hall, Krausman, & Morrison, 1997), herein we refer to the remaining habitats in terrestrial and archipelagic landscapes as "fragments" and "islands," respectively. Meanwhile, the term "patch" is used to encompass both "fragment" and "island." In this study, we assessed bird species responses to forest fragmentation in a vast archipelagic landscape induced by a major hydroelectric dam in eastern Brazilian Amazonia, while addressing the four following questions. First, do habitat generalists show a less steep decline in species richness as a function of island area reduction compared to forest specialists? If so, we predict that assessments of overall species loss relying on species–area relationships also underestimate the loss of forest specialists in reservoir islands as previously shown for forest fragments (Matthews et al., 2014). Second, does forest fragmentation per se exacerbate or reduce the impact of forest loss on species richness for the overall species pool, forest specialists and habitat generalists? We predict a neutral

fragmentation effect on the overall species pool due to a negative effect on forest specialists and a positive effect on habitat generalists. Third, which suite of morpho-ecological traits best explains species rates of island occupancy within the forest archipelago? This allowed us to determine which species are most or least prone to extirpation from anthropogenic island systems to anticipate species losses driven by existing and future hydroelectric impoundments in lowland tropical forests. Fourth, how divergent are observed and detectability-corrected estimates of island occupancy for rarely detected species? We show distinct responses to forest loss between forest specialists and habitat generalists, and that forest fragmentation per se may not affect the overall number of species in forest islands. We also emphasize the use of rarity metrics to assess species vulnerability to forest fragmentation, and caution against the use of occupancy models to infer island occupancy rates when species detection probability is low.

2 | METHODS

2.1 | Study area

This study was carried out within the vast Tucuruí Hydroelectric Reservoir (hereafter, THR; 4°16′ S, 49°34′ W), located in the State of Pará, eastern Brazilian Amazonia (Figure 1). The reservoir was formed in 1984 when the Tocantins River was dammed, flooding over 250,000 ha of pristine lowland forests and creating some 2,200 islands on higher elevation terrain. In 2002, the entire archipelago and surrounding areas were set aside as a sustainable-use reserve (IUCN category VI), spanning 568,667 ha. This protected area—Tucuruí Lake Environmental Protection Area (APA Lago de Tucuruí, in Portuguese)— is a multiple-use mosaic designated to meet both the interests of local communities and wildlife conservation.

The vegetation is typical of Amazonian *terra firme* forests, containing 80%–90% forest cover and an understorey dominated by several palm species (Ferreira, Neckel-Oliveira, Galatti, Fáveri, & Parolin, 2012). The climate is equatorial monsoonal (Am), with a rainy season from December to May and a dry season from June to November (Alvares et al., 2013). Mean annual precipitation and temperature are 2,354 mm and 27.5°C, respectively (Alvares et al., 2013).

The THR is located in the most deforested region of Brazilian Amazonia, known as the "Arc of Deforestation," and encompasses both the Xingú and Belém lowland areas of endemism, which are separated by the Tocantins River (da Silva, Rylands, & Da Fonseca, 2005). To survey the forest avifauna of the reservoir, we selected an even number of islands across a comparable size range on each bank of the former river channel. Many islands and mainland sites surrounding the reservoir were heavily degraded, but we surveyed a set of 36 relatively undisturbed forest islands located within (*n* = 26) or adjacent to (*n* = 10) the two Wildlife Protection Zones (ZPVS): ZPVS 3 on the left bank and ZPVS 4 on the right bank (Figure 1b). The two largest islands (>1,800 ha) were defined as "pseudo-controls," and 34 smaller islands as "treatments," which were selected to maximise the range of island sizes, shapes and degrees of connectivity (see Table S1). The pseudo-control island on the right bank is actually a mainland peninsula that was semi-isolated along a boundary of secondary forest.

2.2 | Avian surveys

We conducted six field campaigns over a 15-month period: 6–25 August and 12–29 November in 2006, and 4–22 March, 12 April–1 May, 14–31 July and 22 September–10 October in 2007. During each field campaign, all 36 islands were surveyed once using 10-min point counts by experienced observers (S.M.D. or L.M.P.H.) accompanied

FIGURE 1 (a) Location of the study area in eastern Brazilian Amazonia; (b) Tucuruí Hydroelectric Reservoir (THR) within the Tucuruí Lake Environmental Protection Area (grey and white areas), showing the two Wildlife Conservation Zones (ZPVS 3 and 4, indicated by dotted lines) and heavily degraded areas surrounding the THR (yellow); and (c) distribution of the 36 surveyed islands (dark grey and black polygons) within or adjacent to the two ZPVS. The background image was extracted from the TerraClass project (de Almeida et al., 2016), available at http://www.inpe.br/cra/projetos_pesquisas/terraclass2008.phpwileyonlinelibrary.com]. [Colour figure can be viewed at wileyonlinelibrary.com]
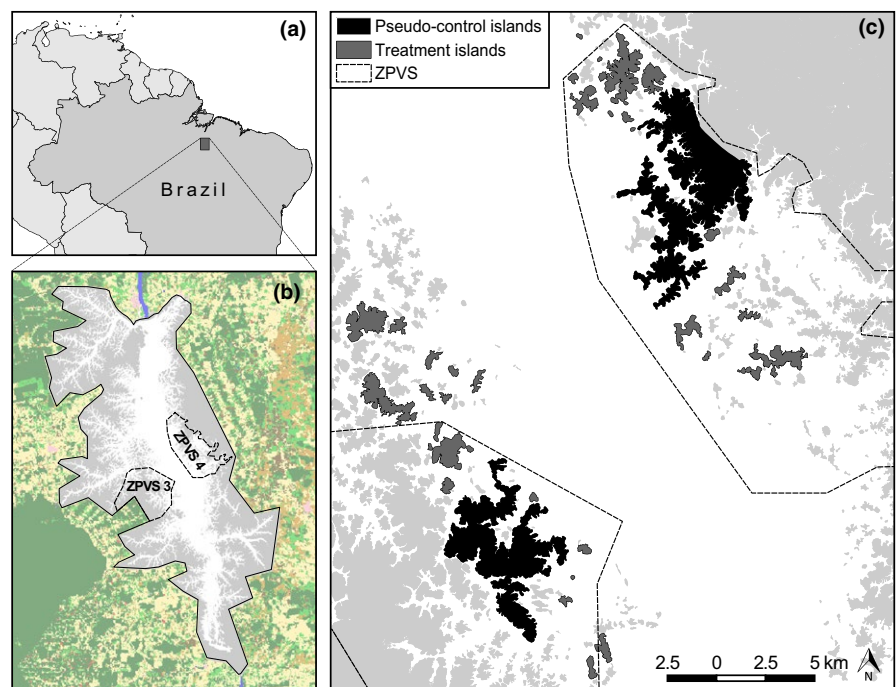
by a field assistant, who simultaneously recorded bird vocal activity (using a Sony TCM-5000 recorder and a semi-directional microphone) as a voucher of species occurrences. To ensure that all birds recorded were within surveyed islands, we restricted all individuals seen or heard to within an estimated 50-m radius from the observer and discarded all flyovers. Given our focus on diurnal forest species, we also discarded all aquatic, nocturnal and aerial species, as well as every species that "does not normally occur in forest" (sensu BirdLife International, 2017). Surveys were usually carried out between 06:00 and 10:00 h avoiding rainy and windy weather. The number of point count stations (hereafter, PCs) surveyed per island, which ranged between 2 and 33 (see Table S1), was roughly proportional to island area on a log–log scale (r^2_{adj} = .863, p < .001). All 36 islands were surveyed along linear transects—three of each placed at the two pseudo-control islands (see Figure S1) and one at each of the 34 treatment islands—along which PCs were distributed at regular 200-m intervals. A total of 240 PCs were visited six times each, amounting to 1,388 samples.

