

# Idiosyncratic responses of Amazonian birds to primary forest disturbance

Nárgila G. Moura<sup>1,2</sup> · Alexander C. Lees<sup>2,3</sup> · Alexandre Aleixo<sup>3</sup> · Jos Barlow<sup>3,4,5</sup> · Erika Berenguer<sup>4</sup> · Joice Ferreira<sup>6</sup> · Ralph Mac Nally<sup>7</sup> · James R. Thomson<sup>7</sup> · Toby A. Gardner<sup>8,9</sup>

Received: 19 May 2015 / Accepted: 22 October 2015  
© Springer-Verlag Berlin Heidelberg 2015

**Abstract** As humans continue to alter tropical landscapes across the world, it is important to understand what environmental factors help determine the persistence of biodiversity in modified ecosystems. Studies on well-known taxonomic groups can offer critical insights as to the fate of biodiversity in these modified systems. Here we investigated species-specific responses of 44 forest-associated bird species with different behavioural traits to forest disturbance in 171 transects distributed across 31 landscapes in two regions of the eastern Brazilian Amazon. We investigated patterns of species occurrence in primary forests varyingly disturbed by selective-logging and fire and examined the relative importance of local, landscape and historical environmental variables in determining species occurrences. Within undisturbed and disturbed primary forest transects, we found that distance to forest edge and the biomass of large trees were the most important predictors

driving the occurrence of individual species. However, we also found considerable variation in species responses to different environmental variables as well as inter-regional variation in the responses of the same species to the same environmental variables. We advocate the utility of using species-level analyses to complement community-wide responses in order to uncover highly variable and species-specific responses to environmental change that remain so poorly understood.

**Keywords** Neotropical birds · Environmental variables · Random forest · Degraded forest · Biodiversity

## Introduction

Land cover change and agricultural expansion are the preeminent threats to tropical biodiversity (Laurance et al. 2014). A significant body of research has assessed patterns of biodiversity persistence in tropical deforestation frontiers, examining patterns of species occurrence in variable-sized forest remnants (e.g. Uezu et al. 2005; Newmark and

Communicated by Christopher N. Johnson.

**Electronic supplementary material** The online version of this article (doi:10.1007/s00442-015-3495-z) contains supplementary material, which is available to authorized users.

✉ Nárgila G. Moura  
nargilamoura@yahoo.com.br

<sup>1</sup> Curso de Pós-Graduação de Zoologia, Universidade Federal do Pará/Museu Paraense Emílio Goeldi, Caixa Postal 399, Belém, Pará CEP 66040-170, Brazil

<sup>2</sup> Cornell Lab of Ornithology, Cornell University, 159 Sapsucker Woods Road, Ithaca, NY 14850, USA

<sup>3</sup> Coordenação de Zoologia, Museu Paraense Emílio Goeldi, Caixa Postal 399, Belém, Pará CEP 66040-170, Brazil

<sup>4</sup> Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK

<sup>5</sup> Universidade Federal de Lavras, Setor de Ecologia e Conservação, Lavras, Minas Gerais CEP 37200-000, Brazil

<sup>6</sup> Embrapa Amazônia Oriental, Trav. Dr. Enéas Pinheiro s/n, CP 48, Belém, Pará CEP 66095-100, Brazil

<sup>7</sup> Institute for Applied Ecology, The University of Canberra, Bruce, ACT 2617, Australia

<sup>8</sup> Stockholm Environment Institute, 87D Linegatan, Stockholm, Sweden

<sup>9</sup> International Institute for Sustainability, Rio De Janeiro CEP 22460-320, Brazil

Stanley 2011), the influence of the surrounding matrix on species persistence in areas of native habitat (e.g. Perfecto and Vandermeer 2002), and patterns of species persistence in production systems (e.g. Daily et al. 2000; Phalan et al. 2011) or native vegetation subject to a specific type of disturbance such as logging (e.g. Wunderle et al. 2006; Edwards et al. 2011), fire (e.g. Uhl 1998; Mestre et al. 2013) and over-hunting (Terborgh et al. 2008). These studies highlight the detrimental influence of disturbance processes such as selective logging which result in changes to forest structure (Veríssimo et al. 1992) and alterations in microclimate (Thiollay 1999) and render forests more susceptible to fire (Holdsworth and Uhl 1997; Nepstad et al. 1999), further disrupting ecosystem processes such as nutrient cycling (Kauffman et al. 1995).

To date, much of our knowledge on biodiversity responses to anthropogenic disturbances in tropical forest ecosystems are based on studies of birds, which continue to be one of the most studied taxonomic groups (Tschamtko et al. 2008; Karp et al. 2012). However, many studies have been limited to examining the pooled responses of entire avian communities through measures of species richness, diversity and community structure (e.g. Aleixo 1999; Lees and Peres 2006; Sodhi et al. 2008) or using specific groups such as understorey insectivores with different degrees of sensitivity (Stotz et al. 1996). Because tropical forest species assemblages have very high levels of alpha diversity (e.g. Lees et al. 2012, 2013), such studies risk masking important species-specific response patterns given the enormous diversity in behavioural traits, even among closely related taxa (Elmqvist et al. 2003). As such, our understanding of the distribution of individual species across human-modified landscapes and the relative importance of different environmental variables in determining observed patterns is often very poor or non-existent (Tylianakis et al. 2006). Moreover, few studies have gathered large-scale data on multiple stressors in primary forest systems which may be subject to multiple interacting anthropogenic stressors such as fire and logging (Gardner et al. 2009). Understanding the variability in species responses to anthropogenic disturbance is an important step towards understanding ecosystem resilience, i.e. the capacity of the environment to recover from disturbance and to continue providing associated ecosystem services (Peterson et al. 1998).

The Brazilian Amazon is one of the most important regions of tropical forest in which we need to understand the impacts of forest disturbance. It is a global priority for biodiversity conservation efforts given its high level of biological diversity and ongoing threats to this diversity from forest clearance and degradation. To date, around 15 % (634,000 km<sup>2</sup>) of the original forested area has been lost and, between 2007 and 2013, a further 103,000 km<sup>2</sup> was detected as being disturbed by fire and logging events

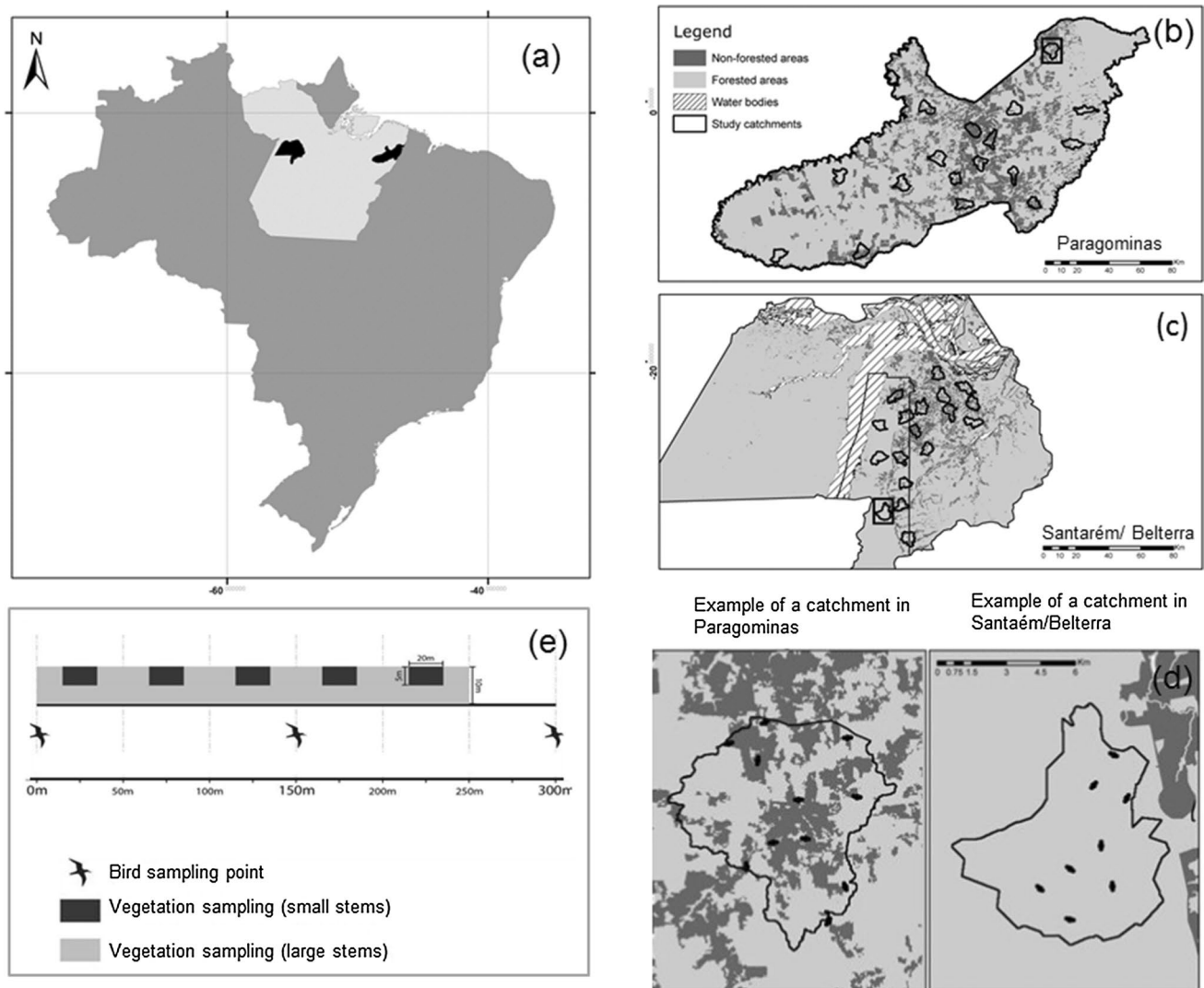
(INPE 2014). The regional avifauna is particularly at risk of widespread human impacts, with 47 bird species recently reported as likely to be locally extinct in the region's oldest deforestation frontier (Moura et al. 2014). However, despite the ubiquitous nature of forest-disturbance events (such as fire and logging) in Amazonia, which likely affect a larger area than deforestation every year (Souza et al. 2013), the nature of species-specific responses to land cover change, forest disturbance and the history of change has been poorly studied in the region.

