Biodivers Conserv
DOI 10.1007/s10531-009-9711-6

ORIGINAL PAPER

Seasonal patterns of spatial variation in understory bird assemblages across a mosaic of flooded and unflooded Amazonian forests

Pedro Beja · Carlos David Santos · Joana Santana · Maria João Pereira · J. Tiago Marques · Hélder Lima Queiroz · Jorge M. Palmeirim

Received: 6 May 2009 / Accepted: 10 August 2009

Abstract We examined seasonal patterns of spatial variation in understory bird assemblages across a mosaic of upland and floodplain forests in central Amazonia, where variation in flooding patterns and floodwater nutrient load shapes a marked spatial heterogeneity in forest structure and composition. Despite great differences in productivity due to flooding by either nutrient-rich “white waters” (várzea) or nutrient-poor “black waters” (igapó), bird assemblages in the two floodplain forest types were relatively similar, showing lower abundances than adjacent upland forests (terra firme) and sharing a set of species that were absent or scarce elsewhere. Species that breed in pensile nests

---

P. Beja (✉) · C. D. Santos · J. Santana
CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Campus Agrário de Vairão, Universidade do Porto, 4485-661 Vairão, Portugal
e-mail: pbeja@mail.icav.up.pt; pbeja@erena.pt

C. D. Santos
e-mail: cdsantos@fc.ul.pt

J. Santana
e-mail: js@erena.pt

P. Beja · J. Santana
ERENA, Rua Robalo Gouveia, 1-1A, 1900-392 Lisbon, Portugal

C. D. Santos · M. J. Pereira · J. T. Marques · J. M. Palmeirim
Centro de Biologia Ambiental, Departamento de Biologia Animal, Faculdade de Ciências, Universidade de Lisboa, C2, Campo Grande1749-016 Lisbon, Portugal

M. J. Pereira
e-mail: mjvpereira@fc.ul.pt

J. T. Marques
e-mail: jtiagomarques@gmail.com

J. M. Palmeirim
e-mail: jmpalmeirim@fc.ul.pt

H. L. Queiroz
Instituto de Desenvolvimento Sustentável Mamirauá, Tefé, Brazil
e-mail: helder@mamiraua.org.br

overhanging water were abundant in floodplain forests, whereas species that feed on the ground were generally scarce. Flooding affected assemblage dynamics in floodplain forests, with some influx of ground-dwelling species such as ant-following birds from adjacent upland during the low-water season, and the occupation by riverine and aquatic species such as kingfishers during floods. Spatial configuration influenced the seasonal pattern of assemblage structuring, with movements from terra firme occurring primarily to adjacent igapó forests. No such influx was detected in várzea forests that were farther from terra firme and isolated by wide river channels. Results support the view that habitat heterogeneity created by flooding strongly contributes to maintain diverse vertebrate assemblages in Amazonia forest landscapes, even in the case of largely sedentary species such as understory forest birds. Including both upland and floodplain forests in Amazonia reserves may thus be essential to preserve bird diversity at the landscape scale.

Keywords Amazonia · Brazil · Conservation · Floodplain forests · Neotropical forests · Igapó · Resource tracking · Terra firme · Várzea

Introduction

Local patterns of species richness, abundance and composition often vary in response to spatiotemporal fluctuations in resource availability (Bissonette and Storch 2007). This is particularly well documented in temperate regions, where mobile animals such as birds are known to track resources over a range of spatial and temporal scales (Herrera 1998; Tellería et al. 2008). In tropical forests, resource tracking has primarily been recognised in large-bodied frugivorous vertebrates, which may undertake large-scale movements matching spatial variation in fruit production (Renton 2001; Holbrook et al. 2002; Haugaasen and Peres 2007, 2008). Yet, resource tracking in these forests may be widespread, as it is becoming apparent that there are major spatial shifts in resource availability (Haugaasen and Peres 2005b; Cotton 2007), and many tropical forest vertebrates may range far more widely than previously assumed (Van Houtan et al. 2007; but see also Moore et al. 2008). Vertebrate assemblages in tropical forests may thus be profoundly influenced by temporal variation in the spatial distribution of resource availability (Cotton 2007; Haugaasen and Peres 2007).

The mosaic of flooded and unflooded forests in lowland Amazonia offers an excellent setting to examine the response of tropical vertebrates to spatiotemporal fluctuations in resource availability (Haugaasen and Peres 2005a, b, c, 2007). This landscape mosaic is dominated by upland forests collectively known as terra firme (Hess et al. 2003), which lie above the maximum flood level of Amazonian rivers and perennial streams and therefore portray heavily leached and nutrient-poor soils. Terra firme is interspersed with floodplain forests, the most extensive of which are eutrophic várzea forests which occur along nutrient-rich white-water rivers originating in the Andes or the pre-Andean region (Prance 1979; Junk 1997). Also prevalent in these landscapes are oligotrophic igapó forests, which are seasonally inundated by nutrient-poor black-water originating in the Amazonian Tertiary lowlands (Prance 1979, Junk 1997). These contrasting environmental conditions determine the occurrence of distinctive plant and animal communities, each contributing with exclusive species to the overall regional biodiversity (Remsen and Parker 1983; Borges and Carvalhaes 2000; Haugaasen and Peres 2005a, b; Pereira et al. 2009).

Differences in flooding regimes among forest types determine asynchronies in the timing of leafing, flowering and fruiting, thereby shaping spatial heterogeneities in the seasonal availability of food resources (Haugaasen and Peres 2005b, 2007). In terra firme there is a tendency towards high levels of fruit production in the early wet season, whereas a marked fruiting peak in seasonally flooded forests occurs during the inundation period (Haugaasen and Peres 2005b). Fruits and seeds that are available in the crowns during the high-water are then deposited on the ground when dry land becomes exposed (Haugaasen and Peres 2007). Once the waters recede, many plants flower highly synchronously and new growth from young seedlings and new leaves on larger trees also start to emerge, providing high-quality resources for nectarivores and herbivores (Cotton 2007; Haugaasen and Peres 2007). Much less is known about the spatial pattern of temporal variation in invertebrate abundance, although forest floor arthropods tend to peak during the wet season in terra firme (Pearson and Derr 1986; Noriega et al. 2007), when the forest floor in igapó and várzea is inundated.

This temporal variation in the spatial distribution of resources prompts significant movements of terrestrial vertebrates that apparently track the receding waters to take advantage of resources available on the recently exposed forest floor (Bodmer 1990; Haugaasen and Peres 2007). Many arboreal species also move seasonally into floodplain forests to explore newly available fruit patches in the canopy (Renton 2002; Haugaasen and Peres 2007). Because of these seasonal dynamics, Haugaasen and Peres (2007) suggested that floodplain forests could act as keystone habitats for the predominantly terra firme vertebrate fauna, contributing to the landscape-scale viability of many species. However, this view is based on observations made for a relatively restricted set of wide-ranging habitat generalists, remaining important to clarify the role of floodplain forests for other groups of vertebrates with different food requirements and behavioural attributes, including species assumed to be largely sedentary such as understory insectivorous birds. Such knowledge is important for the design and implementation of Amazonian forest reserves, since floodplain forests are increasingly threatened by deforestation, logging, agricultural conversion, and the building of hydroelectric dams (Borges and Carvalhaes 2000; Fearnside 2001; Vale et al. 2008), though they are particularly protected by Brazilian federal legislation (Lees and Peres 2008).

This study tests the hypotheses that spatiotemporal heterogeneity in environmental conditions created by seasonal flooding strongly influences the structure and dynamics of understory bird assemblages in tropical forest landscapes. The study was conducted in central Amazonia, examining assemblage variation among upland and floodplain forests and between seasons in terms of (1) species richness and composition, (2) relative species abundances, and (3) relative abundance of dietary and foraging guilds. Variation in assemblage attributes was then interpreted in terms of resource fluctuations, and used to discuss the potential for floodplain forests acting as keystone habitats for understory forest birds.