Sampling sufficiency per island was represented by individual-based rarefaction curves produced with 1,000 bootstrap replications in the INEXT R package (Hsieh, Ma, & Chao, 2016; R Core Team, 2016). Sampling completeness per island was quantified as a percentage between the recorded and the estimated number of species based on the first-order Jackknife estimator (Willie, Petre, Tagg, & Lens, 2012) calculated using the VEGAN package (Oksanen et al., 2017).

2.3 | Species traits

We classified the degree of habitat specialisation of each species into "forest specialist" or "habitat generalist" based on two attributes extracted from BirdLife International (2017), namely "forest dependency" and "habitats". Species had to meet two criteria to be classified as forest specialists: (1) "high" forest dependency, and (2) "Forest— Subtropical/Tropical Moist Lowland"—the equivalent to Amazonian lowland forest—listed as a habitat of "major" importance. Species that did not meet these criteria were classified as habitat generalists. Accordingly, a habitat generalist is a species that occurs in forest (i.e., "low," "medium" or "high" forest dependency) but does not have "Forest—Subtropical/Tropical Moist Lowland" listed as a habitat of "major" importance. For example, *Pitangus sulphuratus* has a "low" forest dependency and occurs throughout nine habitat types, including "Forest—Subtropical/Tropical Moist Lowland" which is listed as a habitat of "suitable" importance. Likewise, *Onychorhynchus coronatus* was classified as a habitat generalist, despite its "high" forest dependency, because this species is mostly associated with riparian habitats (Bueno, Bruno, Pimentel, Sanaiotti, & Magnusson, 2012) and this habitat type (i.e., "Forest—Subtropical/Tropical Swamp") was inundated by the THR floodwaters. Habitat generalist is then a species that may use the "Forest—Subtropical/Tropical Moist Lowland" habitat as an alternative habitat. Habitat specialisation was used to examine whether patterns of species loss differed between forest specialists and habitat generalists.

We also compiled data on seven additional traits associated with avian extinction risk (Sodhi, Liow, & Bazzaz, 2004): body mass,

trophic level, vertical stratum, flocking behaviour, geographic range size, habitat breadth and natural abundance (herein defined as the total number of individuals recorded within pseudo-control islands; see Table S2 for variable descriptions and sources, and Table S3 for species traits). We $\log_{10}$-transformed body mass (g), geographic range size (km²) and natural abundance (n + 1) prior to analysis. Trophic level is a continuous variable estimated from proportional consumption of food items across five diet categories. Vertical stratum and flocking behaviour were converted from nominal to ordinal (rank) variables to produce a gradient from ground to canopy strata, and from low to high levels of gregariousness, respectively. Stotz, Fitzpatrick, Parker, and Moskovits (1996) classified 41 habitats for the Neotropical avifauna and assigned one to seven habitats used by each species. Habitat breadth was then defined as a count variable representing the number of habitats used, with lower and higher values indicating restricted and broad habitat breadth, respectively. These traits were used to assess patterns of species occupancy across all 36 surveyed islands.

2.4 | Island and landscape metrics

We used four RapidEye© imagery tiles (250,000 ha at 5-m resolution) covering all surveyed islands and an unsupervised classification performed in ESRI ARCMAP 10.2 to produce a categorical map with two land-cover classes: island and water (Figure 1c). We then extracted three spatial metrics for each island: island area in hectares (AREA), shape index (SHAPE), and proximity index (PROX). SHAPE is a measure of the deviation in the perimeter of a given island from the perimeter (m) of a perfect circle with the same area (m²), and calculated as perimeter/[2√(π × area)], with lower and higher values indicating simple and complex shapes, respectively (Burchell, Shake, Moorman, Riddle, & Burchell, 2012). PROX (sensu McGarigal, Cushman, & Ene, 2012) was used as a measure of connectivity, and considered the total area of any island (≥1 ha) that was partially or entirely within a 500-m external buffer (Benchimol & Peres, 2015), with smaller values indicating lower connectivity or higher isolation. We arbitrarily assigned a PROX value one order of magnitude greater than the most connected island for pseudo-control islands, and a value of 0.01 for the least connected island. Finally, we $\log_{10}$-transformed both AREA and PROX prior to analysis.

2.5 | Species–area relationships and forest fragmentation effect

The logarithmic form of the species–area relationship (type IV curve sensu Scheiner, 2003) was used to allow us to fit simple linear regression models (hereafter, SAR models; Rosenzweig, 1995) for three data sets—all species, only forest specialists, and only habitat generalists— according to the following equation:

$$\log_{10}(S) = z \times \log_{10}(A) + \log_{10}(c),$$

where S = number of species, z = regression slope, A = island area (ha), c = regression intercept. As forest specialists were not

recorded at one small surveyed island, S was standardised as $\log_{10}$ $(n + 1)$. To test whether z-values for forest specialists and habitat generalists were significantly different ($p \leq .05$), we performed an ANCOVA model with habitat specialisation as the categorical independent variable.

We examined whether forest fragmentation per se either exacerbates or reduces species loss as a function of forest loss (i.e., island area reduction) following Yaacobi et al. (2007). Accordingly, after fitting SAR models for each data set, we extrapolated the number of species to a hypothetical island with the combined area of all 36 surveyed islands (6,502.6 ha). We then compared the overall number of species recorded across the whole set of surveyed islands (i.e., gamma diversity) with the extrapolated number of species to the hypothetical island (i.e., predicted alpha diversity) for each data set. If the gamma diversity is lower or higher than the predicted alpha diversity of the hypothetical island, forest fragmentation will have either exacerbated or reduced species loss, respectively. In other words, additional factors other than forest loss operate in explaining the gamma diversity, which we attributed to forest fragmentation. Values were considered significantly different if the overall number of species recorded was outside the 95% confidence interval of the extrapolated number of species. As the accuracy of this method relies on SAR model fits, we deemed the method as appropriate if the z-value was significant and the r^2_{adj} was $\geq.5$ (Matthews, Triantis et al., 2016).

Previous studies have shown that departures in the overall number of species recorded from that predicted by extrapolating SAR models are related to the nested structure of species assemblages (Matthews, Triantis et al., 2016; Santos et al., 2010). To examine how the degree of nestedness relates to the fragmentation effect on species richness, we quantified the nested structure of the three data sets using the nestedness metric based on overlap and decreasing fill (NODF) as this metric is statically robust to overestimating nestedness (i.e., type I statistical errors; Almeida-Neto, Guimarães, Guimaraes, Loyola, & Ulrich, 2008). We used the NODF-PROGRAM, version 2.0 (Almeida-Neto & Ulrich, 2011), to calculate NODF values for all three data sets and for 1,000 simulated assemblages generated with the proportional-row and proportional-column (PP) null model algorithm (Ulrich & Gotelli, 2012). NODF Z-transformed scores (hereafter, Z-scores) were then used to determine whether the nested (positive Z-scores) or antinested (negative Z-scores) structure of species assemblages were significantly different from those of simulated assemblages (Matthews, Cottee-Jones, & Whittaker, 2015).