Here we undertake the first large-scale species-specific assessment of bird responses to multiple anthropogenic impacts in humid tropical forests, focussing on 44 widely distributed Amazonian forest bird species, sampling 171 primary forest transects distributed across 31 catchments in two regions of the eastern Brazilian Amazon. These catchments encompass a gradient of historical deforestation ranging between 6 and 100 % of the remaining primary forest cover, as well as different levels of disturbance to remaining areas of primary forest from fragmentation, logging and fire. The studied species are representative of the diverse terra firme forest bird community as they have a range of different diets, feeding strategies and flocking responses. First, we use these species to investigate how species-specific occurrence patterns change along the gradient of forest disturbance, examining similarity and differences between regions and visually separating species into response classes. We then use species-environment models to examine how disturbance and other environmental variables that characterise different areas of primary forests, such as forest structure, soil and topography, affect species responses. Finally, we examine whether species' responses to primary forest disturbance can be determined by their behavioural traits or their response to broader land cover changes.

## Materials and methods

### Study regions and sampling design

This study was conducted in two regions of the Brazilian state of Pará in the eastern Amazon (Fig. 1a) comprising the municipality of Paragominas and a region that consists of parts of the three municipalities of Santarém, Belterra and Mojuí dos Campos (Fig. 1b, c). Both are biophysically distinct, present different trajectories of human colonization, yet have both experienced the loss of at least one-third of their native forest cover and have ongoing land-use sustainability initiatives strongly supported by local and state government and civil society organizations (for more details see Gardner et al. 2013). Paragominas (1.9 Mha; PGM), sampled between July and November



**Fig. 1** Paragominas and Santarém/Belterra/Mojui dos Campos (a) showing the location of the 31 catchments surveyed in both municipalities (b, c), an example catchment and location of transects (d) and the sampling design (e)

2010 and again in May 2011, is located in north-east Pará state, 300 km south of the state capital Belém. The municipalities of Santarém/Belterra/Mojuí dos Campos (sampled area equal to approximately 1 Mha; STM), sampled between October 2010 and February 2011, lie immediately south-east of the confluence of the Amazonas and Tapajós rivers (Table 1).

Both regions were divided into approximately evenly sized catchments (ca. 5000 ha), which were delineated using a digital elevation model and the Soil and Water Assessment Tool for ARCGIS 9.3. Eighteen catchments were selected in each region (Fig. 1d), capturing the full gradient of accumulated deforestation until 2010 (6–100 % forest cover in Paragominas; 10–100 % forest cover in Santarém) whilst also ensuring adequate representation of

current land cover practices, the spatial distribution of the rural population, and major soil types.

In each catchment between eight and twelve 300-m transects were allocated (depending on differences in

**Table 1** Total number of transects sampled in each class of primary forest in both Paragominas and Santarém

Land cover type	Paragominas	Santarém
Primary forest		
Undisturbed	9	17
Logged only	44	25
Burnt only	0	9
Logged and burnt	44	23
Total	97	74

catchment size) and distributed using a stratified-random sampling design—stratified only with respect to the proportion of forest cover, and random within forest and non-forest areas to increase the likelihood that they would capture important heterogeneities in habitat condition in either forest and/or production systems (using an even density of 1 transect 400 ha<sup>-1</sup>; Fig. 1e). A distance of at least 1.5 km was maintained between transects, helping to ensure sample independence.

We limited our analysis to primary forests—the region's original physiognomy that has never been clear-felled for agriculture, although may have been extensively degraded by disturbance from logging, fire, fragmentation and unsustainable extraction of other forest resources. Primary forest transects were sub-classified into four classes of disturbance based on a combination of remote-sensing data and ground-truthed observations of past disturbance events (Gardner et al. 2013): 'undisturbed' for which no evidence of recent human-induced disturbance was apparent, 'selectively logged' for forests which have undergone detectable logging, 'burnt' for forests in which fire scars were found on trees and charcoal deposits detected on the ground, and 'logged and burnt' for those forests that have experienced both of these disturbances. In total we sampled 97 primary forest transects in PGM and 74 in STM of primary forest. The transects were classified on visual inspection at the time of the survey and a 20-year time series of Landsat images (Gardner et al. 2013).

### *Bird surveys*

In each transect three point-count (PC) stations were located at 0, 150 and 300 m. We carried out two repetitions of three 15-min, 75-m fixed-width PCs per transect, recording all species seen or heard. Repeat surveys accounted for temporal variation in avian vocal activity. A total of 513 PCs (repeated twice) were conducted across both regions. For more details on survey methodology, full species lists and links to digital vouchers for almost all species (95 % in PGM and 88 % in STM); see Lees et al. (2012, 2013). We recorded 398 species in both regions of which 330 were forest-associated species (forest birds), with 308 species (249 forest birds) in PGM and 304 (271 forest birds) in STM. Forest-associated species are defined as those that occur in undisturbed terra firme forests but are not necessarily restricted to those habitats (for more details see Moura et al. 2013). As our sampling design focused on maximising the spatial extent of sampling—traded off against temporal repetition—we were not able to correct for potential differences in detectability, which we here assume to be uniform among species and habitats (Banks-Leite et al. 2014).

## **Environmental variables**

We chose forest structural characteristics, edaphic variables and landscape attributes that are known to influence avian community composition. These include leaf litter depth (Pearson 1975), the availability of dead trees for foraging or nesting/roosting (Skutch 1961; Cornelius et al. 2008), topography (e.g. Cintra and Naka 2012; Stratford and Stouffer 2013) and edaphic variables known to influence avian community composition including both soil fertility (Pomara et al. 2012) and clay content (Bueno et al. 2012). Variables describing past deforestation and historical forest disturbance have also been shown to be important in explaining fauna recovery in degraded forests (Dunn 2004). We thus used 14 environmental variables, related to both natural biophysical conditions and human disturbance, which we judged a priori to be relevant in influencing patterns of occurrence of forest birds in primary forest transects in both regions. These variables were divided into three categories: local (forest structure and edaphic), landscape, and historical, as described below.

### **Local variables**

#### *Forest structure*

Vegetation sampling was undertaken in 10 × 250-m plots (0.25 ha) where all trees and palms (alive or dead) ≥ 10 cm diameter at 1.3 m height were measured (Fig. 1e). Smaller individual plants (2–9.9 cm diameter) were sampled in five 5 × 20-m subplots (100 m<sup>2</sup>). Sampling design for lianas (woody vines) followed that of trees and palms, but the diameter was measured at 1.3 m from the main root, if this was located inside the plot (for large individuals) or inside the subplots (for smaller individuals). All sampled individuals were identified to species level by experienced parobotanists. These data were compiled to give a total richness of tree, palm and liana species. Understorey density was measured by counting the number of stems between 2 and 9.9 cm diameter in the 100-m<sup>2</sup> subplots. To calculate the biomass of large trees (i.e. ≥ 10 cm diameter) in each transect we used an allometric equation for humid tropical forests which incorporates the diameter of each tree and species-specific wood density (Chave et al. 2005). We used the global wood density database (Zanne et al. 2009) to obtain species-specific wood density data; the only exception was for the genus *Cecropia*, for which we used the allometric equations of Nelson et al. (1999), as these trees are hollow and other equations overestimate their biomass. For more details see Berenguer et al. (2014).

We also estimated the biomass of coarse woody debris ≥ 10 cm diameter in five 5 × 20-m subplots located 30 m apart in each transect (Fig. 1e). Coarse woody debris

consisted of stumps, fallen trunks, fallen branches and fallen palms and lianas (with  $\geq 10$  cm diameter in at least one of its extremities). We measured the length of all individual pieces, as well as their diameter at both extremities. Each piece was also subdivided into five decomposition classes (Harmon and Sexton 1996); ranging from ‘recently dead’ to ‘completely soft, rotten crumbling wood’. Samples sometimes had severe structural damage, so we recorded four damage categories for each sample: 0–25, 25–50, 50–75 and  $>75$  %. All pieces had their individual volumes estimated using Smalian’s formula, which uses length and diameter (Chao et al. 2009). We then discounted the percentage damage from the final volume of each piece of dead wood. The biomass of all individual pieces of coarse woody debris was calculated by multiplying the final volume of each piece by the density of its decomposition class (Keller et al. 2004).

Leaf litter biomass, comprising fallen leaves, fine twigs, fruits and seeds, was sampled every 50 m along the transect in  $50 \times 50$ -cm quadrats at both 5- and 10-m lines perpendicular to the main transect to avoid human trampling. Samples were taken to a laboratory and oven dried to calculate their mass.

#### *Edaphic variables*

Soil was sampled at five points separated by 50 m along each transect, where individual samples were collected at three different depths (0–10, 10–20 and 20–30 cm). Soil analyses were carried out at the Embrapa Amazônia Oriental Soil Laboratory in Belém. Here we used variables of pH (following EMBRAPA 1997) and clay content as a measure of soil texture, determined using a densimeter (Camargo et al. 1986).