Study area

The study was carried out from April to December 2007 at Lago Amanã (02°35′S, 64°40′W) in the lower Japurá River region of central Amazonia, about 500 km west of Manaus (Fig. 1). The study area was within the Amanã Sustainable Development Reserve (ASDR; 23,500 km^2), which is part of the Central Amazon Ecological Corridor (57,660 km^2), one of the largest continuous protected areas of tropical forest in the world. Climate is tropical and humid, with annual rainfall of about 2,500 mm unevenly distributed over the year. The rainy season lasts from January to June, alternating with a dry season from July to December. The joint effect of seasonal variation in local rainfall and in the discharge of rivers originating in the Andean and pre-Andean regions produce fluctuations of up to about 10 m in the water level of the lake and the surrounding rivers and streams.

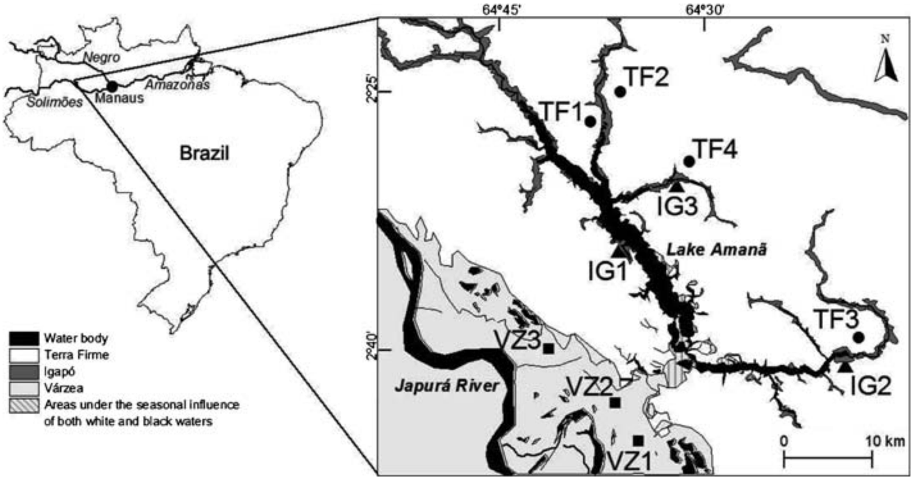

Fig. 1 Map of the study area, showing the sites sampled in terra firme (TF), várzea (VZ) and igapó (IG) forests, within the Amanã Sustainable Development Reserve (central Amazonia, Brazil)

Lago Amanã is mostly a black-water lake fed primarily by streams draining catchments dominated by terra firme forests, although there is some inflow of white-waters from the Rio Japurá during the flooding season. Igapó forests occur primarily along stream and lake margins within the catchment of the Lago Amanã, whereas várzea forests dominate the floodplain of the Rio Japurá. The region remains little disturbed by human activities, although about 4,000 persons live in 23 communities within the ASDR, along the margins of the Lago Amanã and the Rio Japurá. They depend primarily on small-scale agriculture (e.g., cassava, banana, and corn) and fishing, but there is also some subsistence hunting and collection of nuts and fruits from forest trees. There is little data on the bird assemblages of the ASDR, with a single published study reporting on the lacustrine avifauna of seasonally flooded wetlands (Cintra et al. 2007). Far more published information is available for igapó and terra firme habitats of the adjacent Jaú National Park (e.g., Borges and Carvalhaes 2000; Borges et al. 2001).

Methods

Bird sampling

A standardized mist-netting protocol was used to sample the understory avifauna in upland and floodplain forests. Although it is recognised that this method is affected by potential shortcomings due to differences in catchability among species (Thiollay 1994; Remsen and Good 1996), we have assumed in common with other studies that it provides valid comparative information on bird assemblage variation across habitats and sampling occasions (e.g., Karr 1981; Barlow and Peres 2004; Barlow et al. 2007; Blake and Loiselle 2009). Mist nets were set along each of 10 trails open for research purposes in terra firme (4), igapó (3) and várzea (3) forests (Fig. 1). Trails were set far from human settlements to reduce potential effects of human disturbance, and they were as far as possible from ecotones between forest types to minimise edge-effects (e.g., Terborgh et al. 1990). Distance to the nearest forest type was shortest in the case of igapó trails, because these forests always occurred in relatively narrow bands bordering terra firme. Each site was sampled once each wet (April-June) and dry (October-December) season using ten 12 × 3 m mist-nets, during four consecutive days. During the wet season, nets in flooded forests were tied to long poles (about 8 m) or trees and they were set about 20 cm above water to prevent birds from drowning (e.g., Pollock and Paxton 2006). These nets were thus about 2–4 m higher than nets set in terra firme during both seasons, and in igapó and várzea during the dry season, though remaining at less than 1/3 of canopy height. During floods, nets were set and checked using small boats and canoes. Nets remained open between 6h30–11h00 in the morning and 16h30–18h30 in the afternoon, except during rainy periods, and were checked every 30 min. All captured birds were identified, aged and sexed, and wing, tail and bill lengths were measured. Most individuals were photographed, particularly if representing a new species to the sample or showing any unusual feature. To avoid double counting birds recaptured within the same season and site, the tip of the third primary from the right or left wing was clipped during the wet and dry season, respectively. Marking of just one specific primary with a sharp clip and the short duration of seasonal mist-netting within each site made it unlikely that a bird with broken or worn feathers could be misidentified as a recaptured bird. Bird nomenclature follows Remsen et al. (2009).

Data analysis

A set of quantitative approaches was used to examine how bird assemblage patterns varied between seasons and forest types. Various methods were selected to allow comparisons with previous studies, and to encompass variability in a range of assemblage attributes from species richness to relative abundances (Barlow et al. 2007). Analyses were based on species incidence and relative abundance data, as well as on the relative abundances of birds categorized according to foraging and dietary guilds. Guild classification followed Terborgh et al. (1990), with additional information extracted from the literature (e.g., Stotz et al. 1996; Barlow and Peres 2004; Barlow et al. 2007, and references therein). Analysis based on guilds aimed at detecting changes in assemblage structure that may be largely independent of variation in species composition. Significance of statistical tests was assessed at $\alpha = 0.05$. In common with other studies (e.g., Van Bael et al. 2007), however, we have also documented weaker tendencies revealed by marginally significant results ($\alpha = 0.10$), as low power of statistical tests due to small sample sizes could inflate Type II error rates (e.g., Taylor and Gerrodette 1993).

Species richness patterns were assessed with individual-based rarefaction curves, constructed using EcoSim with 1000 iterations and independent sampling (Gotelli and Entsminger 2007). These curves describe species richness while controlling for the confounding effect of sampling effort and bird density (Gotelli and Graves 1996). Because there was large seasonal and between-habitat variation in the number of individuals captured, comparisons across forest types and seasons were made by truncating the rarefaction curves at the minimum number of individuals recorded on any sample being compared. Analyses were based on catch data combined according to season and forest type, because there were not enough observations in some individual sampling sites to construct meaningful rarefaction curves.