2.6 | Species vulnerability to forest fragmentation

Species vulnerability to forest fragmentation corresponds to the risk of a species to become locally extinct across the whole set of forest patches remaining in the landscape. Hence, species occurring in a few patches would be more extinction-prone than those occurring in many patches, particularly if an extinction debt has yet to be paid and patch colonization rates are low, which is likely the case of forest archipelagos within hydroelectric reservoirs (Jones, Bunnefeld, Jump, Peres, &

Dent, 2016). In this case, patch occupancy is inversely related to vulnerability to forest fragmentation. However, species absences from a patch does not necessarily imply that local extinctions had occurred because such species could be initially absent from the patch at the time of its creation (Bolger, Alberts, & Soule, 1991), meaning that patch occupancy may not always indicate vulnerability to forest fragmentation (Keinath et al., 2017). Therefore, we first examined whether local extinction had actually occurred across surveyed islands by comparing the SARs for birds in pseudo-control islands with that in much smaller treatment islands (Bolger et al., 1991; Brown, 1971; Wang, Zhang, Feeley, Jiang, & Ding, 2009). To accomplish this, we used the number of bird species as a function of surveyed area (number of PCs × point count area), and performed an ANCOVA model with island type as the categorical independent variable (see Appendix S1 for further details). We found that the predicted line derived from treatment islands was well below and had a steeper slope than that of pseudo-control islands (see Figure S2a), indicating that local extinctions had occurred in the former. Subsequently, we estimated the number of local extinctions that had occurred in each treatment island by subtracting the predicted number of species in pseudo-control islands from the recorded number of species in treatment islands (Bolger et al., 1991). Accordingly, we estimated a total of 788 local extinctions across all 34 treatment islands over 22–23 years of post-isolation history at the THR landscape (see Figure S2b). Given these results, we used estimates of island occupancy (i.e., proportion of islands occupied—PIO) as a measure of species vulnerability to forest fragmentation based on species occurrence across all 36 surveyed islands.

Due to potential biases introduced by imperfect detectability, we calculated both the observed and detectability-corrected PIO for each species (Thornton et al., 2011; Wang et al., 2015). The latter was calculated using single-season occupancy models (MacKenzie et al., 2002) implemented in the UNMARKED package (Fiske & Chandler, 2011). As some species can occasionally disperse across islands by traversing the water matrix and our bird surveys were conducted over six discrete field campaigns, we relaxed the closure assumption of single-season models, which is defensible as long as (1) changes in island occupancy status occur at random— which is likely the case—and (2) "occupancy" is interpreted as "use" (Mackenzie & Royle, 2005).

We modelled species occupancy probability (ψ) as a function of island AREA, SHAPE and PROX, assuming an interactive effect between AREA and SHAPE due to their combined effects in determining the severity of edge effects. As sampling effort increases the chances of detecting any given species, we modelled the detection probability (p) as a function of the number of PCs per island (EFFORT). We also considered both ψ and p as constants across islands. Accordingly, we built 16 competitive occupancy models for each species (Table 1). We then used the Akaike information criterion (AIC) to rank models and to calculate Akaike weights to indicate the best-fit models (Burnham & Anderson, 2002). From model-averaging based on all models with high support (ΔAIC ≤ 2), we summed the occupancy probability at each island and divided this by the total number of surveyed islands to obtain the detectability-corrected PIO for each species (Thornton et al., 2011;

TABLE 1 Structure of the 16 occupancy models used to estimate detectability-corrected proportions of islands occupied for 207 bird species surveyed across 36 islands at the Tucuruí Hydroelectric Reservoir landscape. Probability of occupancy (ψ) was modelled as a function of $\log_{10}$ island area in hectares (AREA), shape index (SHAPE), and $\log_{10}$ proximity index (PROX). The probability of detection (p) was modelled as a function of the number of point count stations surveyed per island (EFFORT)

Model description
$\psi(.) \, p(.)$
$\psi(\text{AREA}) \, p(.)$
$\psi(\text{SHAPE}) \, p(.)$
$\psi(\text{PROX}) \, p(.)$
$\psi(\text{AREA} \times \text{SHAPE}) \, p(.)$
$\psi(\text{AREA} + \text{PROX}) \, p(.)$
$\psi(\text{SHAPE} + \text{PROX}) \, p(.)$
$\psi(\text{AREA} \times \text{SHAPE} + \text{PROX}) \, p(.)$
$\psi(.) \, p(\text{EFFORT})$
$\psi(\text{AREA}) \, p(\text{EFFORT})$
$\psi(\text{SHAPE}) \, p(\text{EFFORT})$
$\psi(\text{PROX}) \, p(\text{EFFORT})$
$\psi(\text{AREA} \times \text{SHAPE}) \, p(\text{EFFORT})$
$\psi(\text{AREA} + \text{PROX}) \, p(\text{EFFORT})$
$\psi(\text{SHAPE} + \text{PROX}) \, p(\text{EFFORT})$
$\psi(\text{AREA} \times \text{SHAPE} + \text{PROX}) \, p(\text{EFFORT})$

Wang et al., 2015). We also summed the detection probability for each visit per island and divided by 216 (36 islands × 6 surveys) to obtain the overall detection probability for each species.

2.7 | Species traits and vulnerability to forest fragmentation

It is widely assumed that closely related species share more traits than distantly related species (Webb, Ackerly, McPeek, & Donoghue, 2002). Thus, analyses involving species as sampling units should be corrected for phylogenetic non-independence among traits (Freckleton, Harvey, & Pagel, 2002). To account for this, we built a majority-rule consensus tree based on 1,000 trees obtained from birdtree.org ("Hackett All Species"; Jetz, Thomas, Joy, Hartmann, & Mooers, 2012) using the APE package (Paradis, Claude, & Strimmer, 2004). As a consensus tree does not include branch lengths, we set all branch lengths equal to one. We then performed Phylogenetic Generalised Least Squares (PGLS) models using the CAPER package (Orme et al., 2013) and Pagel's lambda branch length transformation optimised by maximum likelihood (Freckleton et al., 2002). We examined both observed and detectability-corrected PIO separately as response variables and species traits as explanatory variables.

To assess the role of morpho-ecological traits in explaining species vulnerability to forest fragmentation, we built 13 competing PGLS models: a univariate model for each of the seven traits, three

additive models and three interactive models. Additive and interactive models were built under the same combination of traits. The first included natural abundance, habitat breadth and geographic range size, and is referred to as "rarity model" as it combines all three dimensions of rarity (sensu Rabinowitz, 1981). The second included natural abundance, body mass and trophic level, and is referred to as "population size model," following Meyer et al. (2008). The third included trophic level, vertical stratum and flocking behaviour, and is referred to as "foraging model."