#### *Landscape variables*

The topographic variables elevation and slope were obtained using Shuttle Radar Topography Mission images (90-m resolution; National Aeronautics and Space Administration) and represent the average elevation and slope of each transect. In addition, a remote sensing analysis was performed using a 30-m ( $900\text{-m}^2$ ) pixel resolution Landsat image time series from 1988 to 2010 in Paragominas and 1990–2010 in Santarém with ArcGIS 9.3 software. The images were classified using a decision tree algorithm after being corrected for atmospheric haze and smoke interferences (see Gardner et al. 2013). To capture the importance of edge effects we used the mean distance to the nearest forest edge calculated across all pixels located within a 100-m buffer around the transect (where forest is considered to be both primary forest and secondary forest  $>10$  years mapped in 2010).

#### *Historical deforestation and forest-disturbance variables*

To measure differences in the timing (vs. extent) of deforestation in the area around each transect we calculated the deforestation curvature profile within a 500-m buffer based on a biannual time series of classified satellite images spanning two decades prior to when field observations were made (1988–2010). The deforestation curvature profile illustrates the deviation of the observed deforestation relative to the average rate for the time series, providing a unitless measure that is positive if deforestation occurred more at the start of the time series (i.e. observed line falls below the average line) and negative if deforestation occurred more recently (i.e. observed line falls above average line) (Ferraz et al. 2009).

The classification of primary forest disturbance for each transect was based on evidence from a combination of both field observations and a visual inspection of degradation scars from remote-sensing images, providing measures of the number of times each transect was logged and burnt. In addition to the ground-truthed classification of different types of forest disturbance we used a semi-supervised classification of degraded forest pixels to estimate the percentage of forest pixels degraded at least once in the time series within a 100-m buffer around each transect.

#### **Data analysis**

We reduced our choice of candidate species for all analyses by first selecting all forest birds occurring in both regions and with records from at least 20 point counts (PCs) per region in primary forest, thus excluding rarer species. This left a shortlist of 44 species, which we classified with respect to behavioural traits: diet, flocking behaviour and forest strata occupied (based on Stotz et al. 1996; Cohn-Haft et al. 1997; Stouffer and Bierregaard 1995; del Hoyo et al. 2014). Our final selection included 27 species of insectivores, 14 frugivores, two granivores and one nectarivore (Supplementary Material Appendix 1). Our taxonomy follows the checklist of Brazilian birds compiled by the Comitê Brasileiro de Registros Ornitológicos (CBRO 2011).

To assess how study species responded to different class of primary forest, we calculated the percentage occurrence of species within transects of each category of primary forest for both regions. For instance if one species was recorded in all 44 logged forest transects in PGM, we considered it to have a 100 % occurrence rate. Then, to investigate the relative importance of each candidate predictor variable for each study species, we used Random Forest (RF) regression trees. The RF analyses were performed using 2000 regression trees, using the package extendedForest (Ellis et al. 2012) in R version 2.15.1 (R

Core Development Team 2011). We modified the RF fitting and cross-validation procedure to account for spatial autocorrelation of transects sampled within the same catchment using a variant of the residual autocovariate method (Crase et al. 2012). Specifically, for each catchment in turn, we used data from all other catchments to predict occurrence within the held-out catchment, and calculated the mean residual. We then included the catchment mean residuals as an additional predictor variable (analogous to a catchment-level random intercept) in a final RF model fitted with all data combined. Following Ellis et al. (2012) we calculated  $R^2$  weighted mean importance values for each predictor variable, which indicate the relative importance of each variable in predicting the assemblage as a whole. After modelling we discarded poorly modelled species with  $r^2 \leq 0.4$  and then plotted a cluster heat map, using the heatmap.2 function to visualize differences in species-environment relationships across both individual species and variables.

## Results

### Species occurrence patterns across forest-disturbance classes

Across the gradient of disturbed primary forests, our 44 study forest species exhibited considerable response diversity both among different forest types and between regions (Fig. 2; Supplementary Material Appendix 2). We visually identified five broad response categories among our study species (Fig. 2; Supplementary Material Appendix 2). The first response category (Fig. 2a) involved species such as the Pará foliage-gleaner *Automolus paraensis* and thrush-like schiffornis *Schiffornis turdina*, which exhibited a rapid decline in occurrence from undisturbed to disturbed primary forests (either logged, burnt, or both). The second response category (Fig. 2b) included species such as the cinereous antshrike *Thamnomanes caesius* and red-billed pied tanager *Lamprospiza melanoleuca* that showed a gradual decline with increasing forest disturbance. The third response category (Fig. 2c) included those species whose occurrence remained relatively stable despite a deterioration in forest condition (e.g. white-shouldered antshrike *Thamnophilus aethiops* and helmeted pygmy-tyrant *Lophotriccus galeatus*). The fourth category (Fig. 2d) included species (e.g. plumbeous pigeon *Patagioenas plumbea* and black-necked aracari *Pteroglossus aracari*) that were more frequently encountered in disturbed forests. Finally, a few species (Fig. 2e; e.g. squirrel cuckoo *Piaya cayana* and white-tailed trogon *Trogon viridis*) exhibited marked differences in responses between regions.

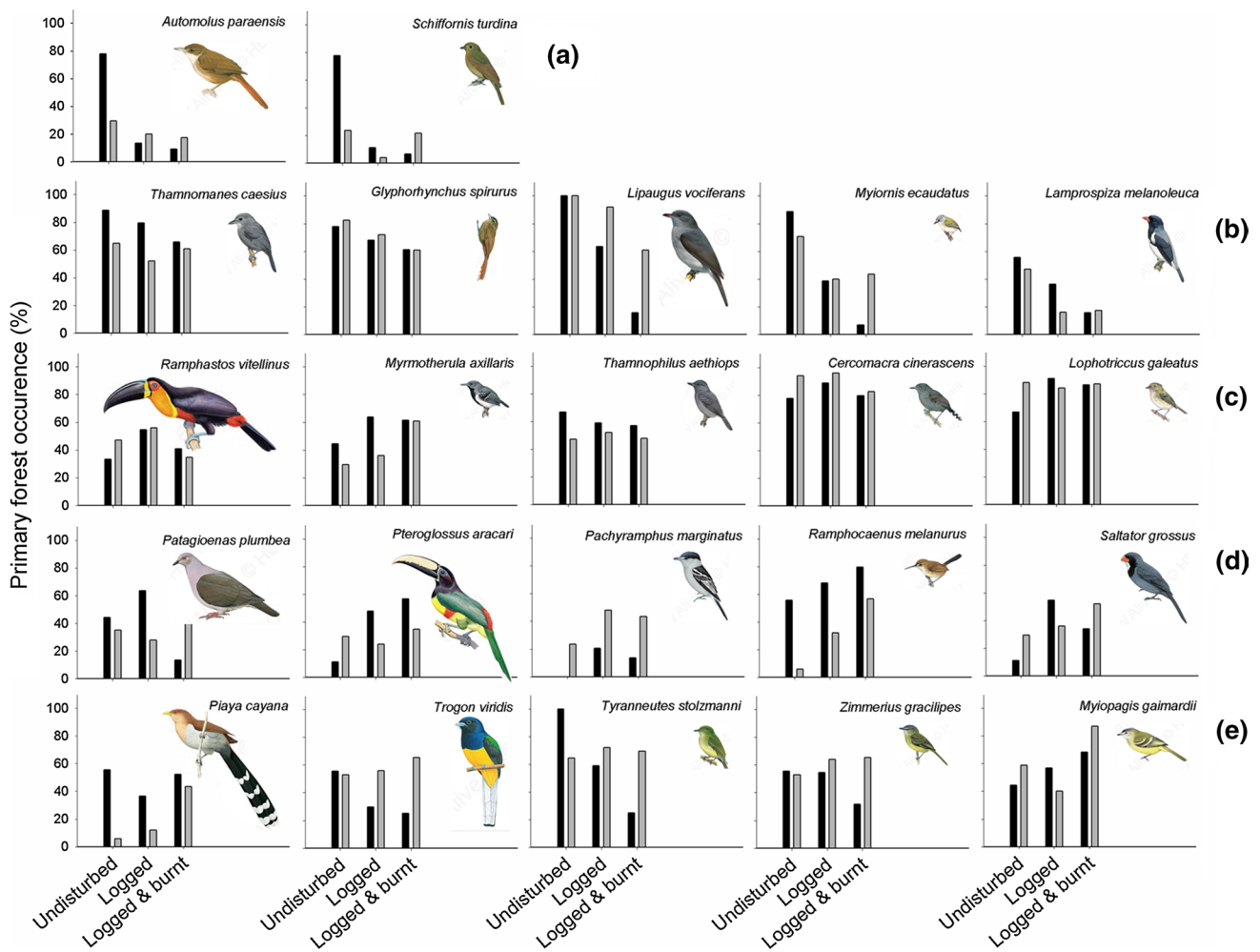
### Predicting species occurrence in primary forests

Considering our set of study species, we found that the most important predictors of species occurrence in primary forest transects for both landscapes were biomass of large trees and the distance to the forest edge (Fig. 3). However elevation and percentage of degraded forest pixels were also important for PGM and STM, respectively.

The partial dependence plots (Fig. 4) indicated a near-linear increase in the probability of occurrence of study species with increasing tree biomass in both regions. The probability of occurrence of forest species increased with increasing distance from the forest edge until approximately 200 m, after which occurrence levels remained constant. In PGM the occurrence of study species decreased with increasing primary forest degradation until a threshold of around 30 %, after which probability remains constant, while in STM species probability of occurrence decreased slightly with increasing elevation until around 80 m and then underwent a slight but consistent increase.