Variation in assemblage structure was investigated using a range of analyses implemented in the software package Primer v6 (Clarke and Gorley 2006), following procedures adopted in other studies of tropical bird assemblages (Barlow and Peres 2004; Barlow et al. 2007). Before analyses, relative abundance data was standardized per site to account for differences in total abundances, and then square-root transformed to reduce the influence of the most abundant species and to overcome the unity-sum constraint. Overall assemblage patterns were described using non-metric multidimensional scaling (MDS) and the Bray-Curtis similarity index. The presence of spatial patterns in assemblage structure was investigated by comparing the Bray-Curtis similarity matrix and the matrix of Euclidean distances between sampling sites using the Relate test, a non-parametric version of the Mantel test (Clarke and Gorley 2006). Analysis of Similarity (ANOSIM), a non-parametric permutations test that is analogous to an ANOVA for similarity matrices (Clarke and Gorley 2006), was used to test for significant differences in assemblage structure between seasons and among forest types. Similarity Percentage (SIMPER) analysis was used to examine the contribution of each bird species or guild towards differentiating seasons and the three forest types (Clarke and Gorley 2006). The sum of the average dissimilarity divided by the standard deviation was taken as the best measure of both the consistency and strength of the contribution that each species made toward the dissimilarity values generated (e.g., Barlow et al. 2007). Species and guilds captured very occasionally ($n < 5$) were excluded from these analyses, because they would introduce variation in assemblage structure that could not be consistently related to habitat or season effects.

Results

Differences between forest types

Species richness and abundance

Mist nets captured 796 birds (about one bird per 6.5 mist-net hours), of which 92 were recaptures within the same season and sampling site, and were thus discarded from further analyses. The remaining 704 birds represented 105 species, though 58 species were rarely caught ($n < 5$) and together accounted for only 17.5% of the catches (see Appendix Table 5). Excluding these rare species, there were 40.4% of species captured in a single forest type, with 34.0% in terra firme, 6.4% in várzea, and none in igapó. Also excluding the rarest species, 31.9% of species were only captured in floodplain forests, accounting for 40.6% of the birds caught in these forests.

There was significant overall variation among forest types in the number of birds captured (Kruskall Wallis test, $H = 7.436$, df $= 2$, $P = 0.024$), resulting primarily from much lower capture rates in igapó than in terra firme (multiple comparisons z-value $= 2.667$, $P = 0.023$; Table 1). Significant between-habitat variation in bird capture rates during the wet season (Kruskall Wallis test, $H = 8.018$, df $= 2$, $P = 0.018$) also resulted from differences between igapó and terra firme (multiple comparisons z-value $= 2.811$, $P = 0.015$), whereas no significant variation was found during the dry season (Kruskall Wallis test, $H = 3.000$, df $= 2$, $P = 0.223$). After controlling for differences in bird catches using rarefaction curves (Fig. 2), there was no between-habitat variation in species richness, despite the higher number of species captured in terra firme than in either igapó or várzea (Table 1). Similar results were obtained when data were analysed per season, although dry-season rarefaction curves showed lower richness in várzea than in other forest types (Table 1).

Species assemblage structure

The structure of understory bird assemblages varied significantly among forest types (ANOSIM: Global $R = 0.904$, $P = 0.0005$). This variation was primarily determined by

Table 1 Summary of bird mist net captures and the observed and estimated species richness in Amazon flooded and unflooded forests sampled during the wet and dry seasons at the Amanã Sustainable Development Reserve, central Amazonia, Brazil

Forest	Season	Captures[a]	Richness per site[b]	Total richness[c]	Rarefaction richness[d]
Terra Firme	Wet	60.0 ± 8.8	21.8 ± 8.8	53	26.7 (22,31)
(*n* = 4 sites)	Dry	41.3 ± 18.9	28.0 ± 1.8	46	27.8 (23,32)
	Total[e]	101.2 ± 16.3	37.2 ± 5.7	60	27.5 (23,33)
Igapó	Wet	19.3 ± 6.1	13.0 ± 4.4	27	25.2 (23,27)
(*n* = 3 sites)	Dry	22.3 ± 8.5	14.7 ± 3.2	29	24.9 (22,28)
	Total[e]	41.7 ± 14.1	22.7 ± 5.0	40	27.2 (23,31)
Várzea	Wet	39.7 ± 6.8	19.0 ± 3.5	38	24.4 (21,29)
(*n* = 3 sites)	Dry	18.3 ± 15.6	9.0 ± 6.0	21	20.2 (18,21)
	Total[e]	58.0 ± 20.7	23.0 ± 6.1	43	25.6 (21,30)
Overall	Wet	41.7 ± 19.0	28.7 ± 17.6	92	27.5 (23,32)
(*n* = 10 sites)	Dry	20.8 ± 7.2	15.8 ± 8.2	71	25.5 (21,30)
	Total[e]	70.4 ± 31.3	28.6 ± 9.0	105	33.7 (29,39)

[a] Average captures per site ± SD

[b] Average number of species recorded per site ± SD

[c] Total number of species recorded

[d] Species richness and 95% confidence intervals derived from rarefaction curves truncated at 50 individuals

[e] Computed by combining wet and dry season samples for each site

differences between terra firme and both igapó (ANOSIM: $R = 1.0$, $P = 0.029$) and várzea (ANOSIM: $R = 1.0$, $P = 0.029$), while differences between the two floodplain forests were only marginally significant (ANOSIM: $R = 0.37$, $P = 0.10$). The same patterns were observed in comparisons made separately for each season, though the dissimilarity between igapó and várzea was highest during the dry season, whereas that between igapó and terra firme was highest during the wet season (Table 2). The MDS biplot reflected these patterns, with terra firme samples forming a distinct cluster, while a great scatter and overlap of samples was found for igapó and várzea (Fig. 3a). Igapó samples tended to converge to the terra firme cluster during the dry season (Fig. 3a). Assemblage similarity varied inversely with distance between sampling sites, irrespective of forest type (Relate test; Rho = 0.325, $P = 0.026$). The effects of spatial structure on assemblage similarity were stronger in the dry (Relate test; Rho = 0.372, $P = 0.014$) than in the wet season (Relate test; Rho = 0.275, $P = 0.053$) season.

SIMPER analysis showed that dissimilarity among forest types resulted from variation in the capture rates of a large number of species, with rather small contributions of each individual species (Table 3). Woodcreepers were among the species which contributed the most to the dissimilarity between floodplain forests and terra firme. This group contained species that associated either with the former (*Dendroplex picus* and *Xiphorhynchus obsoletus*) or the latter habitats (*Xiphorhynchus ocellatus*, and *Glyphorynchus spirurus*). Another two woodcreepers (*Dendrocincla fuliginosa* and *Dendrocincla merula*) were mainly captured in igapó, contributing to the dissimilarity between this and other forests. Kingfishers also made a consistent contribution to the dissimilarity between terra firme and floodplain forests (Table 3), with *Megaceryle torquata* and *Chloroceryle aenea* dominating in várzea, and *Chloroceryle inda* dominating in igapó. Birds breeding in pensile nests overhanging water (mainly *Hypocnemoides melanopogon*), were also caught frequently in