3 | RESULTS

Considering all 36 surveyed islands, we recorded 10,575 individuals representing 207 bird species, 150 genera and 31 families (see Table S3). The number of individuals recorded per island ranged from 28 to 1,997 (mean ± *SD* = 293.8 ± 359.1), and the number of species from 7 to 128 (46.3 ± 26.8). The number of individuals recorded per species ranged widely from 1 to 1,385 (51.1 ± 124.2).

Despite our large sampling effort, individual-based rarefaction curves indicate that further surveys would be necessary to reach sampling sufficiency (i.e., to approach the asymptote of the curves; see Figure S3). Completeness of the inventories per island ranged from 64% to 89% (73.6 ± 5.1%; see Figure S3). As near-exhaustive inventories (>80% completeness) were only obtained at four islands (see Figure S3), the number of species in most surveyed islands should be regarded as conservative.

3.1 | Species–area relationships and forest fragmentation effect

Island area had a significant positive effect on the number of species for all species, forest specialists and habitat generalists (Figure 2). The *z*-value for habitat generalists was significantly lower than for forest specialists (*p* = .028; Figure 2), indicating that the rate of species loss as a function of island area reduction was higher for forest specialists.

The SAR models were deemed as appropriate to assess the forest fragmentation effect on avian species richness as the *z*-value was significant and the r^2_{adj} was ≥.5 for all three data sets (Figure 2). We recorded a higher overall number of species in surveyed islands than that extrapolated to an unfragmented forest area of 6,502.6 ha, the aggregate size of all 36 surveyed islands, considering both all species (207 + 1 > 201.6; Figure 2a) and only habitat generalists (124 + 1 > 104.7; Figure 2b). In contrast, this trend was reversed for forest specialists (83 + 1 < 109.1; Figure 2c). However, the difference between the recorded and extrapolated number of species was not significant for all three data sets.

The *Z*-scores for all species (−0.34), forest specialists (0.24) and habitat generalists (−0.64) were not statistically significant, indicating that the structure of all three data sets could not be described as either nested or antinested (Figure 2).
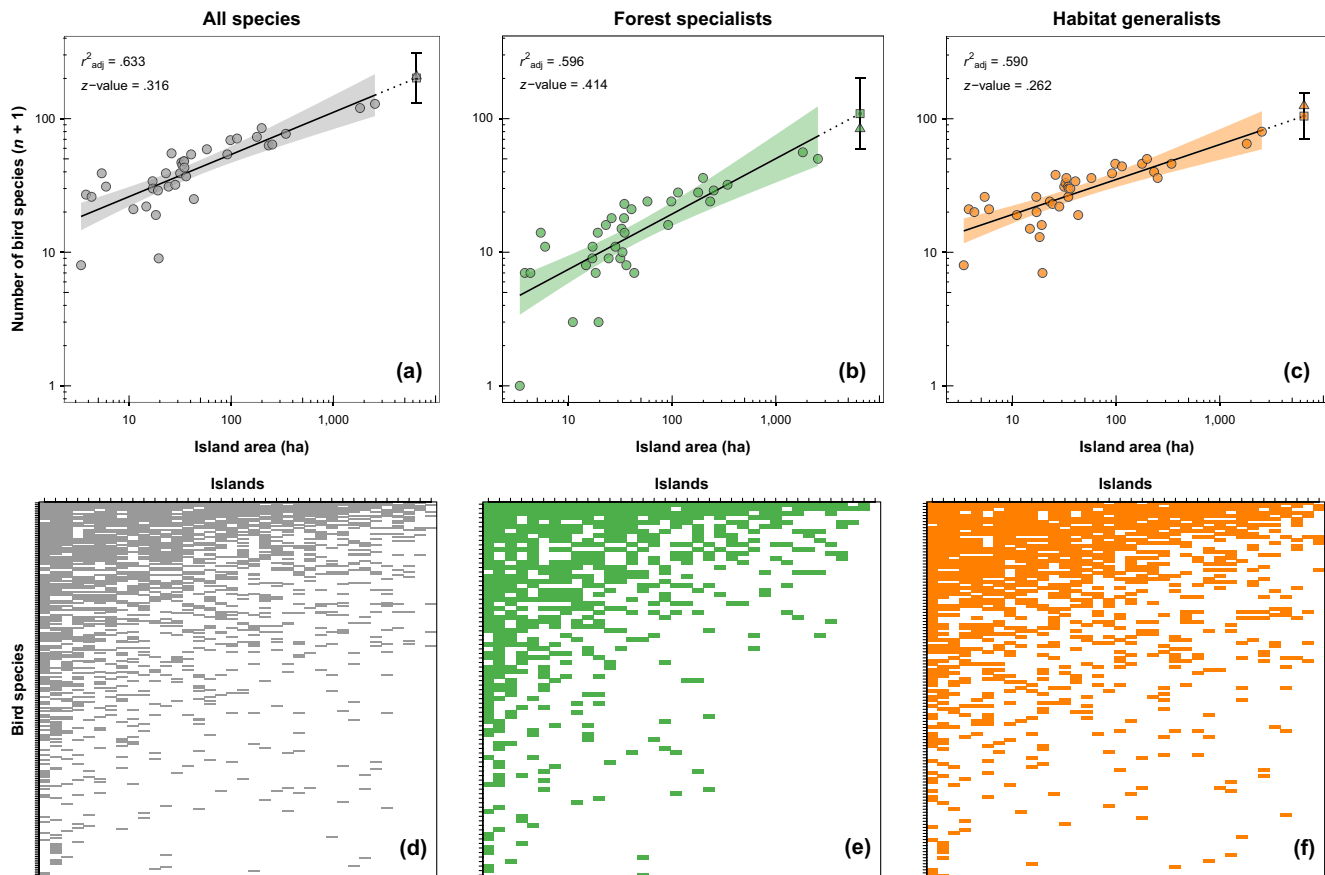
FIGURE 2 Plots at the top show the species–area relationships, and their r^2- and z-values for (a) all species; (b) forest specialists; and (c) habitat generalists surveyed across 36 islands at the Tucuruí Hydroelectric Reservoir landscape ($p < .001$ in all instances). Dotted lines indicate null predicted numbers of species if forest fragmentation had no effect. Circles, squares and triangles correspond to the recorded, extrapolated, and overall number of species, respectively. Coloured regions and error bars show the 95% confidence intervals of predicted lines and extrapolated values, respectively. Note the base 10 logarithmic scales along both axes. Plots at the bottom show the maximally packed matrices for (d) all species; (e) forest specialists; and (f) habitat generalists based on the NODF nestedness metric (Almeida-Neto et al., 2008). Coloured bars indicate the islands (x-axis) where each species (y-axis) was recorded. None of the data sets was either significantly nested or antinested. [Colour figure can be viewed at wileyonlinelibrary.com]

3.2 | Trait-based vulnerability to forest fragmentation

Considering the observed PIO as a response variable, only the interactive PGLS "rarity model" including natural abundance, habitat breadth and geographic range size was highly supported based on AIC values (Table 2). This model explained most of the variance in observed PIO ($R^2_{adj} = .649$), outperforming the univariate PGLS models of natural abundance ($r^2_{adj} = .554$), habitat breadth ($r^2_{adj} = .031$) and geographic range size ($r^2_{adj} = .017$). Accordingly, species with higher natural abundance (Figure 3), broader habitat breadth and wider geographic range tended to have higher values of observed PIO (see Figure S4).