Thirteen species were considered to be satisfactorily modelled ( $R^2 > 0.4$ ) in PGM and 17 in STM (Fig. 5). Of the 13 species satisfactorily modelled in PGM, 12 were suboscine passerines: nine insectivores and three frugivores (screaming piha *Lipaugus vociferans*, purple-throated fruit-crow *Querula purpurata* and slender-footed tyrannulet *Zimmerius gracilipes*) and one granivore (blue-headed parrot *Pionus menstruus*—the only non-passerine). In STM, the 17 (Supplementary Material Appendix 4) satisfactorily modelled species comprised 12 suboscines, of which ten were insectivorous species, five frugivorous and five were non-passerines of which two were frugivores (plumbeous pigeon and black-necked aracari), one insectivore (white-fronted nunbird *Monasa morphoeus*), and two granivores (blue-headed parrot and mealy parrot *Amazona farinosa*). Of these 30 species, seven were well modelled in both regions.

We found that local and landscape variables were apparently more important in determining the distribution of study species in anthropogenic landscape than our landscape history variables. In PGM forest structure and soil variables were the most important in determining the presence of eight of the 13 species (Supplementary Material Appendix 3). Forest structure was most important for cinereous antshrike, scale-backed antbird *Willisornis poecilinotus*, Spix's woodcreeper *Xiphorhynchus spixii*, thrush-like schiffornis, screaming piha and slender-footed tyrannulet, while soil variables were more important for dwarf tyrant-manakin *Tyrannetes stolzmanni* and purple-throated fruitcrow. Meanwhile, landscape variables such as distance to primary forest edge were important for the blue-headed parrot and short-tailed pygmy-tyrant *Myiornis ecaudatus*,



**Fig. 2** Species occurrence in different primary forest-disturbance classes for 17 out of 44 study species (the remaining species can be found in Appendix 2) in the municipalities of Paragominas (black bars) and Santarém (grey bars). Each row of panels corresponds to a response category: **a** species that exhibited a rapid decline in occurrence from undisturbed to disturbed primary forests, **b** species that showed a gradual decline with increasing forest disturbance, **c** species

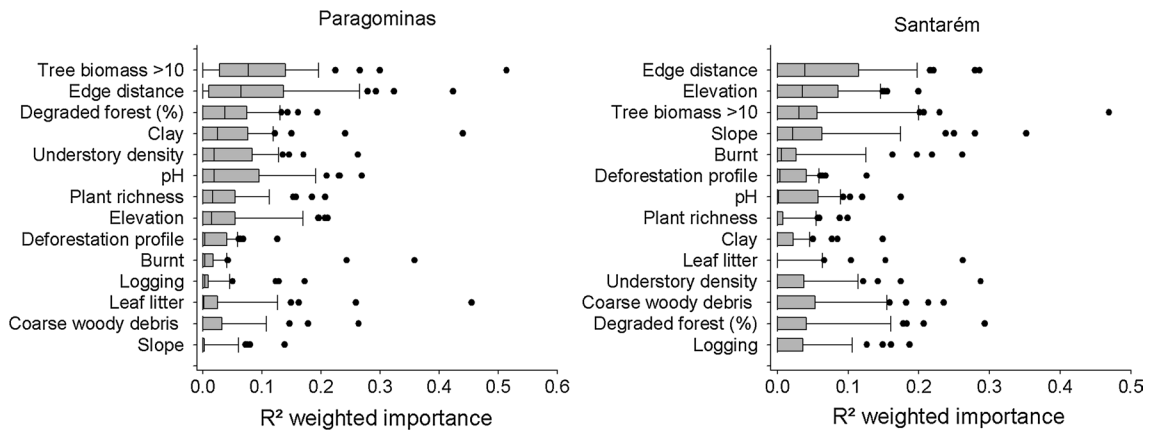
whose occurrence remained relatively stable despite a deterioration in forest condition, **d** species that were more frequently encountered in disturbed forests, **e** species that exhibited marked differences in responses between regions. Species illustrations are reproduced with the permission of Lynx and are approximately proportional to body size

and elevation was important for Pará foliage-gleaner and black-capped becard *Pachyramphus marginatus*. Finally, the grey antbird *Cercomacra cinerascens* was the only species for which historical variables (the number of times that a transect burned) were among the most important.

In STM (Supplementary Material Appendix 4), the biomass of live trees was potentially the most important variable influencing occurrence patterns of each of screaming piha, cinereous antshrike, and short-tailed pygmy-tyrant, while leaf litter biomass was the most important variable for black-necked aracari. Elevation was found to be important for white-fronted nunbird and long-billed gnatwren *Ramphocaenus melanurus*, whilst slope was important for red-billed pied tanager. Soil clay content was the most

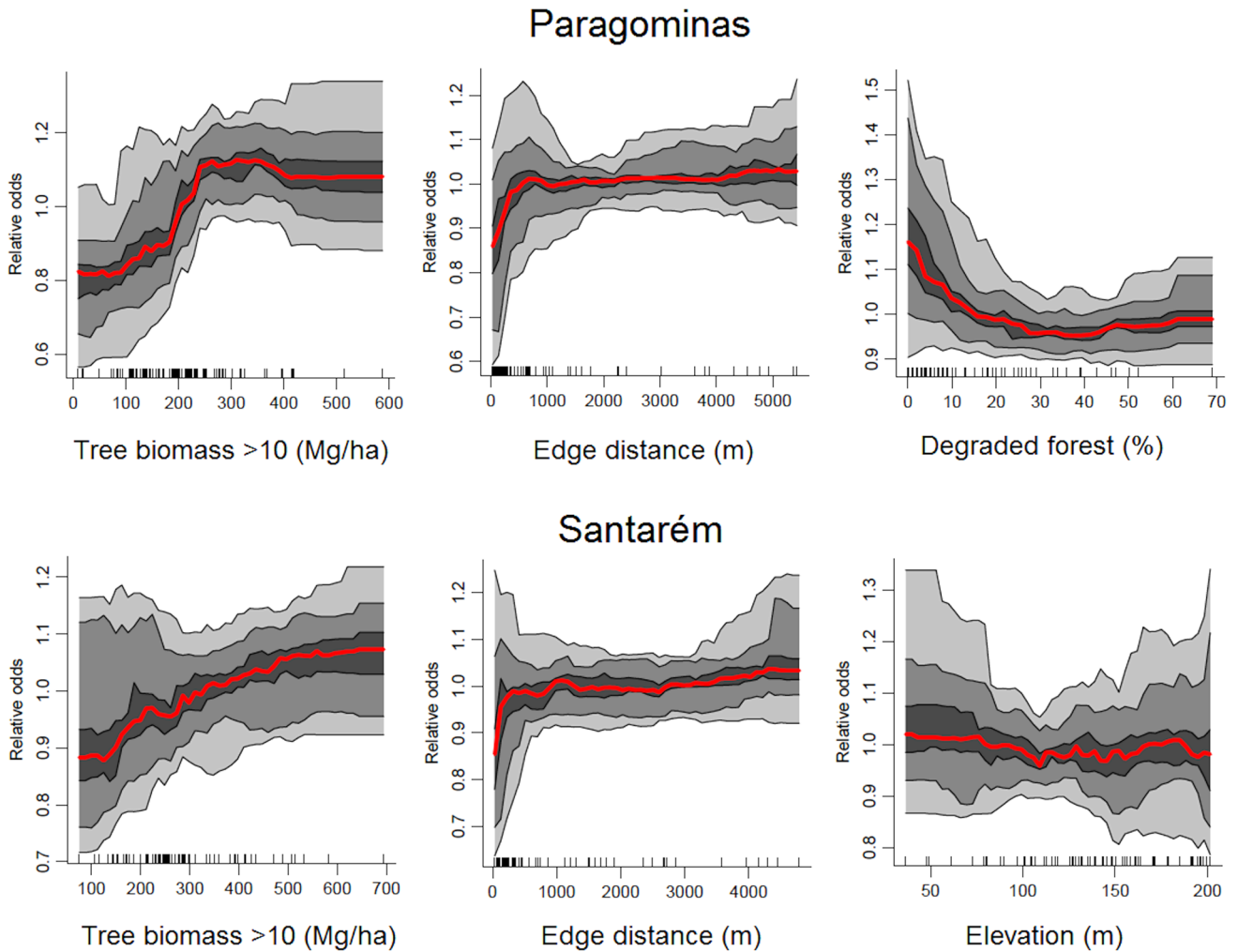
important variable for thrush-like schiffornis, and distance to primary forest edge for plumbeous pigeon, gray antwren *Myrmotherula menetriesii* and scale-backed antbird. Landscape history variables were less important, although the number of times that transects were logged and the deforestation curvature profile were more important for blue-headed parrot and grey antbird, respectively.

Finally, we found no clear taxonomic or functional groupings or associations between either closely related species or those sharing similar behavioural strategies in their responses to environmental disturbance (Supplementary Material Appendix 5) indicating significant response diversity within both phylogenetically conserved groups and broad functional guilds.