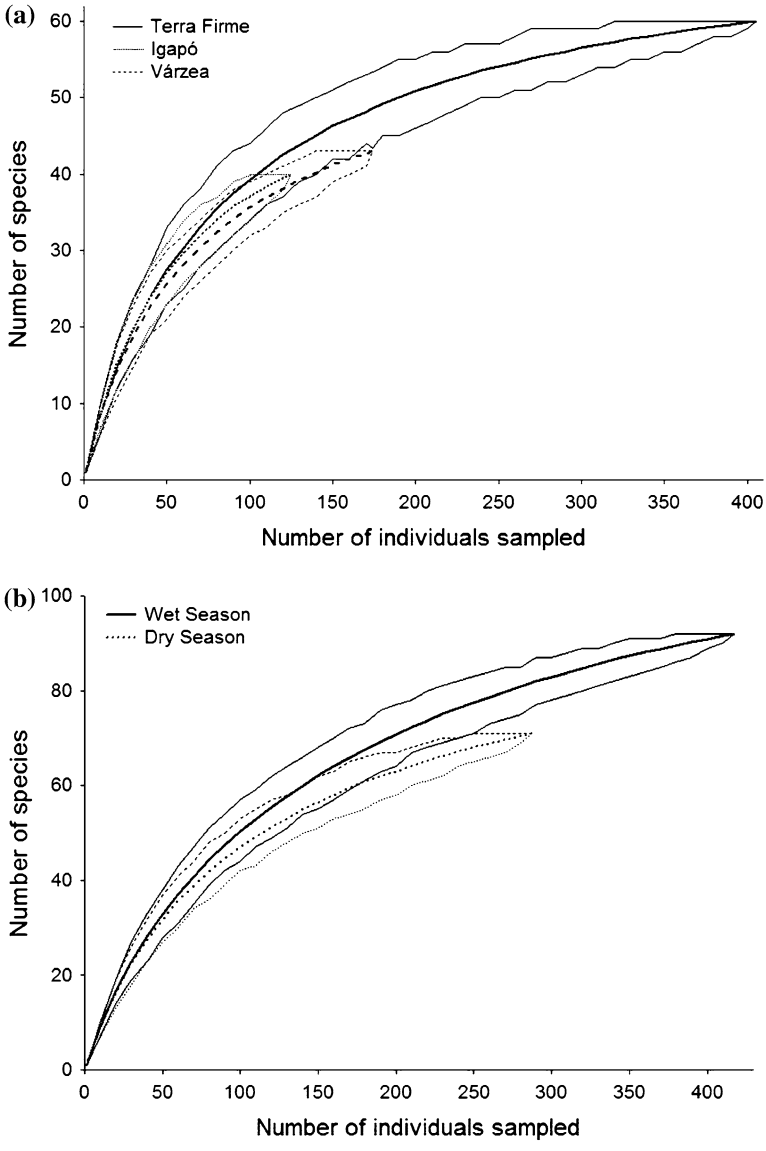

Fig. 2 Individual-based rarefaction curves of species richness for samples combined according to forest types (**a**) and seasons (**b**). Thick lines indicate mean richness and thin lines indicate 95% confidence intervals

igapó and várzea, contributing markedly to dissimilarity between these forests and terra firme. Conversely, ground-dwelling birds such as *Pithys albifrons* and *Gymnopithys leucaspis* were often recorded in terra firme but they were rare or absent in floodplain forests. Manakins (*Lepidothrix coronata* and *Pipra erythocephala*) were frequently caught in igapó but not in várzea, whereas the opposite was recorded for hummingbirds (mainly *Phaethornis hispidus*) and woodpeckers (mainly *Colaptes punctigula*).

Table 2 Average dissimilarity values based on the Bray-Curtis similarity index on bird species and guilds within and between forest types, at the Amanã Sustainable Development Reserve, central Amazonia, Brazil

Forest types[a]	Species			Guilds		
	Overall (%)	Wet season (%)	Dry season (%)	Overall (%)	Wet season (%)	Dry season (%)
Within habitats						
TF	29.4	38.4	52.9	15.4	16.0	25.8
IG	45.2	63.0	56.5	21.1	25.4	28.0
VZ	49.7	48.3	79.0	21.2	19.6	68.5
Between habitats						
TF and IG	75.4*	89.8*	75.5*	31.4*	41.2*	34.0^{ns}
TF and VZ	94.5*	95.4*	97.9*	39.4*	41.7*	59.3*
IG and VZ	$54.0^{\S}$	57.2^{ns}	71.3^{ns}	$24.8^{\S}$	23.3^{ns}	46.8^{ns}

[a] Forest types: *IG*, Igapó; *TF*, Terra Firme, *VZ*, Várzea

* $P < 0.05$, $^{\S}P < 0.10$, $^{ns}P > 0.10$

Guild structure

Analysis based on guilds also showed significant variation among forest types (ANOSIM: Global $R = 0.854$, $P = 0.0001$), with the largest differences between terra firme and both igapó (ANOSIM: $R = 0.907$, $P = 0.029$) and várzea (ANOSIM: $R = 1.0$, $P = 0.029$), while the difference between the two floodplain forests was only marginally significant (ANOSIM: $R = 0.481$, $P = 0.10$). This pattern was similar during the wet season, whereas during the dry season only the difference between terra firme and várzea remained significant (Table 2). Dissimilarity between igapó and terra firme was highest during the wet season, whereas those between várzea and both igapó and terra firme were highest during the dry season (Table 2). The MDS biplot for foraging and dietary guilds was similar to that based on species captures, showing an overall separation between terra firme and the two floodplain forests, though with a tendency for igapó dry season samples to converge to the terra firme cluster (Fig. 3b).

SIMPER analysis showed that ground-dwelling and aquatic feeding birds had the most consistent contribution to dissimilarity between terra firme and floodplain forests (Table 3). Ant-following and terrestrial gleaning insectivores were often recorded in terra firme, whereas they were absent or scarce in floodplain forests. The guild of dead-leaf gleaning insectivores was never recorded outside terra firme. Aquatic feeding birds and both internal and external bark-searching insectivores were mainly caught in floodplain forests. Although the guild structure of várzea and igapó forests were broadly similar, there was a tendency for higher capture rate of kingfishers, nectarivores and internal bark-searching insectivores in várzea, and ant-following insectivores, terrestrial sallying insectivores and arboreal frugivores in igapó (Table 3).

Differences between seasons

Species richness and abundance

There was an overall tendency for the lowest bird captures during the dry season, though this difference was only marginally significant (Wilcoxon matched pairs test, $z = 1.784$,

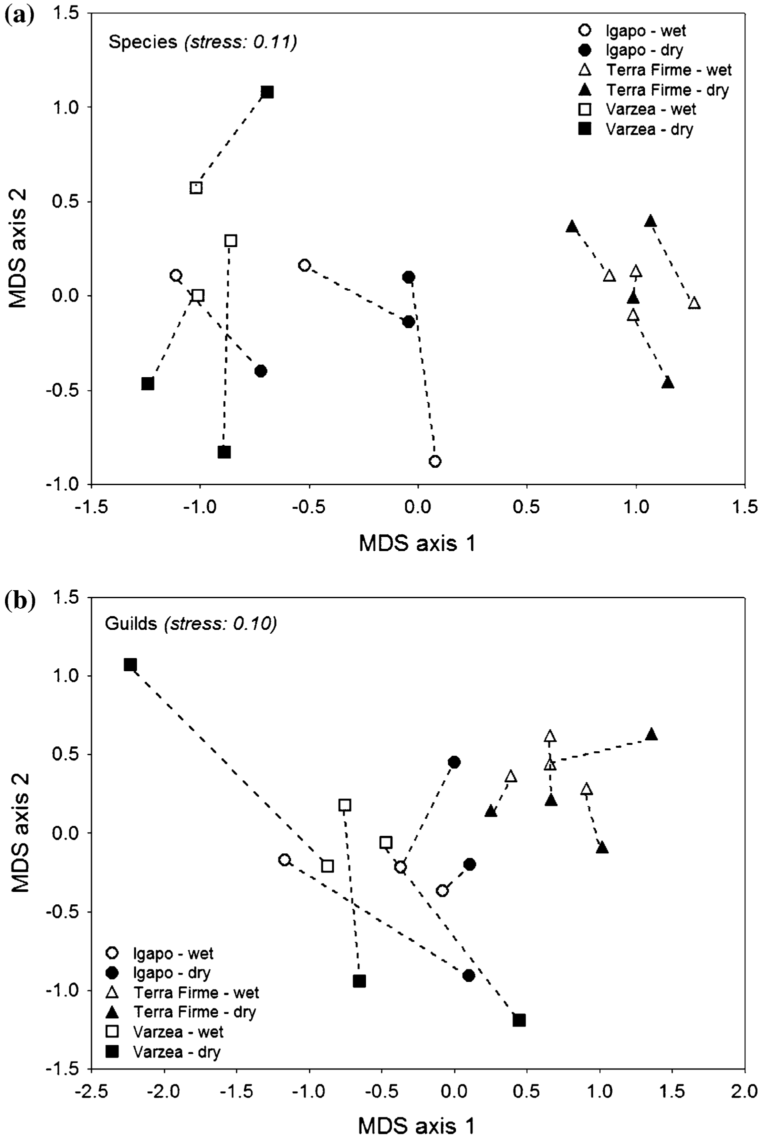

Fig. 3 Non-metric multidimensional scaling (MDS) biplots of bird assemblage variation among forest types and seasons, as assessed from the relative abundances of species (**a**) and foraging and dietary guilds (**b**). Hatched lines link seasonal samples of each sampling site