Considering the detectability-corrected PIO as a response variable, only the interactive PGLS "rarity model" was highly supported based on AIC values (Table 2). This model explained a fifth of the variance in detectability-corrected PIO ($R^2_{adj} = .199$), outperforming the univariate models of natural abundance ($r^2_{adj} = .113$), habitat breadth ($r^2_{adj} = .047$) and geographic range size ($r^2_{adj} = .018$). Accordingly,

species with higher natural abundance, broader habitat breadth and wider geographic range tended to have higher values of detectability-corrected PIO (see Figure S4).

3.3 | Observed versus detectability-corrected estimates of island occupancy

Vulnerability to forest fragmentation was widely variable across the 207 species in terms of the proportion of islands occupied (PIO), regardless of whether we considered observed or detectability-corrected PIO (see Table S3). The variation in observed PIO ranged from 2.8% to 94.4% (22.4 ± 22.5%), whereas the variation in detectability-corrected PIO ranged from 5.6% to 96.4% (42.4 ± 24.4%). Estimates of island occupancy corrected for imperfect detectability were higher than those observed for 200 species, identical for five, and slightly lower for two (see Table S3). For 30 species with detection probabilities below 30%, the detectability-corrected PIO was at least tenfold higher than the observed PIO (16.0 ± 5.1%; Figure 4; see Table S3). Conversely, differences between these two

TABLE 2 Performance of 13 Phylogenetic Generalised Least Squares (PGLS) models relating either observed or detectability-corrected estimates of island occupancy to seven morpho-ecological traits, and combinations thereof, for 207 bird species surveyed across 36 islands at the Tucuruí Hydroelectric Reservoir landscape

| Model description	df	AIC	ΔAIC	ω_i	R^2_{adj}
Response variable: observed proportion of islands occupied					
Univariate models					
Natural abundance	2	1,697.151	43.918	2.901×10^{-10}	.554
Habitat breadth	2	1,847.325	194.091	7.126×10^{-43}	.031
Geographic range size	2	1,850.594	197.361	1.390×10^{-43}	.017
Body mass	2	1,851.311	198.077	9.713×10^{-44}	.015
Flocking behaviour	2	1,854.150	200.917	2.349×10^{-44}	−.001
Vertical stratum	2	1,854.443	201.209	2.029×10^{-44}	−.002
Trophic level	2	1,854.845	201.611	1.659×10^{-44}	−.004
Additive models					
Rarity: natural abundance + habitat breadth + geographic range size	4	1,666.006	12.773	0.0016815	.620
Population size: natural abundance + body mass + trophic level	4	1,700.690	47.457	4.945×10^{-11}	.551
Foraging: trophic level + vertical stratum + flocking behaviour	4	1,857.672	204.438	4.037×10^{-45}	−.007
Interactive models					
Rarity: natural abundance × habitat breadth × geographic range size	8	1,653.233	0	0.9983185	.649
Population size: natural abundance × body mass × trophic level	8	1,703.471	50.238	1.231×10^{-11}	.553
Foraging: trophic level × vertical stratum × flocking behaviour	8	1,862.848	209.614	3.035×10^{-46}	−.015
Response variable: detectability-corrected proportion of islands occupied					
Univariate models					
Natural abundance	2	1,877.104	15.115	4.063×10^{-04}	.113
Habitat breadth	2	1,891.950	29.962	2.427×10^{-07}	.047
Geographic range size	2	1,898.307	36.319	1.011×10^{-08}	.018
Body mass	2	1,901.063	39.074	2.549×10^{-09}	.005
Trophic level	2	1,902.062	40.074	1.546×10^{-09}	−.001
Flocking behaviour	2	1,902.317	40.328	1.361×10^{-09}	−.002
Vertical stratum	2	1,902.804	40.815	1.067×10^{-09}	−.004
Additive models					
Rarity: natural abundance + habitat breadth + geographic range size	4	1,864.512	2.524	0.2203577	.173
Population size: natural abundance + body mass + trophic level	4	1,875.745	13.756	0.0008016	.128
Foraging: trophic level + vertical stratum + flocking behaviour	4	1,905.494	43.505	2.780×10^{-10}	−.008
Interactive models					
Rarity: natural abundance × habitat breadth × geographic range size	8	1,861.988	0	0.7782926	.199
Population size: natural abundance × body mass × trophic level	8	1,879.215	17.227	0.0001414	.130
Foraging: trophic level × vertical stratum × flocking behaviour	8	1,909.816	47.828	3.202×10^{-11}	−.010
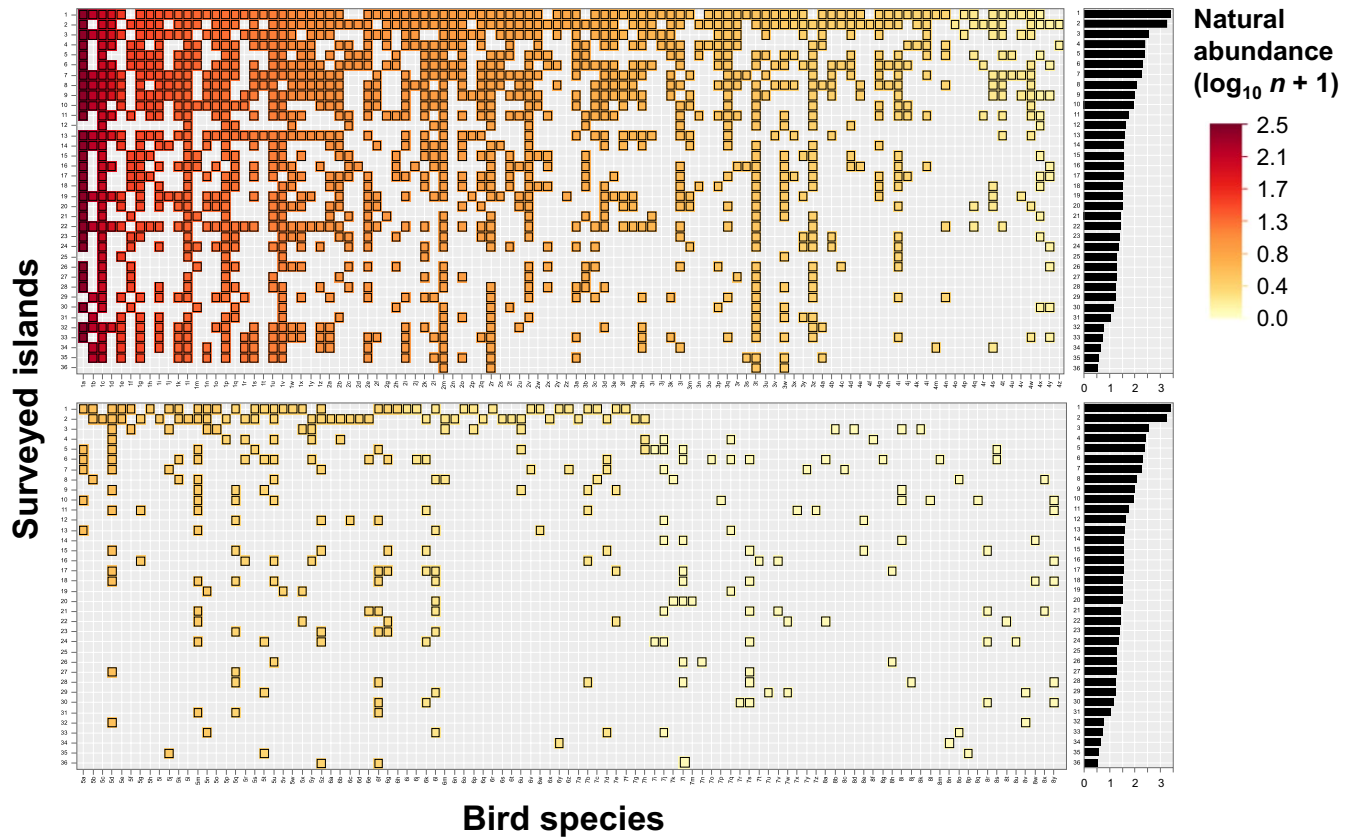
FIGURE 3 Site-by-species incidence matrix for 207 bird species surveyed across 36 islands at the Tucuruí Hydroelectric Reservoir landscape. Squares representing at least one individual recorded per island are coloured according to the natural abundance of each species, defined as the total number of individuals recorded within pseudo-control islands. Islands are ordered from the largest to the smallest (black bars on a $\log_{10}$ scale; see Table S1); species are ordered from the most to the least naturally abundant (see Table S3 for species codes). [Colour figure can be viewed at wileyonlinelibrary.com]