**Fig. 3** Distribution of the weighted importance values of environmental variables in primary forests for the 44 study species in Paragominas and Santarém/Belterra/Mojuí dos Campos. *Logging* number of times the transect was logged; *Burnt* number of times the transect was burnt; *edge distance* average distances to forest edges (primary forests + secondary forests >10 years); *degraded forest* percentage of

forest pixels degraded; *plant richness* total number of tree, palm and liana species; *leaf litter* biomass of leaf litter; *tree biomass >10* biomass of trees with diameter  $\geq 10$  cm; *coarse woody debris* biomass of coarse woody debris; *deforestation profile* deforestation curvature profile



**Fig. 4** Partial dependence plot for the three most important variables from an analysis of random forest regression trees in Paragominas (*top panels*) and Santarém (*bottom panels*). For abbreviations, see Fig. 3



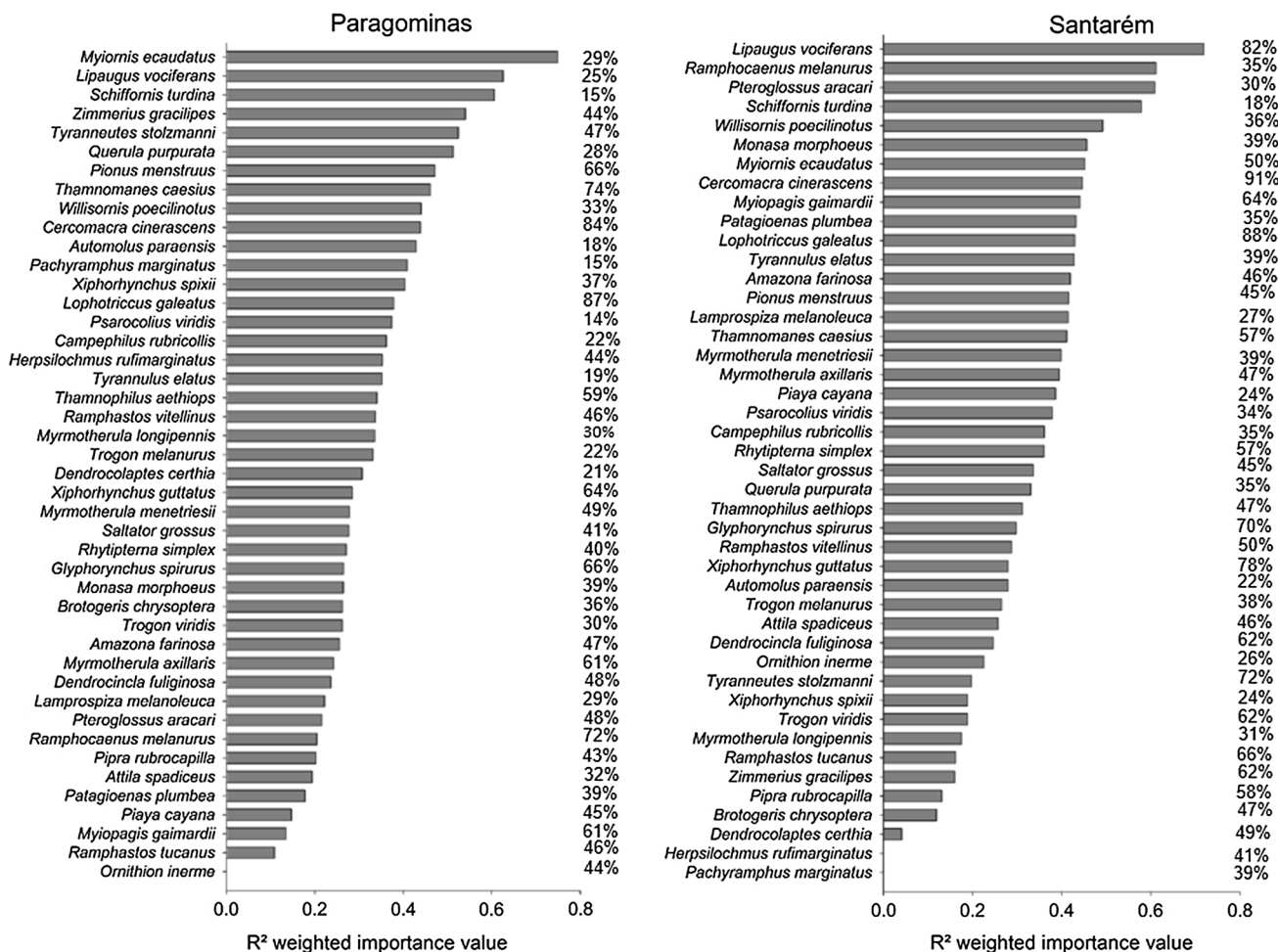


Fig. 5 Ranked goodness-of-fit (pseudo- $R^2$ ) of the models for each study species in Paragominas and Santarém

Discussion

Interpreting species-specific patterns of avian occurrence across different forest-disturbance classes

Our large-scale species-specific assessment of bird responses to multiple anthropogenic impacts in human-modified tropical forests reveals how most study species declined with increasing forest disturbance. However, the manner in which species declined differed among taxa and between regions. Those showing the most rapid decrease in occurrence in more disturbed forests, e.g. the Pará foliage-gleaner and long-winged antwren *Myrmotherula longipennis*, were typically insectivorous flock obligate species of the forest mid- and understorey, known to exhibit low tolerance to forest fragmentation and disturbance (Henriques et al. 2008; Moura et al. 2013). That elevation was an important predictor of the former may reflect its dependency on slopes to build burrow-nests (Remsen 2003).

However, not all flock-following species responded in this way: the cinereous antshrike *Thamnomanes caesius*, a nuclear flock leader (Powell 1985) known to be sensitive to forest disturbance (e.g. Stouffer and Bierregaard 1995; Barlow et al. 2002), declined less rapidly, indicating a greater resistance or resilience to forest disturbance. In logged and burnt forests this species typically leads impoverished flock networks comprising predominantly facultative flock-following members such as white-flanked antwren *Myrmotherula axillaris*, wedge-billed woodcreeper *Glyphorhynchus spirurus* and plain xenops *Xenops minutus* (see also Powell et al. 2013, Mokross et al. 2014).

Canopy flocking species such as red-billed pied-tanager and green oropendola *Psarocolius viridis* also declined gradually across the full forest disturbance gradient. Canopy species may be more tolerant to disturbance (Cohn-Haft and Sherry 1994) as they may be pre-adapted to more open environments and longer-distance movements (Karr and James 1975), and may need to track spatio-temporarily variable food resources such as fruit. Moreover, selective

logging may not be as detrimental to canopy species, whose habitat structure is less affected by the removal of some trees, in the same way as understorey species are highly dependent on humid micro-climates beneath the forest canopy (Mason and Thiollay 2001). Some species such as the grey antbird, helmeted pygmy-tyrant and long-billed gnatwren exhibited similar patterns of occurrence in all levels of disturbed primary forest, and this tolerance is likely related to their preference for dense forest understorey or vine tangle habitats which are maintained or even proliferate in disturbed forests (Thiollay 1999; Berenguer et al. 2014). The grey antbird provided an exception to the rule that landscape history variables were of generally low value in predicting avian occurrence relative to local and landscapes variables given that historical logging frequency was the best predictor of this species' occurrence, perhaps as a reflection of its association with these mid-storey vine tangles.

The species that were more frequently recorded in disturbed than in undisturbed primary forests were mostly the large-bodied canopy frugivores such as the plumbeous pigeon and black-necked aracari. These species are both highly vagile (Lees and Peres 2009) and may benefit from an increase in fruit production seen in some tree species in once-burnt forests (Barlow and Peres 2006).

Not all species exhibited similar patterns between regions, for instance in PGM, the squirrel cuckoo slowly decreased in abundance with increasing forest disturbance, whilst in STM the opposite was true. We interpret this difference as potentially due to a release from competition with its sister species, the congeneric black-bellied cuckoo *Piaya melanogaster* (not modelled in STM and absent from PGM), which was restricted to undisturbed and logged forests. It seems likely that *P. cayana* is competitively excluded from less-disturbed forest habitats by the canopy specialist *P. melanogaster* (Pearson 1971). Moreover, Wolfe et al. (2014) recently uncovered evidence for marked geographical differences in survival rates for several common Amazonian bird species, suggesting that regional variation in population processes, even in undisturbed forest landscapes may be significant across the basin. However, it may be difficult to tease apart intra-specific response variation from potentially significant endogenous differences between these major regions. The landscape divergence hypothesis (Laurance et al. 2007) posits that species assemblages may diverge in disturbed areas because of the different effects of disturbance, or because of interaction between disturbance processes and underlying differences in environmental heterogeneity. Such variability in consequences of disturbance, which there is some evidence for in our region (Solar et al. 2015), highlight the challenges in understanding regional differences in species responses.

Finally, our results should be viewed as a conservative overview of avian species responses to forest disturbance. We were unable to model the most disturbance-sensitive forest species (e.g. variegated antpitta *Grallaria varia*, tawny-crowned greenlet *Hylophilus ochraceiceps*) as these were rarely recorded in our study region where disturbed forests predominate. We anticipate that these species are likely to exhibit far more sensitive responses to forest disturbance than those modelled here. This bias towards a focus on more abundant and disturbance-tolerant forest species is typical of most studies in human-modified landscapes, and should be borne in mind when interpreting our results and those of other studies (e.g. Banks-Leite et al. 2014).

### Avian species-environment relationships in modified primary tropical forests

Overall, we found that distance to the forest edge and the biomass of large live trees were likely the most important variables driving patterns of occurrence of our study species in varyingly disturbed primary forests in our two study regions. Edge effects are among the most studied types of disturbance in tropical forests, with proximity to edges typically resulting in marked patterns of bird species turnover with increases in gap-specialist species and a loss of forest-interior specialists (e.g. Terborgh et al. 1990; Laurance 2004). That we were able to uncover evidence for edge effects stretching beyond 200 m into forests is further support for the pervasive effects of edges on forest bird distributions. Not all species responded strongly to edges, however; medium- to large-bodied frugivores (e.g. Psittacids and Ramphastids) are less affected, given their natural affinity for edges and good gap-crossing ability (Lees and Peres 2008, 2009).