$n = 10$, $P = 0.074$). This tendency was observed in várzea and terra firme forests, but not in igapó (Table 1). Less species were also observed during the dry season (Table 1), with rarefaction curves suggesting that differences in species richness were independent of capture rates (Fig. 2b). When data were analysed by forest type, rarefaction curves showed that species richness was lowest in várzea during the dry season, but the differences between seasons were not significant in igapó and terra firme (Table 1).

Table 3 The ten species and guilds making the highest contributions to between-habitat assemblage dissimilarity in terra firme (TF), igapó (IG) and várzea (VZ) forests, at the Amanã Sustainable Development Reserve, central Amazonia, Brazil

Species	Abund[a]		Diss/ SD[b]	Cum%[c]	Guilds	Abund[a]		Diss/ SD[b]	Cum%[c]
IG-TF	IG	TF			IG-TF	IG	TF		
Dendroplex picus	3.0	0.0	3.3	4.6	Ant-following insect.	2.0	4.8	1.5	16.9
Xiphorhynchus obsoletus	3.0	0.0	4.2	9.1	Terrestrial gleaning insect.	0.0	2.6	4.6	31.6
Hypocnemoides melanopogon	2.8	0.0	19.0	13.3	Aquatic	2.4	0.6	2.1	41.8
Dendrocincla fuliginosa	2.6	0.0	2.7	17.4	Arboreal sallying insect.	4.7	3.2	1.8	51.1
Turdus hauxwelli	2.6	0.0	11.5	21.4	Bark-searching insect. (ext.)	5.0	3.6	1.3	59.9
Pithys albifrons	1.0	2.9	1.6	24.8	Dead-leaf gleaning insect.	0.0	1.4	1.6	67.7
Gymnopithys leucaspis	0.5	2.6	2.4	28.2	Arboreal nectarivore	1.9	3.0	1.0	75.2
Chloroceryle inda	2.0	0.0	19.0	31.1	Arboreal omnivore	3.0	1.9	1.8	81.6
Lathrotriccus euleri	2.0	0.0	19.0	34.1	Bark-searching insect. (int.)	1.0	0.0	1.3	87.5
Xiphorhynchus ocellatus	0.0	1.9	3.1	37.1	Terrestrial granivores	0.0	0.9	1.5	92.4
IG-VZ	IG	VZ			IG-VZ	IG	VZ		
Megaceryle torquata	0.0	2.5	1.3	6.4	Aquatic	2.4	4.5	2.1	15.6
Phaethornis hispidus	0.0	2.6	1.3	12.6	Ant-following insect.	2.0	0.0	1.1	30.3
Dendrocincla fuliginosa	2.6	0.6	1.7	18.2	Arboreal nectarivore	1.9	3.3	1.4	44.7
Chloroceryle aenea	1.5	3.3	1.0	23.3	Arboreal frugivore	2.7	1.4	1.4	56.0
Dendrocincla merula	1.8	0.0	1.3	27.6	Bark-searching insect. (int.)	1.0	1.8	1.6	66.6
Pipra erythocephala	1.7	0.0	1.3	31.8	Terrestrial granivore	0.0	1.2	1.1	75.6
Lepidothrix coronata	1.7	0.0	1.1	36.0	Arboreal sallying insect.	4.7	4.3	1.3	83.4
Turdus hauxwelli	2.6	1.1	1.6	40.1	Arboreal omnivore	3.0	2.1	1.6	90.6
Glyphorynchus spirurus	1.7	0.8	1.2	44.2	Bark-searching insect. (ext.)	5.0	4.6	1.4	96.8
Colaptes punctigula	0.6	1.8	1.3	48.3	Arboreal gleaning insectivore	3.8	3.6	1.5	100.0
TF-VZ	TF	VZ			TF-VZ	TF	VZ		
Dendroplex picus	0.0	3.5	2.7	4.7	Ant-following insect.	4.8	0.0	5.1	21.8
Lepidothrix coronata	3.3	0.0	5.9	9.0	Aquatic	0.6	4.5	3.7	39.3
Xiphorhynchus obsoletus	0.0	3.1	4.5	13.2	Terrestrial gleaning insect.	2.6	0.0	4.6	51.0
Hypocnemoides melanopogon	0.0	3.0	2.4	17.3	Arboreal frugivore	3.5	1.4	1.7	60.7
Pithys albifrons	2.9	0.0	3.4	21.1	Bark-searching insect. (int.)	0.0	1.8	1.3	68.7
Chloroceryle aenea	0.7	3.3	1.5	24.8	Dead-leaf gleaning insect.	1.4	0.0	1.6	74.9

Table 3 continued

Species	Abund[a]		Diss/SD[b]	Cum%[c]	Guilds	Abund[a]		Diss/SD[b]	Cum%[c]
Gymnopythis leucaspis	2.6	0.0	4.7	28.3	Arboreal sallying insect.	3.2	4.3	1.4	80.6
Megaceryle torquata	0.0	2.5	1.3	31.6	Arboreal nectarivore	3.0	3.3	3.5	85.8
Phaethornis hispidus	0.0	2.6	1.4	34.8	Bark-searching insect. (ext.)	3.6	4.6	1.2	90.8
Glyphorynchus spirurus	2.9	0.8	1.7	37.7	Terrestrial granivores	0.9	1.2	1.3	95.0

[a] Average number of captures per site (square-root transformation of site-standardised data)

[b] Average dissimilarity/standard deviation of similarity

[c] Cumulative percentage contribution to dissimilarity

Species assemblage structure

Overall, there was a significant seasonal variation in assemblage structure (two-way ANOSIM: Global $R = 0.228$, $P = 0.046$), though comparisons for each forest type did not yield statistically significant differences. Nevertheless, there was a tendency for higher seasonal dissimilarity in igapó (ANOSIM: $R = 0.370$, $P = 0.10$), than in either terra firme (ANOSIM: $R = 0.146$, $P = 0.257$) and várzea (ANOSIM: $P = 0.259$, $P = 0.300$). Samples from várzea tended to be less homogeneous in the dry than in the wet season (Table 2). In the MDS biplot there was no separation of samples according to season (Fig. 3a).

SIMPER analysis showed that the higher capture rates during the wet season of birds breeding in pensile nests overhanging water (*Hypocnemoides melanopogon* and *Hypocnemis cantator*) contributed markedly to seasonal dissimilarity in igapó (Table 4). In the same way, birds breeding on land exposed when water levels drop such as *Monasa nigrifrons*, were mainly captured during the dry season. Seasonal dissimilarity in igapó was also shaped by the increased number of manakins and of species feeding frequently on the ground (*Dendrocincla fuliginosa* and *Dendrocincla merula*) captured in the dry season, and by the increased capture rates of kingfishers during the wet season. Similar patterns were found in várzea, although ground-dwelling birds remained largely absent in both seasons, while there was a high contribution of hummingbirds during the dry season. In terra firme there were only small changes in the capture rates of the most frequently caught species (Table 4).