estimates were negligible or non-existent (1.02 ± 0.02%) for all 31 species with detection probabilities exceeding 45.5% (Figure 4; see Table S3). Once phylogenetic non-independence was accounted for, detection probabilities was higher for more naturally abundant species (r^2_{adj} = .202, p < .001; Figure 4).

4 | DISCUSSION

Here, we present one of the most comprehensive landscape-scale efforts to date to assess the role of morpho-ecological traits in explaining species vulnerability to forest fragmentation, in terms of the number of surveyed islands (n = 36), range of island sizes (3.4–2,551.5 ha), overall sampling effort (n = 1,388 samples) and number of species surveyed (n = 207). This effort exploited a quasi-experimental anthropogenic tropical forest archipelago, following an even-aged post-isolation history of 22–23 years, and allowed us to uncover which traits pose the greatest threats to bird species in forest islands within hydroelectric reservoirs. We also highlight potentially misleading applications of species occupancy models by contrasting observed and detectability-corrected estimates of island occupancy.

4.1 | Species–area relationships and forest fragmentation effect

Although SARs are arguably the most ironclad relationship in ecology (Rosenzweig, 1995), rates of species loss induced by declining habitat areas are highly variable. Triantis, Guilhaumon, and Whittaker (2012) synthesised 449 data sets from log–log SAR applications to islands in inland, continental-shelf and oceanic systems, and reported z-values ranging from 0.064 to 1.312 (mean ± SD = 0.321 ± 0.164). Such variance was attributed to several factors, namely island type, taxonomic group and range of island areas (Triantis et al., 2012). A reliable comparison of z-values among studies should therefore take these factors into account.

Z-values derived for forest islands have been shown to be higher than for forest fragments (Matthews, Guilhaumon, Triantis, Borregaard, & Whittaker, 2016), rendering forest fragmentation induced by hydroelectric dams (i.e., forest insularization) a more severe threat to biodiversity than that induced by agro-pastoral activities. We largely attribute such difference in z-values to the permeability of the intervening matrix, which may either preclude (increasing z-values; Moore, Robinson, Lovette, & Robinson, 2008) or allow species to disperse among forest patches, offsetting species losses through the rescue
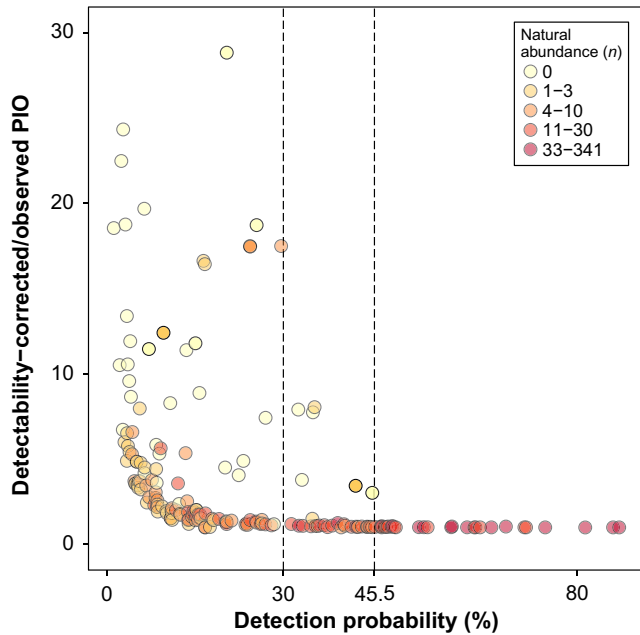
FIGURE 4 Ratio between detectability-corrected and observed estimates of proportion of islands occupied (PIO) as a function of species detectability for 207 bird species surveyed across 36 islands at the Tucuruí Hydroelectric Reservoir landscape; y-values indicate how many times detectability-corrected estimates are higher than observed estimates. Circles are coloured according to the natural abundance of each species, defined as the total number of individuals recorded within pseudo-control islands. [Colour figure can be viewed at wileyonlinelibrary.com]

effect (decreasing z-values; Stouffer, Strong, & Naka, 2009). For instance, in a fragmented southern Amazonian landscape dominated by cattle pasture—where 338 bird species were surveyed across 30 forest fragments (1–14,476 ha)—Lees and Peres (2008) derived a z-value of 0.191, which is considerably lower than in this study (0.316). Although we do not have direct evidence on species dispersal in these two landscapes, both studies are comparable in most factors affecting z-values (Triantis et al., 2012), except for the intervening matrix. Therefore, we predict that forest islands in existing and future hydroelectric reservoirs will experience a pronounced species richness decay, resulting in depauperate avian assemblages shaped by selective extinction (Mendenhall et al., 2014; Si, Baselga, Leprieur, Song, & Ding, 2016; Wolfe et al., 2015).

Predictions of species losses based on the species–area relationship are affected by the degree of habitat specialisation of the species included in the analysis. In 16 of 23 data sets, avian species richness decreased at a greater rate as a function of fragment area reduction for forest specialists than for habitat generalists (Matthews et al., 2014). Moreover, the inclusion of habitat generalist and edge species can even reverse the generally positive species–area relationship, whereby small patches will counter-intuitively harbour the most species-rich assemblages (Lövei, Magura, Tóthmérész, & Ködöböcz, 2006). In archipelagic landscapes, colonisation of habitat generalists into forest islands is expected to be hindered by the aquatic matrix, ultimately reducing their impact in reducing z-value estimates. In fact,

our z-value derived for all species (0.316) approaches the mean value of island systems (0.321; Triantis et al., 2012) rather than that of terrestrial landscapes (0.202; Watling & Donnelly, 2006). However, our z-value estimate for forest specialists (0.414) was significantly greater than that for habitat generalists (0.262). Including habitat generalists in the species pool therefore reduced our assemblage-wide rate of species loss, obscuring the more severe impact of habitat loss on forest specialists, which reinforces the notion that habitat patches must be defined from the perspective of target species (Lövei, Magura, Tóthmérész, & Ködöböcz 2006).