The biomass of large live trees closely reflects patterns of historical logging as well as fire frequency and intensity (Berenguer et al. 2014), with the death or removal of large emergent tree species altering the canopy structure and hence understorey micro-climate and vegetation composition (Uhl and Vieira 1989) and potentially availability of nesting sites (Cockle et al. 2015) to the detriment of specialist understorey species, such as brown-winged *Psophia dextralis* and dark-winged *P. obscura* trumpeters, variegated antpitta and musician wren *Cyphorhinus arada*, which were only recorded in our region in undisturbed forests (Moura et al. 2013).

Variation in Amazonian soils can be responsible for the heterogeneity of lowland forest physiognomies (Tuomisto et al. 1995) with consequences for avian distribution patterns and community structuring (Bueno et al. 2012; Pomara et al. 2012). Changes in soil variables such as clay content and pH were found to be associated with species

with different life strategies, including mid-storey frugivore (e.g. dwarf tyrant-manakin), and canopy frugivores (e.g. slender-footed tyrannulet). These results echo those of Cintra and Naka (2012) who also found an association between avian community structure and clay content in central Amazonia, which is also positively associated with tree biomass (Laurance et al. 1999; Castilho et al. 2006) perhaps because larger trees offer a larger resource base in terms of providing food, nesting sites and microhabitats.

We did not find any clear patterns of congruence between our environmental predictor variables and different functional groups (diet, flocking behaviour or association with different forest strata) of our study species. Some species were poorly modelled by our environmental variables, and it is of course possible that observed occurrence patterns are associated with factors that we did not measure, including biotic interactions such as inter-specific competition, predation or parasitism (Connell and Orias 1964; Robinson and Terborgh 1995). Furthermore, the species most affected by human-induced disturbance and land cover change are likely to be the first to disappear and probably were not included in our models, as the cut-off point for model inclusion was species occurrence in at least 20 PCs. The difficulty of modelling the rarest species supports our choice of occurrence models over the data-hungry detectability approaches (Banks-Leite et al. 2014).

We were able to model the occurrence of some species much better than others, and given the strong response of some to primary forest disturbance, we can recommend these species as indicators of good-quality forest habitat that can contribute towards ongoing work to validate and refine a suite of indirect and direct indicators as part of a forest biodiversity monitoring program (Gardner 2010). Suboscine passerines were better modelled than most other phylogenetic groups, reinforcing their importance as effective study systems for ecological enquiries (Tobias et al. 2012). One indicator species that stands out was the screaming piha, a mid-storey frugivore, which was well modelled in both regions and appears to be strongly influenced by edge effects, differences in tree species richness, biomass of large live trees, and understorey density. This is particularly notable given that this species is one of the loudest birds on earth (Nemeth 2004) and thus provides an easily detectable proxy of forest condition given its general affinity for areas of forest with high basal area and removed from edges.

Although crude metrics of biodiversity value such as richness or phenotypic diversity (Owens and Bennett 2001) are useful in conservation planning, the high level of intra- and inter-specific variation uncovered here illustrates the importance of using detailed multi-taxon studies to refine our knowledge of the value of human-modified tropical forests for biodiversity (Solar et al. 2015). The heterogeneity of forest bird species responses to disturbance in primary

forests likely reflects both species-specific variation in the width of each species' realized and fundamental niches and the lack of clear guild-specific variation, which can be attributed to the coarseness of current classifications and unappreciated fine-scale variation in avian morphology and behavioural traits (e.g. Bravo et al. 2014). Knowing that such avian 'response diversity' (sensu Elmquist et al. 2003) exists within primary forests suggests that many important processes and ecosystem services may still be performed by some species in even the most degraded of primary forests. Understanding the impact on ecosystem resilience ought to be a research priority given variation—in some cases even intra-specifically between regions—in avian responses to disturbance and the spatially variable nature of anthropogenic threats to tropical forests (Malhi et al. 2014).

**Acknowledgments** We thank the Instituto Nacional de Ciência e Tecnologia—Biodiversidade e Uso da Terra na Amazônia (CNPq 574008/2008-0), the National Environment Research Council (NE/G000816/1), the Darwin Initiative (17-023), the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior—CAPES, Lancaster University, Embrapa Amazonia Oriental (SEG 02.08.06.005.00), and the Nature Conservancy for funding, as well as the Nature Conservancy for access to detailed land cover maps of the municipality. We also thank the farmers' and workers' unions of Santarém, Belterra and Paragominas and all collaborating private landowners for their support. We thank the Large-scale Biosphere–Atmosphere Experiment in Amazonia for logistic support. We are indebted to support from our field team including C. B. Andretti, W. Ávila, A. S. Costa, F. C. S. Cunha, B. J. Davis, R. M. Freitas, M. Cordeiro, V. C. Nascimento, E. P. Oliveira, G. J. Oliveira, J. M. Oliveira, the late M. A. Nascimento, N. Rosa, A. S. Silva, J. C. Silva and the late E. D. Silva. We also thank I. C. G. Vieira for logistical support and R. C. Solar for the map. J. B. and E. B. were supported by a Natural Environment Research Council grant (NE/K016431/1), J. B. by CNPq 400640/2012-0, T. A. G. by Formas 2013-1571, N. G. M. and A. C. L. thank CNPq for scholarships. A. A. thanks CNPq for a research productivity fellowship. This paper is no. 44 in the Rede Amazônia Sustentável publication series.

**Author contribution statement** T. A. G., J. F., J. B., A. C. L. and E. B. conceived and designed the experiments. A. C. L., N. G. M., T. A. G., E. B. and J. R. T. collected and analysed the data. N. G. M. wrote the manuscript, and all authors revised the manuscript.

## References

- Aleixo A (1999) Effects of selective logging on a bird community in the Brazilian Atlantic forest. *Condor* 101:537–548. doi:10.2307/1370183
- Banks-Leite C, Pardini R, Boscolo D, Cassano CR, Püttker T, Barros CS, Barlow J (2014) Assessing the utility of statistical adjustments for imperfect detection in tropical conservation science. *J Appl Ecol* 51:849–859. doi:10.1111/1365-2664.12272
- Barlow J, Peres CA (2006) Effects of single and recurrent wildfires on fruit production and large vertebrate abundance in a central Amazonian forest. *Biodiv Conserv* 15:985–1012
- Barlow J, Haugaasen T, Peres CA (2002) Effects of ground fires on understorey bird assemblages in Amazonian forests. *Biol Conserv* 105:157–169. doi:10.1016/S0006-3207(01)00177-X