Guild structure

Guild structure showed low overall variation between seasons (two-way ANOSIM: Global $R = 0.138$, $P = 0.093$), with comparisons for each forest type only yielding marginally significant seasonal differences in the case of igapó (ANOSIM: $R = 0.370$, $P = 0.10$). Seasonal dissimilarity in guild structure was low for both várzea (ANOSIM: $R = 0.111$, $P = 0.300$) and terra firme (ANOSIM: $R = 0.042$, $P = 0.343$). As observed at the species level, there was no separation of samples according to season in the MDS biplot based on guilds (Fig. 3b).

Table 4 The ten species and guilds making the highest contributions to between-season assemblage dissimilarity in terra firme, igapó and várzea, at the Amanã Sustainable Development Reserve, central Amazonia, Brazil

Species	Abund[a]		Diss/SD[b]	Cum%[c]	Guilds	Abund[a]		Diss/SD[b]	Cum%[c]
	Dry	Wet				Dry	Wet		
Igapó									
Hypocnemoides melanopogon	0.6	4.0	2.8	8.1	Ant-following insect.	2.7	0.0	1.1	16.9
Dendrocincla fuliginosa	3.0	0.8	1.3	15.0	Arboreal gleaning insect.	2.6	4.7	3.0	30.7
Monasa nigrifons	2.1	0.0	1.2	20.2	Arboreal omnivore	3.7	1.7	1.5	43.4
Dendrocincla merula	2.3	0.0	1.3	25.3	Arboreal sallying insect.	4.9	4.4	1.3	54.3
Chloroceryle inda	0.6	2.6	1.9	30.2	Arboreal nectarivore	1.9	2.0	1.1	64.2
Glyphorynchus spirurus	1.5	1.5	1.3	35.0	Arboreal frugivore	3.0	2.0	1.1	74.1
Lepidothrix coronata	1.3	1.8	1.3	39.5	Bark-searching insect. (int.)	0.0	1.4	1.3	83.6
Pipra erythocephala	1.9	1.1	1.1	44.0	Bark-searching insect. (ext.)	4.5	5.4	1.3	92.4
Dendroplex picus	2.6	2.7	1.8	48.4	Aquatic	1.9	2.6	0.9	100.0
Hypocnemis cantator	0.0	1.9	1.2	52.8					
Várzea									
Hypocnemoides melanopogon	0.0	3.6	2.6	9.9	Aquatic	3.4	4.7	1.8	15.0
Phaethornis hispidus	3.7	1.8	1.6	18.2	Arboreal nectarivore	3.7	2.6	3.8	29.5
Megaceryle torquata	0.0	2.8	1.3	26.0	Arboreal gleaning insect.	1.4	4.0	1.7	43.5
Chloroceryle aenea	3.2	3.1	1.5	33.8	Bark-searching insect. (ext.)	3.9	5.0	1.3	56.4
Xiphorhynchus obsoletus	1.3	3.5	1.4	40.7	Arboreal sallying insect.	3.2	4.1	1.3	69.1
Monasa nigrifons	2.6	0.0	1.3	47.1	Arboreal omnivore	2.3	1.6	2.1	78.4
Xiphorhynchus guttatus	1.7	0.6	0.8	52.7	Arboreal frugivore	1.3	1.0	1.5	86.6
Dendroplex picus	2.6	3.8	1.4	58.0	Bark-searching insect. (int.)	0.9	1.8	1.1	94.8
Chloroceryle inda	0.6	2.1	1.2	62.9	Terrestrial Granivores	0.6	0.8	0.9	100.0
Colaptes punctigula	0.9	1.9	1.2	67.6					
Terra firme									
Gymnopythis leucaspis	2.0	2.7	2.0	5.5	Ant-following insect.	4.3	5.1	1.9	14.9
Glyphorynchus spirurus	2.6	2.4	1.2	10.0	Arboreal gleaning insect.	3.3	3.9	0.9	27.2
Pipra erythocephala	1.6	0.0	1.7	14.1	Bark-searching insect. (ext.)	3.2	3.7	1.3	37.7
Xiphorhynchus ocellatus	0.8	2.3	1.5	18.1	Arboreal omnivore	1.8	1.8	1.8	48.1

Table 4 continued

Species	Abund[a]		Diss/SD[b]	Cum%[c]	Guilds	Abund[a]		Diss/SD[b]	Cum%[c]
	Dry	Wet				Dry	Wet		
Thamnomanes caesius	1.9	0.7	1.7	22.0	Arboreal sallying insect.	3.5	2.7	1.2	58.5
Hylophylax poecilinotus	1.3	1.8	1.3	25.8	Terrestrial granivore	0.0	1.1	1.6	67.8
Phaethornis malaris	2.0	1.4	1.8	29.6	Dead-leaf gleaning insect.	1.5	1.3	1.3	76.9
Plathyrinchus coronatus	0.3	1.6	1.4	33.3	Terrestrial gleaning insect.	2.3	2.8	1.4	83.9
Hylophylax naevius	1.4	0.7	1.4	36.9	Aquatic	0.5	0.7	1.1	90.6
Xenops minutus	0.6	1.6	3.1	40.3	Arboreal frugivore	3.8	3.3	1.8	95.5

[a] Average number of captures per site (square-root transformation of site-standardised data)

[b] Average dissimilarity/standard deviation of similarity

[c] Cumulative percentage contribution to dissimilarity

SIMPER analysis showed that the dry season captures of ant-following insectivores, which were absent during the wet season, had the highest contribution to seasonal dissimilarity in igapó. Arboreal omnivores were also caught more often in igapó during the dry season, whereas the opposite was found for arboreal gleaning insectivores. Seasonal dissimilarity in vázea and terra firme was low, resulting from small variation in the relative abundance of some frequently caught guilds. In várzea, there was a tendency for increased capture rates of aquatic birds and arboreal gleaning insectivores during the wet season, and that of arboreal nectarivores during the dry season.

Discussion

General patterns

This study showed that understory bird assemblages of floodplain forests (várzea and igapó) are significantly distinct from that of adjacent upland forests (terra firme), sharing a set of species that are absent or scarce elsewhere. Furthermore, the study provided evidence that flooding affected the seasonal assemblage dynamics in floodplain forests, with some influx of ground-dwelling species from adjacent terra firme during the dry season, and of riverine and aquatic-feeding species during flooding season. Spatial configuration of the forest types contributed to the seasonal pattern of bird assemblage structure. Movements of terra firme birds occurred primarily to adjacent igapó forests, whereas no such influx was detected in várzea forests that were further from terra firme and isolated by wide river channels.

These general patterns are unlikely to be shaped by methodological artefacts, although mist-netting is prone to several potential biases (Thiollay 1994; Remsen and Good 1996). In our case, for example, birds could have responded to flooding by migrating vertically, consequently being missed with this sampling method. However, this is unlikely to have represented a serious problem as nets in flooded forests were raised by 2–4 m in synchrony with increasing water levels. This seasonal change in the vertical position of nets is also unlikely to have biased the results due to variation in capture efficiency or by increasing the representation of canopy birds, because the capture efficiencies of nets set at ground level and above water are generally considered similar (Pollock and Paxton 2006) and nets were always set well below the canopy level. The occasional capture of species normally associated with the upper forest levels was controlled by dropping from analysis all species caught rarely ($n < 5$).

Bird assemblage variation between upland and floodplain forests

The differences between bird assemblages of floodplain and adjacent upland forests recorded in this study are similar to those reported elsewhere in Amazonia (Remsen and Parker 1983; Borges and Carvalhaes 2000; Haugaasen and Peres 2008). However, to the best of our knowledge, only this study and Haugaasen and Peres (2008) directly compared the three main Amazonian forest types within the same region. Both studies showed a much higher similarity between the two floodplain forests than between any of these and adjacent upland forests. This was partly because many species abundant in terra firme were absent or rare in floodplain forests, whereas a range of other species was largely absent from terra firme but abundant in both igapó and várzea. The only relatively abundant species that was exclusive to just one floodplain forest type was *Phaethornis hispidus*, which was only captured in várzea.