Forest fragmentation per se neither significantly decreased nor increased the overall number of species predicted by forest loss (i.e., island area reduction) regardless of the data set used, which corroborates our prediction regarding the fragmentation effect on all species (neutral) but not on both forest specialists (positive) and habitat generalists (negative). Likewise, species richness was unrelated to fragmentation in previous studies undertaken in different landscapes across a wide range of taxonomic groups. For instance, fragmentation effects on the overall number of species in forest fragments were not evident for perennial flowering plants and two beetle families in an agricultural landscape (Tenebrionidae and Carabidae; Yaacobi et al., 2007), and for butterflies in an urban landscape (Soga & Koike, 2012). Yet this failed to hold true for lizards in an archipelagic landscape, where the overall number of species in forest islands was significantly decreased by fragmentation (Wang et al., 2009). Hypothetically, terrestrial matrices can then buffer fragmentation effects as they are more permeable to species movements than water matrices (Soga & Koike, 2012), or even increase gamma diversity as shown for spider species in forest fragments of two agricultural landscapes in Israel (Gavish, Ziv, & Rosenzweig, 2012). To test this hypothesis, we reanalysed the bird data available from the Thousand Island Lake forest archipelago in China (Si, Baselga, & Ding, 2015) applying the same analysis carried out here (Yaacobi et al., 2007). We found no support for that hypothesis as forest fragmentation per se significantly increased the overall number of bird species in forest islands (60 recorded > 42.6 extrapolated; see Figure S5), which is partially explained by the low z-value (0.098; see Yu, Hu, Feeley, Wu, & Ding, 2012) and the antinested structure (Si et al., 2015) of the avian assemblages in the Thousand Island Lake (Matthews, Triantis et al., 2016; Santos et al., 2010). Accordingly, antinested assemblages (i.e., species present at an island are not present at other islands) are expected to have a higher gamma diversity than nested assemblages (i.e., species present in smaller islands are subsets of larger islands; Santos et al., 2010), ultimately determining the direction (positive or negative) and magnitude of the fragmentation effect on species richness. In this study, the lack of fragmentation effects on species richness for the data sets including all species, forest specialists, and habitat generalists was thus unsurprising given the non-significant nested structure of these avian assemblages. Collectively, this indicates that the extrapolation of SAR models is an indirect method to infer the nested structure of species assemblages (this study; Santos et al., 2010; Matthews, Triantis et al., 2016).

In a recent SLOSS-type analysis, Fahrig (2017) uncovered a significantly higher overall number of species in several small patches

compared to a single large patch based on 60 compiled data sets. This suggests that habitat fragmentation per se increases the overall number of species in habitat patches, but we caution against such assertion for three reasons. First, antinested assemblages are shaped by species turnover, which depends on landscape-dispersal processes determined by isolation (with lower isolation leading to greater antinested structure; Santos et al., 2010), matrix permeability (Stouffer, Johnson, Bierregaard, & Lovejoy, 2011) and species dispersal ability (Si, Pimm, Russell, & Ding, 2014). Second, methodological choices may lead to biased outcomes as exemplified by the widespread nested structure of species assemblages in fragmented landscapes (Watling & Donnelly, 2006; n = 67 data sets), which were recently deemed as an analytical artefact as most species assemblages were neither significantly nested nor antinested (Matthews et al., 2015; n = 97 data sets). As fragmentation effects on species richness are strictly related to the nested structure of species assemblages, we believe that a fragmentation effect on species richness would not be evident for most studies compiled by Matthews et al. (2015). This contradicts Fahrig's (2017) conclusions, which were largely grounded on the positive fragmentation effect on species richness when comparing species accumulation curves of sites ordered according to either increasing or decreasing patch area (Quinn & Harrison, 1988). Nevertheless, this method is biased towards detecting higher species richness in several small patches compared to a single large patch due to unequal sampling intensity (i.e., proportion of patch area that is surveyed) among surveyed patches (Gavish et al., 2012). Third, an assemblage-level approach may mask fragmentation effects on individual species, as measures of species richness completely disregard species identity.

4.2 | Trait-based vulnerability to forest fragmentation

Rarity is an intrinsic property of certain species that results from variable cross-scale combinations of small local population size, restricted habitat breadth and narrow geographic range (Rabinowitz, 1981). Rare species are inherently predisposed to high extinction risk, which justifies the use of rarity as a measure of species vulnerability to a wide range of anthropogenic stressors (Kattan, 1992; Mace et al., 2008). Using a global-scale analysis, Newbold et al. (2014) reported that forest specialists and narrow-range bird species from tropical and subtropical forest biomes are more vulnerable to land-use change than habitat generalists and wide-range species. We corroborate this outcome at the scale of an archipelagic landscape, and endorse other comparative analyses incorporating field data (i.e., estimates of local population size; Feeley et al., 2007) and synergistic interactions among species traits that amplify the power of predictive models (Wang et al., 2015). Moreover, we identified rarity as a decisive factor exacerbating species vulnerability at all three spatial dimensions defined by Rabinowitz (1981), particularly because rarity is unrelated to several key traits, such as body mass and flocking behaviour (Thiollay, 1994; but see Kattan, 1992). As such, species with higher natural abundance, broader habitat breadth and wider geographic range were in general those with the highest rates of island occupancy at the THR

landscape. Nevertheless, natural abundance played a disproportionately important role compared to habitat breadth and geographic range size, a pattern corroborated in another Amazonian fragmented landscape (Lees & Peres, 2008). A positive abundance-occupancy relationship, in which more abundant species occupy more sites, is widely considered a general rule in ecology (Hartley, 1998). Although many underlying mechanisms have been proposed to explain this relationship, there is no broadly accepted consensus as to why locally abundant species should be more ubiquitous (Gaston et al., 2000). We stress that our findings can be extended to other fragmented landscapes, including those dominated by variable-quality terrestrial matrices, in which non-random extirpations could also be predicted by metrics of rarity.

Based on our PGLS models, we failed to find support for some morpho-ecological traits that are often associated with avian extinction risk in human-modified tropical forest landscapes, namely body mass, trophic level, vertical foraging stratum and flocking behaviour (Sodhi et al., 2004). However, this does not imply that these traits are not meaningful (Hamer et al., 2015), although body mass, foraging specialisation and vertical stratum were unrelated to bird species vulnerability in a fragmented Atlantic Forest of southern Brazil (dos Anjos, 2006). In some instances, the role of species traits in predicting vulnerability to forest fragmentation depends on the scale (global vs. landscape) and the response variable (e.g., population size vs. global extinction risk scores) used in the study (Keinath et al., 2017). For example, body mass has been often reported as a meaningful trait in broad-scale studies using global extinction risk scores (Keinath et al., 2017). Moreover, in model selection approaches, the best-fit models depend on the entire set of plausible competitive models (Aho, Derryberry, & Peterson, 2014). Had we considered only univariate models including each of those four traits separately, body mass (ΔAIC $\leq$ 2 in this instance) would have emerged as the most important trait in explaining observed island occupancy rates (Table 2), with small-bodied species occupying more islands than large-bodied species (r^2_{adj} = .015). Any given trait or combination of traits may therefore play a role in a comparative analysis, but collectively may operate as less meaningful variable (Keinath et al., 2017). Furthermore, the large number of species included in the analysis (n = 207) can obscure the role of ecological traits associated with only a few species (e.g., obligate ant-followers, n = 2), as the deviance of a few values may change the balance of strength in competing traits but not the main outcome.