- Berenguer E, Ferreira J, Gardner TA, Aragão LEOC, De Camargo PB, Cerri CE, Durigan M, Oliveira Junior RC, Vieira ICG, Barlow J (2014) A large-scale field assessment of carbon stocks in human-modified tropical forests. *Glob Change Biol* 20:3713–3726. doi:10.1111/gcb.12627
- Bravo GA, Remsen JV, Brumfield T (2014) Adaptive processes drive ecomorphological convergent evolution in antwrens (Thamnophilidae). *Evolution* 68:2757–2774. doi:10.1111/evo.12506
- Bueno AS, Bruno RS, Pimentel TP, Sanaiotti TM, Magnusson WE (2012) The width of riparian habitats for understory birds in an Amazonian forest. *Ecol Appl* 22:722–734. doi:10.1890/11-0789.1
- Camargo OA, Moniz AC, Jorge JA, Valadares JMA (1986) Métodos de análise química, mineralógica e física de solos do Instituto Agronômico de Campinas. *Boletim Técnico* 106:77
- Castilho CV, Magnusson WE, Araújo RNO, Luizao RC, Luizao FJ, Lima AP, Higuchi N (2006) Variation in aboveground tree live biomass in a central Amazonian forest: effects of soil and topography. *For Ecol Manage* 234:85–96. doi:10.1016/j.foreco.2006.06.024
- Chao KJ, Phillips OL, Baker TR, Peacock J, Lopez-Gonzalez G, Vásquez Martínez R, Monteagudo A, Torres-Lezama A (2009) After trees die: quantities and determinants of necromass across Amazonia. *Biogeosciences* 6:1615–1626. doi:10.5194/bg-6-1615-2009
- Chave J, Andalo C, Brown S, Cairns MA, Chambers JQ, Eamus D, Fölster H, Fromard F, Higuchi N, Kira T, Lescure JP, Nelson BW, Ogawa H, Puig H, Riéra B, Yamakura T (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* 145:87–99. doi:10.1007/s00442-005-0100-x
- Cintra R, Naka LN (2012) Spatial variation in bird community composition in relation to topographic gradient and forest heterogeneity in a Central Amazonian rainforest. *Int J Ecol* 2012:1–25. doi:10.1155/2012/435671
- Cockle KL, Bodrati A, Lammertink M, Martin K (2015) Cavity characteristics, but not habitat, influence nest survival of cavity-nesting birds along a gradient of human impact in the subtropical Atlantic Forest. *Biol Conserv* 184:193–200. doi:10.1016/j.biocon.2015.01.026
- Cohn-Haft M, Sherry TW (1994) Evolution of avian foraging stereotypes in tropical rain forest habitats. *J Ornithol* 135:481
- Cohn-Haft M, Whittaker A, Stouffer PC (1997) A new look at the “species-poor” central Amazon: the avifauna north of Manaus, Brazil. *Ornithol Monogr* 48:205–235
- Comitê Brasileiro de Registros Ornitológicos (2011) Listas das aves do Brasil. Electronic database. [www.cbro.org.br](http://www.cbro.org.br). Accessed 1 Oct 2014
- Connell JH, Orias E (1964) The ecological regulation of species diversity. *Am Nat* 98:399–414. doi:10.2307/40157535
- Cornelius C, Cockle K, Politi N, Berkunsky I, Sandoval L, Ojeda V, Rivera L, Hunter M Jr, Martin K (2008) Cavity-nesting birds in Neotropical forests: cavities as a potentially limiting resource. *Ornitol Neotrop* 19:253–268
- Cruse B, Liedloff AC, Wintle BA (2012) A new method for dealing with residual spatial autocorrelation in species distribution models. *Ecography* 35:879–888. doi:10.1111/j.1600-0587.2011.07138.x
- Daily GC, Ehrlich PR, Sanchez-Azofeifa GA (2000) Country-side biogeography: utilization of human dominated habitats by the avifauna of southern Costa Rica. *Ecol Appl* 11:1–13. doi:10.1890/1051-0761(2001)011[0001:CBUOHD]2.0.CO;2
- del Hoyo J, Elliott A, Sargatal, Christie DA, de Juana E (eds) (2014) *Handbook of the birds of the world alive*. Lynx, Barcelona. <http://www.hbw.com>. Accessed January 2015
- Dunn RR (2004) Recovery of faunal communities during tropical forest regeneration. *Conserv Biol* 18:302–309. doi:10.1111/j.1523-1739.2004.00151.x
- Edwards DP, Larsen TH, Docherty TD, Ansell FA, Hsu WW, Derhé MA, Hamer KC, Wilcove DS (2011) Degraded lands worth protecting: the biological importance of Southeast Asia’s repeatedly logged forests. *Proc R Soc B* 278:82–90. doi:10.1098/rspb.2010.1062
- Ellis N, Smith SJ, Pitcher CR (2012) Gradient forests: calculating importance gradients on physical predictors. *Ecology* 93:156–168. doi:10.1890/11-0252.1
- Elmqvist T, Folke C, Nyström M, Peterson G, Bengtsson J, Walker B, Norberg J (2003) Response diversity, ecosystem change, and resilience. *Front Ecol Environ* 1:488–494. doi:10.1890/1540-9295(2003)001[0488:RDECAR]2.0.CO;2
- EMBRAPA-CNPS (1997) Manual de métodos de análise de solo. Embrapa Solos, Rio de Janeiro, p 212p
- Ferraz SDB, Vettorazzi CA, Theobald DM (2009) Using indicators of deforestation and land-use dynamics to support conservation strategies: a case study of central Rondônia, Brazil. *For Ecol Manage* 257:1586–1595. doi:10.1016/j.foreco.2009.01.013
- Gardner TA (2010) Monitoring forest biodiversity. Improving conservation through ecologically responsible management. Earthscan, London
- Gardner TA, Barlow J, Chazdon R, Ewers RM, Harvey CA, Peres CA, Sodhi NS (2009) Prospects for tropical forest biodiversity in a human-modified world. *Ecol Lett* 12:561–582. doi:10.1111/j.1461-0248.2009.01294.x
- Gardner TA, Ferreira J, Barlow J, Lees AC, Parry L, Vieira ICG, Berenguer E, Abramovay R, Aleixo A, Andretti C, Aaragao LEO, Araujo I, Souza de Avila W, Bardgett RD, Batistella M, Begotti RA, Beldini T, Ezzine de Blas D, Braga RF, de Lima Braga D, de Brito JG, de Camargo PB, Campos dos Santos F, Campos de Oliveira V, Cordeiro ACN, Cardoso TM, de Carvalho DR, Castellani SA, Chaul JCM, Cerri CE, De Assis Costa F, da Costa CDF, Coudel E, Coutinho AC, Cunha D, D’Antona A, Dezincourt J, Dias-Silva K, Durigan M, Esquerdo JCD, Feres J, de Barros Ferraz SF, de Melo Ferreira AE, Fiorini AC, da Silva LVF, Frazao FS, Garrett R, dos Santos Gomes A, da Silva Gonçalves K, Guerrero JB, Hamada N, Hughes RM, Iglioni DC, da Conceição Jesus E, Juen L, Junior M, de Oliveira Junior JMB, de Oliveira Junior RC, Junior CS, Kaufmann P, Korasaki V, Leal CG, Leitao R, Lima N, de Almeida MFL, Lourival R, Louzada J, Mac Nally RC, Marchand S, Maués MM, Moreira FMS, Morsello C, Moura NG, Nessimian J, Nunes S, Oliveira VHF, Pardini R, Pereira HC, Pompeu PS, Ribas CR, Rossetti F, Schmidt FA, da Silva R, da Silva RCV, da Silva TFM, Silveira J, Siqueira JV, de Carvalho TS, Solar RRC, Tancredi NSH, Thomson JR, Torres PC, Vaz-de-Mello FZ, Veiga RCS, Venturieri A, Viana C, Weinhold D, Zanetta R, Zuanon J (2013) A social and ecological assessment of tropical land uses at multiple scales: the Sustainable Amazon Network. *Philos Trans R Soc Lond B* 368(1619):20120166. doi:10.1098/rstb.2012.0166
- Harmon ME, Sexton J (1996) Guidelines for measurements of woody detritus in forest ecosystems. US LTER publication no. 20. US LTER Network Office, University of Washington, Seattle
- Henriques LMP, Wunderle JM Jr, Oren DC, Willig MR (2008) Efeitos da exploração Madeireira de Baixo impacto sobre uma comunidade de aves de sub-bosque na Floresta Nacional do Tapajós, Pará, Brasil. *Acta Amaz* 38:267–290
- Holdsworth AR, Uhl C (1997) Fire in Amazonian selectively logged rain forest and the potential for fire reduction. *Ecol Appl* 7:713–725. doi:10.1890/1051-0761(1997)007
- INPE (2014) DEGRAD. Available at: <http://www.obt.inpe.br/degrad/>. Accessed November 2014
- Karp DS, Rominger AJ, Zook J, Ranganathan J, Ehrlich PR, Daily GC (2012) Intensive agriculture erodes  $\beta$ -diversity at large scales. *Ecol Lett* 15:963–970. doi:10.1111/j.1461-0248.2012.01815.x