The most common floodplain species identified in this study, mainly *Phaethornis hispidus*, *Dendroplex picus*, *Xyphorhynchus obsoletus* and *Hypocnemoides melanopogon*, have been consistently associated with either várzea or igapó in the literature (see Appendix Table 5), suggesting that they may be specialists in seasonally flooded forests. Other species, such as *Dendrocincla fuliginosa*, *Turdus hauxwelli*, and *Lathrotriccus euleri*, were also captured most often in floodplain forests, but they are generally regarded as habitat generalists (see Appendix Table 5). The occurrence of a distinctive set of understory bird species common to both floodplain forests may seem rather surprising, given the high dissimilarity between várzea and igapó in terms of floristic composition, structure and productivity (Haugaasen and Peres 2005b, 2006). However, these two forest types also share similarities resulting primarily from seasonal flooding, including an open understory, a tree assemblage dominated by Euphorbiaceae and Fabaceae, and largely synchronous tree phenologies (Haugaasen and Peres 2005b, 2006). These results thus suggest that flooding is a primary environmental filter (*sensu*, Poff 1997) in Amazonian floodplain forests, strongly determining the composition of understory forest bird assemblages independently of water nutrient loads. This idea is supported by a recent study on bat assemblages carried out within the same area, which showed a higher similarity between the two seasonally flooded forests, than between these and terra firme (Pereira et al. 2009).

Seasonal assemblage variation: is there evidence for resource tracking?

Seasonal flooding was associated with temporal variation in assemblage structure, which may reflect at least partly bird tracking of resources that are temporarily available in floodplain forests. This was probably in the case for dietary and foraging guilds such as aquatic-feeding birds, ground-dwelling insectivores, and nectarivores. For instance, kingfishers were caught most frequently in the interior of flooded forests during the high-water season, when fish migrate into floodplain forests seeking food and shelter (Saint-Paul et al. 2000; Castello 2008). The influx of kingfishers was much higher in várzea than in igapó, probably reflecting differences in fish abundance between white- and black-waters (Saint-Paul et al. 2000; but see Henderson and Crampton 1997). As the water receded, the abundance of kingfishers was greatly reduced and the abundance of species feeding at low forest levels or even on the forest floor increased. Ground-dwelling insectivores, including obligate ant-followers, were also found moving between upland and floodplain forests, probably tracking changes in resource availability. Indeed, when floodwaters recede the exposed forest floor is recolonised by invertebrates surviving floods in adjacent upland forests or in refugia such as high ground within flooded forests (*restinga*), treetops, and floating wood and mats of vegetation (Adis and Junk 2002; Ballinger et al. 2007). Expanding the foraging range into floodplain forests may thus be attractive for ground-dwelling insectivores during the dry season, when the abundance of forest floor arthropods is at its lowest in terra firme (Pearson and Derr 1986; Noriega et al. 2007) and competition with other individuals for resources is likely to be high. Shortage of food resources may have forced insectivorous birds such as *Dendrocincla fuliginosa* to use peripheral habitats due to inter- or intraspecific competitive displacement (Willis 1966; Pierpont 1986), thereby explaining their increased abundance in floodplain forests during the dry season. Hummingbirds were also captured primarily in floodplain forests during the dry season, probably due to the seasonal availability of plants flowering highly synchronously once the flood waters receded (Cotton 2007).

The influx of ground-dwelling birds from terra firme into floodplains involved primarily igapó forests, with little evidence of such movements between terra firme and várzea. For instance, ant-following insectivores such as *Gymnopithys leucaspis* and *Pithys albifrons* that were common in terra firme, were captured during the dry season in adjacent igapó forests, but not in várzea. This was probably related to the spatial distribution of forest types; igapó patches were always adjacent to vast expanses of terra firme forests, whereas the várzea forests sampled in this study were much farther from terra firme and were isolated by wide river channels. These channels probably served as effective fluvial barriers to dispersal and movements of most understory terra firme birds (Gascon et al. 2000). These patterns corroborate the idea that physical connectivity and proximity to adjacent terra firme forests is a factor greatly influencing the structure of floodplain vertebrate assemblages (Haugaasen and Peres 2007).

For other bird groups, variation in capture rates between seasons was likely to reflect variation in catchability, rather than movements among forest types. This was probably the case of species breeding in pensile nests overhanging water, including *Hypocnemoides melanopogon* and *Hypocnemis cantator* (Sick 1997; Cadena et al. 2000), which were mainly caught during the breeding season. The former species is largely restricted to seasonally inundated forests (Borges and Carvalhaes 2000; Appendix), where they were often sighted and heard at all times, though they were infrequently captured during the dry season. The latter species is generally considered a habitat generalist (Borges and Carvalhaes 2000; Appendix), but in this study was never captured in terra firme. This suggests that variation in the capture rates of these species was primarily due to their lower catchability outside the breeding season. Changes in catchability may also have affected species breeding in holes in the forest floor, such as *Monasa nigrifons* (Rasmussen and Collar 2002). This species was only captured in floodplain forests during the dry season, though it was often sighted and heard therein all through the year.

Conservation implications

Results from this study add to the growing evidence that seasonally flooded forests play a significant role for the maintenance of bird diversity in Amazonian lowlands (Remsen and Parker 1983; Borges and Carvalhaes 2000; Haugaasen and Peres 2008; Vale et al. 2008), as it has been shown for other vertebrates (Haugaasen and Peres 2007; Pereira et al. 2009). Although terra firme holds the richest bird assemblages, floodplain forests contribute with several unique understory species for the overall diversity of Amazonian forest birds, providing habitats for a range of specialists that are rare or absent elsewhere. These include some of the bird species with the most restricted geographical ranges in Amazonian, making riparian forests essential to their conservation at the global scale (Vale et al. 2008). Floodplain forests also appear to provide seasonal foraging habitats for some bird species from adjacent terra firme and riverine habitats, which may be essential to safeguard their long-term viability at the landscape scale (Haugaasen and Peres 2007, 2008, this study).

Conservation efforts targeted at floodplain forests are thus particularly important, especially considering that these habitats seem to be underrepresented in Amazonian reserve networks (Fearnside and Ferraz 1995), and that they are highly susceptible to a range of impacts resulting from human disturbance, logging, agricultural conversion and the building of hydroelectric dams (Fearnside and Ferraz 1995; Borges and Carvalhaes 2000; Fearnside 2001; Haugaasen and Peres 2008; Vale et al. 2008). Deforestation models for Amazonia also suggest that areas near river will be at the greatest risk (Laurance et al. 2001), with strongly negative consequences for riparian forests and their associated biodiversity (Vale et al. 2008).

Although these forests are protected to some extent by Brazilian federal legislation, which require that clearcutting operations by private landowners should set aside a riparian forest strip along rivers and perennial streams in the form of "permanent protection areas", these forest remnants only retain a small proportion of vertebrate species richness found in riparian forests within large forest patches (Lees and Peres 2008). There is thus a need for incorporating in natural reserves sufficiently large and heterogeneous habitat mosaics of both terra firme and seasonally flooded forests to guarantee the long-term persistence of Amazonian biota (Peres 2005). The presence of such habitat mosaics might also be important in fragmented landscapes, where well-connected patches of both upland and floodplain habitats could provide conditions for a complement of species with different habitat requirements (Lees and Peres 2008), including wide-ranging generalists that habitually move across forest types (e.g., Peres 2005; Keuroghlian and Eaton 2008).