It has been widely reported that insectivore species are particularly vulnerable to forest fragmentation (Bregman et al., 2014; Powell, Cordeiro, & Stratford, 2015), especially ground insectivores (Stratford & Stouffer, 1999) and obligate flocking species (i.e., mixed-species flock attendants and ant-followers; Van Houtan, Pimm, Bierregaard, Lovejoy, & Stouffer, 2006). Hence, species at higher trophic levels, using lower forest strata, and joining flocks were expected to exhibit lower rates of island occupancy. We failed to corroborate these expectations, which we largely attribute to differences in sampling design and analytical approaches among studies (Powell et al., 2015). For example, in an anthropogenic tropical forest archipelago in Malaysia, avian insectivores showed the steepest decline in the number of

species with decreasing island area compared to either omnivores or frugivores (Yong et al., 2011). Had we applied the semi-log form of the species–area relationship [$S \sim \log_{10}(A)$] to the same three avian foraging guilds, as the authors did, we would also have identified insectivores (sensu Wilman et al., 2014) as the most impaired foraging guild (see Figure S6). To provide further evidence of the impact of the analytical approach on the outcomes, we additionally applied the log–log form of the species–area relationship to both our data set and the data set available from the Malaysian archipelago (Yong et al., 2011). Although the outcomes converged between studies, at this time, frugivores emerged as the most impaired foraging guild, rather than insectivores (see Figure S6). Another noteworthy point is that species grouped into a foraging guild may span more than an entire trophic level (Hamer et al., 2015). As such, the trophic level of an insectivore species could overlap that of a carnivore (Hamer et al., 2015), omnivore or granivore species (see Figure S7). In Bornean rainforests, insectivore species showed variable responses to selective logging, with species at higher trophic levels more adversely affected than those at lower trophic levels (Hamer et al., 2015). These authors used stable isotopes to quantify trophic levels, a more accurate approach than our energetic score, preventing a direct comparison between studies.

Ground insectivores were extirpated from small Amazonian forest remnants (≤ 10 ha) following fragmentation (Stratford & Stouffer, 1999) as edge-dominated remnants could no longer sustain critical foraging microhabitats for these species (Stratford & Stouffer, 2013). Likewise, none of the five ground insectivores we recorded (*Conopophaga aurita*, *Conopophaga roberti*, *Formicarius analis*, *Formicarius colma* and *Hylopezus macularius*) was found in islands smaller than 30 ha (see Figure S8). Moreover, obligate flocking species were extirpated from small fragments (≤ 10 ha) after isolation (Stouffer & Bierregaard, 1995), a pattern corroborated at the THR landscape, where smaller islands also harboured depauperate assemblage of these social species (see Figure S8). Although mixed-species flocks and obligate ant-followers can reassemble and recolonize small fragments following the regrowth of the intervening matrix (Stouffer & Bierregaard, 1995; Stouffer et al., 2011), these rebounds, by definition, cannot occur within hydroelectric reservoirs. Finally, the only comparable avian island biogeography study (Thousand Island Lake, China; Wang et al., 2015)—in terms of both the sampling design and analytical approach used here—is largely consistent with our findings, in which only natural abundance and habitat breadth had sufficiently high support in explaining species occupancy patterns in forest islands.

4.3 | Observed versus detectability-corrected estimates of island occupancy

Occupancy modelling is assumed to derive more reliable estimates of patch occupancy as it accounts for potentially present species that go undetected in a given patch (MacKenzie et al., 2002). As a result, estimates of patch occupancy corrected for imperfect detectability are, as a general rule, equal to or higher than observed estimates (this study; Thornton et al., 2011; Wang et al., 2015). In an archipelagic landscape created by China's Thousand Island Lake, detectability-corrected

proportions of islands occupied were up to sevenfold higher than that observed for a small raptor (*Accipiter soloensis*; Wang et al., 2015). At the THR landscape, those estimates were at least tenfold higher for 30 bird species, and almost 29-fold higher for two of them (Figure 4; see Table S3). These large discrepancies can be explained by overestimates of patch occupancy for species with detection probabilities below 30% (MacKenzie et al., 2002). Overcoming this artefact to obtain more reliable estimates of patch occupancy would require increasing the number of samples per patch, but this is not always feasible due to logistical constraints (Mackenzie & Royle, 2005).

Estimates of patch occupancy for species with low detection probabilities (< 30%) can be misleading and the large uncertainties they carry should be interpreted with caution (Welsh, Lindenmayer, & Donnelly, 2013). Such species may be defined as ubiquitous due to overestimates of patch occupancy, even though they have been recorded at only a few patches (Banks-Leite et al., 2014), which would invalidate species–specific predictions of vulnerability based on rates of patch occupancy. This was the case for *Myiopagis caniceps* and *Psarocolius bifasciatus*, which were recorded in only one island but were estimated to occupy 29. As species detectability tends to increase with increasing natural abundance, occupancy models yield far more reliable estimates of patch occupancy for common species than for those that are rare (Banks-Leite et al., 2014). Because over 200 species distributed across many lineages were considered in this study, identifying morpho-ecological characteristics that can best explain species vulnerability to forest fragmentation was largely unbiased. However, the same cannot be stated for species-poor assemblages in which most species have low detection probabilities. We argue that estimates of detectability-corrected proportions of patches occupied should always be reported and examined together with species detectability and observed estimates, to avoid misleading assessments of species vulnerability based on rates of patch occupancy.

5 | CONCLUSIONS

On the basis of a comprehensive bird survey undertaken in forest islands within a major Amazonian hydroelectric reservoir, we addressed four questions: (1) Do habitat generalists show a less steep decline in species richness as a function of island area reduction compared to forest specialists? (2) Does forest fragmentation per se exacerbate or reduce the impact of forest loss on species richness for the overall species pool, forest specialists and habitat generalists? (3) Which suite of morpho-ecological traits best explains species rates of island occupancy within the forest archipelago? (4) How divergent are observed and detectability-corrected estimates of island occupancy for rarely detected species? Our findings show that (1) rates of species loss of forest specialists in land–bridge islands are underestimated if habitat generalists are included in the species pool because habitat generalists are less impacted by island area reduction than forest specialists; (2) fragmentation per se does not necessarily exacerbate the impact of forest loss on species richness; (3) rare species, especially those with low natural local abundance,

are the most extinction-prone in fragmented landscapes; and (4) detectability-corrected estimates of island occupancy can be much higher than observed estimates for species with low detection probability, ultimately limiting the use of occupancy models for rare or elusive species. Finally, we conclude that forest islands within hydroelectric reservoirs are expected to typically harbour depauperate avian assemblages, mostly consisting of naturally abundant and habitat generalist species.

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SUPPORTING INFORMATION

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