- Karr JR, James FC (1975) Eco-morphological configurations and convergent evolution in species and communities. In: Cody ML, Diamond JM (eds) Ecology and evolution of communities. Belknap Press of Harvard University Press, Cambridge, pp 258–291
- Kauffman JB, Cummings DL, Ward DE, Babbitt R (1995) Fire in the Brazilian Amazon. 1. Biomass, nutrient pools, and losses in slashed primary forests. *Oecologia* 104:397–408. doi:10.1007/BF00341336
- Keller M, Palace M, Asner GP, Pereira R, Silva JNM (2004) Coarse woody debris in undisturbed and logged forests in the eastern Brazilian Amazon. *Glob Change Biol* 10:784–795. doi:10.1111/j.1529-8817.2003.00770.x
- Laurance SG (2004) Responses of understory rain forest birds to road edges in central Amazonia. *Ecol Appl* 14:1344–1357. doi:10.1890/03-5194
- Laurance WF, Fearnside PM, Laurance SG, Delamonica P, Lovejoy TE, Rankin-de Merona JM, Chambers JQ, Gascon C (1999) Relationship between soils and Amazon forest biomass: a landscape-scale study. *For Ecol Manage* 118:127–138. doi:10.1016/S0378-1127(98)00494-0
- Laurance WF, Nascimento HE, Laurance SG, Andrade A, Ewers RM, Harms KE, Luizão RCC, Ribeiro JE (2007) Habitat fragmentation, variable edge effects, and the landscape-divergence hypothesis. *PLoS ONE* 2:e1017. doi:10.1371/journal.pone.0001017
- Laurance WF, Sayer J, Cassman KG (2014) Agricultural expansion and its impacts on tropical nature. *Trends Ecol Evol* 29:107–116. doi:10.1016/j.tree.2013.12.001
- Lees AC, Peres CA (2006) Rapid avifaunal collapse along the Amazonian deforestation frontier. *Biol Conserv* 133:198–211. doi:10.1016/j.biocon.2006.06.005
- Lees AC, Peres CA (2008) Avian life history determinants of local extinction risk in a fragmented Neotropical forest landscape. *Anim Conserv* 11:128–137. doi:10.1111/j.1469-1795.2008.00162.x
- Lees AC, Peres CA (2009) Gap-crossing movements predict species occurrence in Amazonian forest fragments. *Oikos* 118:280–290. doi:10.1111/j.1600-0706.2008.16842.x
- Lees AC, Moura NG, Santana A, Aleixo A, Barlow J, Berenguer E, Ferreira J, Gardner TA (2012) Paragominas: a quantitative baseline inventory of an eastern Amazonian avifauna. *Rev Bras Ornitol* 20:93–118
- Lees AC, Moura NG, Andretti CB, Davis BJ, Lopes EV, Henriques LMP, Aleixo A, Barlow J, Ferreira J, Gardner TA (2013) One hundred and thirty-five years of avifaunal surveys around Santarém, central Brazilian Amazon. *Rev Bras Ornitol* 21:16–57
- Malhi Y, Gardner TA, Goldsmith GR, Silman MR, Zelazowski P (2014) Tropical forests in the Anthropocene. *Annu Rev Env Resour* 39:125–159
- Mason D, Thiollay JM (2001) Tropical forestry and the conservation of Neotropical birds. In: Fimbel RA, Grajal A, Robinson JG (eds) The cutting edge: conserving wildlife in logged tropical forests. Columbia University Press, New York, pp 167–191
- Mestre LA, Cochrane MA, Barlow J (2013) Long-term changes in bird communities after wildfires in the Central Brazilian Amazon. *Biotropica* 45:480–488. doi:10.1111/btp.12026
- Mokross K, Ryder TB, Côrtes MC, Wolfe JD, Stouffer PC (2014) Decay of interspecific avian flock networks along a disturbance gradient in Amazonia. *Proc R Soc B* 281:20132599. doi:10.1098/rspb.2013.2599
- Moura NG, Lees AC, Andretti CB, Davis BJ, Solar RR, Aleixo A, Barlow J, Ferreira J, Gardner TA (2013) Avian biodiversity in multiple-use landscapes of the Brazilian Amazon. *Biol Conserv* 167:339–348. doi:10.1016/j.biocon.2013.08.023
- Moura NG, Lees AC, Aleixo A, Barlow J, Dantas SM, Ferreira J, Lima MFC, Gardner TA (2014) Two hundred years of local avian extinctions in Eastern Amazonia. *Conserv Biol* 28:1271–1281. doi:10.1111/cobi.12300
- Nelson BW, Mesquita R, Pereira JL, Souza SGA, Batista GT, Couto LB (1999) Allometric regressions for improved estimate of secondary forest biomass in the central Amazon. *For Ecol Manage* 117:149–167. doi:10.1016/S0378-1127(98)00475-7
- Nemeth E (2004) Measuring the sound pressure level of the song of the screaming Piha *Lipaugus vociferans*: one of the loudest birds in the world? *Bioacoustics* 14:225–228. doi:10.1080/09524622.2004.9753527
- Nepstad D, Verissimo A, Alencar A, Nobre C, Lima E, Lefebvre P, Schlesinger P, Potter C, Moutinho P, Mendoza E, Cochrane M, Brooks V (1999) Large-scale impoverishment of Amazonian forests by logging and fire. *Nature* 398:505–508. doi:10.1038/19066
- Newmark WD, Stanley TR (2011) Habitat fragmentation reduces nest survival in an Afrotropical bird community in a biodiversity hotspot. *Proc Natl Acad Sci USA* 108:11488–11493. doi:10.1073/pnas.1104955108
- Owens IP, Bennett PM (2001) Quantifying biodiversity: a phenotypic perspective. *Conserv Biol* 14:1014–1022. doi:10.1046/j.1523-1739.2000.98509.x
- Pearson DL (1971) Vertical stratification of birds in a tropical dry forest. *Condor* 73:46–55
- Pearson DL (1975) The relation of foliage complexity to ecological diversity of three Amazonian bird communities. *Condor* 77:453–466
- Perfecto I, Vandermeer J (2002) Quality of agroecological matrix in a tropical montane landscape: ants in coffee plantations in southern Mexico. *Conserv Biol* 16:174–182. doi:10.1046/j.1523-1739.2002.99536.x
- Peterson G, Allen CR, Holling CS (1998) Ecological resilience, biodiversity, and scale. *Ecosystems* 1:6–18. doi:10.1007/s100219900002
- Phalan B, Onial M, Balmford A, Green RE (2011) Reconciling food production and biodiversity conservation: land sharing and land sparing compared. *Science* 333:1289–1291. doi:10.1126/science.1208742
- Pomara LY, Ruokolainen K, Tuomisto H, Young KR (2012) Avian composition co-varies with floristic composition and soil nutrient concentration in Amazonian upland forests. *Biotropica* 44:545–553. doi:10.1111/j.1744-7429.2011.00851.x
- Powell GVN (1985) Sociobiology and the adaptive significance of interspecific foraging flocks in the Neotropics. *Ornithol Monogr* 36:713–732. doi:10.2307/40168313
- Powell LL, Stouffer PC, Johnson EI (2013) Recovery of understory bird movement across the interface of primary and secondary Amazon rainforest. *Auk* 130:459–468. doi:10.1525/auk.2013.12202
- R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org>
- Remsen JV Jr (2003) Family Furnariidae (ovenbirds). In: del Hoyo J, Elliott A, Christie DA (eds) Handbook of the birds of the world: broadbills to tapaculos, vol 8. Lynx, Barcelona, pp 162–357
- Robinson SK, Terborgh J (1995) Interspecific aggression and habitat selection by Amazonian birds. *J Anim Ecol* 64:1–11. doi:10.2307/5822
- Skutch AF (1961) Life history of the white-tailed Trogon *Trogon viridis*. *Ibis* 104:301–313. doi:10.1111/j.1474-919X.1962.tb08660.x
- Sodhi NS, Posa MRC, Lee TM, Warkentin IG (2008) Perspectives in ornithology: effects of disturbance or loss of tropical rainforest on birds. *Auk* 125:511–519. doi:10.1525/auk.2008.1708
- Solar RRC, Barlow J, Ferreira J, Berenguer E, Lees AC, Thomson JR, Louzada J, Maués M, Moura NG, Oliveira VHF, Chaul J, Schoreder JH, Vieira ICG, Mac Nally R, Gardner TA (2015) How

- pervasive is biotic homogenization in human-modified tropical forest landscapes? *Ecol Lett* 18:1108–1118. doi:[10.1111/ele.12494](https://doi.org/10.1111/ele.12494)
- Souza CM Jr, Siqueira JV, Sales MH, Fonseca AV, Ribeiro JG, Numata I, Cochrane MA, Barber CP, Roberts DA, Barlow J (2013) Ten-year Landsat classification of deforestation and forest degradation in the Brazilian Amazon. *Remote Sens* 5:5493–5513. doi:[10.3390/rs5115493](https://doi.org/10.3390/rs5115493)
- Stotz DF, Fitzpatrick JW, Parker TA III, Moskowitz DK (1996) Neotropical birds: ecology and conservation. University of Chicago Press, Chicago
- Stouffer PC, Bierregaard RO Jr (1995) Use of Amazonian forest fragments by understory insectivorous birds. *Ecology* 76:2429–2445. doi:[10.2307/2265818](https://doi.org/10.2307/2265818)
- Stratford JA, Stouffer PC (2013) Microhabitat associations of terrestrial insectivorous birds in Amazonian rainforest and second-growth forests. *J Field Ornithol* 84:1–12. doi:[10.1111/jofo.12000](https://doi.org/10.1111/jofo.12000)
- Terborgh J, Robinson SK, Parker TA III, Munn CA, Pierpont N (1990) Structure and organization of an Amazonian forest bird community. *Ornithol Monogr* 60:213–238. doi:[10.2307/1943045](https://doi.org/10.2307/1943045)
- Terborgh J, Nuñez-Iturri G, Pitman NC, Valverde FHC, Alvarez P, Swamy V, Pringle EG, Paine CT (2008) Tree recruitment in an empty forest. *Ecology* 89:1757–1768. doi:[10.1890/07-0479.1](https://doi.org/10.1890/07-0479.1)
- Thiollay JM (1999) Responses of an avian community to rain forest degradation. *Biodivers Conserv* 8:513–534. doi:[10.1023/A:1008912416587](https://doi.org/10.1023/A:1008912416587)
- Tobias JA, Brawn JD, Brumfield R, Derryberry EP, Kirschel AN, Seddon N (2012) The importance of suboscine birds as study systems in ecology and evolution. *Ornithol Neotrop* 23:259–272
- Tscharntke T, Sekercioglu CH, Dietsch TV, Sodhi NS, Hoehn P, Tylianakis JM (2008) Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. *Ecology* 89:944–951. doi:[10.1890/07-0455.1](https://doi.org/10.1890/07-0455.1)
- Tuomisto H, Ruokolainen K, Kalliola R, Linna A, Danjoy W, Rodriguez Z (1995) Dissecting Amazonian biodiversity. *Science* 269:63–66. doi:[10.1126/science.269.5220.63](https://doi.org/10.1126/science.269.5220.63)
- Tylianakis JM, Klein AM, Lozada T, Tscharntke T (2006) Spatial scale of observation affects  $\alpha$ ,  $\beta$  and  $\gamma$  diversity of cavity-nesting bees and wasps across a tropical land use gradient. *J Biogeogr* 33:1295–1304. doi:[10.1111/j.1365-2699.2006.01493.x](https://doi.org/10.1111/j.1365-2699.2006.01493.x)
- Uezu A, Metzger JP, Vielliard JM (2005) Effects of structural and functional connectivity and patch size on the abundance of seven Atlantic Forest bird species. *Biol Conserv* 123:507–519
- Uhl C (1998) Perspectives on wildfire in the humid tropics. *Conserv Biol* 12:942–943. doi:[10.1046/j.1523-1739.1998.012005942.x](https://doi.org/10.1046/j.1523-1739.1998.012005942.x)
- Uhl C, Vieira ICG (1989) Ecological impacts of selective logging in the Brazilian Amazon: a case study from the Paragominas region of the state of Pará. *Biotropica* 21:98–106. doi:[10.2307/2388700](https://doi.org/10.2307/2388700)
- Veríssimo A, Barreto P, Mattos M, Tarifa R, Uhl C (1992) Logging impacts and prospects for sustainable forest management in an old Amazonian frontier: the case of Paragominas. *For Ecol Manage* 55:169–199. doi:[10.1016/0378-1127\(92\)90099-U](https://doi.org/10.1016/0378-1127(92)90099-U)
- Wolfe JD, Stouffer PC, Seeholzer GF (2014) Variation in tropical bird survival across longitude and guilds: a case study from the Amazon. *Oikos* 123:964–970. doi:[10.1111/oik.00849](https://doi.org/10.1111/oik.00849)
- Wunderle JM, Henriques LMP, Willig MR (2006) Short-Term Responses of birds to forest gaps and understory: an assessment of reduced-impact logging in a lowland Amazon forest. *Biotropica* 38:235–255. doi:[10.1111/j.1744-7429.2006.00138.x](https://doi.org/10.1111/j.1744-7429.2006.00138.x)
- Zanne AE, Lopez-Gonzalez G, Coomes, DA, Ilic J, Jansen S, Lewis SL, Miller RB, Swenson NG, Wiemann, MC, Chave J (2009) Global wood density database. Dryad. Retrieved from: <http://hdl.handle.net/10255/dryad.235>