Acknowledgments This study was funded by the Fundação para a Ciência e Tecnologia, through grants SFRH/BD/19629/2004 to MJP, SFRH/BD/22829/2005 to JTM, and POCI/BIA-BDE/60710/2004 to the research project, and by the Fundação Gulbenkian through grant 89185 to CDS. We thank the Brazilian Ministério de Ciências e Tecnologia and Ministério do Meio Ambiente for permissions to do this research, and the Instituto de Desenvolvimento Sustentável de Mamirauá and its staff, especially M. Marmontel, J. Valsecchi and A. Nunes, for logistical assistance. We are very grateful for support from the local communities and the field assistance by Jerry, José Penha, Bento, Deusa, Otávio, Gilmar, Jesui, Raimundo, Sineca, António, Manuel, Gladson, and Rosinaldo. We also thank P. Santos for advice in study planning, L. Reino, C. Miranda and N. Castanheira for help in field work, M. Dias for help with Fig. 1, and T. Haugaasen for critical reading of the manuscript. We thank the thorough review of the manuscript by the associate editor and two anonymous referees.

Appendix

See Table 5.

Table 5 Number of birds captured with mist nets in terra firme, várzea and igapó forests, during the wet (April-June) and dry (October-December) seasons of 2007, within the Amanã Sustainable Development Reserve, central Amazonia, Brazil. Bird nomenclature follows Remsen et al. (2009). Each species was assigned to a trophic and foraging guild and to a preferential habitat (forest type), based on bibliographic sources

Common name	Species	Guilds[a]	Habitat[b]	Terra firme		Várzea		Igapó	
				Wet	Dry	Wet	Dry	Wet	Dry
PSOPHIDAE									
Grey-winged Trumpeter	*Psophia crepitans*	OT	TF	0	1	0	0	0	0
COLUMBIDAE									
Ruddy Quail-dove	*Geotrygon montana*	GT	TF	4	0	0	1	0	0
CUCULIDAE									
Little Cuckoo	*Coccycua minuta*	IAG	G	0	0	1	0	0	0
STRIGIDAE									
Tawny-bellied screech owl	*Megascops watsonii*	RNA	G	0	0	0	0	0	1
Ferruginous Pygmy-Owl	*Glaucidium brasilianum*	RNA	G	0	0	0	3	0	0
CAPRIMULGIDAE									
Common Pauraque	*Nyctidromus albicollis*	ITS	G	0	0	0	0	0	3
TROCHLIDAE									
Rufous-breasted Hermit	*Glaucis hirsutus*	NA	G	0	0	2	2	0	0
Pale-tailed Barbthroat	*Threnetes leucurus*	NA	G	2	0	0	0	0	0
Reddish Hermit	*Phaethornis ruber*	NA	TF	1	2	0	0	0	0
White-bearded Hermit	*Phaethornis hispidus*	NA	VZ	0	0	5	12	0	0
Straight-billed Hermit	*Phaethornis bourcieri*	NA	TF	5	4	0	0	0	2
Great-billed Hermit	*Phaethornis malaris*	NA	TF	8	5	0	0	1	1
Gould's Jewelfront	*Heliodoxa aurescens*	NA	G	1	2	0	0	1	0
Blue-chinned Sapphire	*Chlorestes notata*	NA	G	0	0	2	0	1	0
Fork-tailed Woodnymph	*Thalurania furcata*	NA	G	3	3	0	0	1	1
ALCEDINIDAE									
Ringed Kingfisher	*Megaceryle torquata*	Aqu	VZ	0	0	11	0	0	0
Green Kingfisher	*Chloroceryle americana*	Aqu	VZ, IG	0	0	2	0	0	0
Green-and-rufous Kingfisher	*Chloroceryle inda*	Aqu	VZ, IG	0	0	7	1	3	1
American pygmy Kingfisher	*Chloroceryle aenea*	Aqu	G	2	1	8	4	1	3
GALBULIDAE									
Yellow-billed Jacamar	*Galbula albirostris*	IAS	G	1	0	0	0	0	0
White-chinned Jacamar	*Galbula tombacea*	IAS	VZ	0	0	1	2	0	0
BUCCONIDAE									
White-chested Puffbird	*Malacoptila fusca*	IAS	TF	0	1	0	0	0	0
Black-fronted Nunbird	*Monasa nigrifrons*	IAS	VZ, IG	0	0	0	6	0	4

Table 5 continued

Common name	Species	Guilds[a]	Habitat[b]	Terra firme		Várzea		Igapó	
				Wet	Dry	Wet	Dry	Wet	Dry
CAPITONIDAE									
Gilded Barbet	*Capito auratus*	OA	TF	0	0	0	0	0	1
RAMPHASTIDAE									
Chestnut-eared Aracari	*Pteroglossus castanotis*	FA	G	0	0	1	0	0	0
Ivory-billed Aracari	*Pteroglossus azara*	FA	G	2	0	0	0	0	0
PICIDAE									
Spot-breasted Woodpecker	*Colaptes punctigula*	IBI	G	0	0	5	1	1	0
Chestnut Woodpecker	*Celeus elegans*	IBI	G	0	0	1	0	1	0
FURNARIIDAE									
Short-billed Leaftosser	*Sclerurus rufigularis*	ITG	TF	1	0	0	0	0	0
Striped Woodhaunter	*Hyloctistes subulatus*	IDL	TF	1	1	0	0	0	0
Cinnamon-rumped Foliage-gleaner	*Philydor pyrrhodes*	IDL	G	1	0	0	0	0	0
Buff-throated Foliage-gleaner	*Automolus ochrolaemus*	IDL	TF	4	4	0	0	0	0
Rufous-tailed Xenops	*Xenops milleri*	IBS	TF	1	0	0	0	0	0
Plain Xenops	*Xenops minutus*	IBS	G	5	1	0	0	0	0
Plain-brown Woodcreeper	*Dendrocincla fuliginosa*	IAS	G	0	0	1	1	1	6
White-chinned Woodcreeper	*Dendrocincla merula*	IAF	TF	12	5	0	0	0	6
Olivaceous Woodcreeper	*Sittasomus griseicapillus*	IBS	VZ, IG	0	0	0	0	2	0
Wedge-billed Woodcreeper	*Glyphorynchus spirurus*	IBS	TF	16	15	3	0	2	2
Long-billed Woodcreeper	*Nasica longirostris*	IBS	VZ, IG	0	0	4	0	2	0
Amazonian Barred-Woodcreeper	*Dendrocolaptes certhia*	IAS	G	0	0	0	0	0	1
Straight-billed Woodcreeper	*Dendroplex picus*	IBS	VZ, IG	0	0	12	2	6	4
Striped Woodcreeper	*Xiphorhynchus obsoletus*	IBS	VZ, IG	0	0	10	2	5	6
Ocellated Woodcreeper	*Xiphorhynchus ocellatus*	IBS	TF	11	2	0	0	0	0
Buff-throated Woodcreeper	*Xiphorhynchus guttatus*	IBS	G	1	2	1	1	1	1
THAMNOPHILIDAE									
White-shouldered Antshrike	*Thamnophilus aethiops*	IAG	TF	1	1	0	0	0	0
Pearly Antshrike	*Megastictus margaritatus*	IAG	TF	2	4	0	0	0	0
Dusky-throated Antshrike	*Thamnomanes ardesiacus*	IAS	TF	4	3	0	0	0	0

Table 5 continued

Common name	Species	Guilds[a]	Habitat[b]	Terra firme		Várzea		Igapó	
				Wet	Dry	Wet	Dry	Wet	Dry
Cinereous Antshrike	*Thamnomanes caesius*	IAS	TF	2	7	0	0	0	0
Stipple-throated Antwren	*Epinecrophylla haematonota*	IAG	TF	7	3	0	0	0	0
Plain-throated Antwren	*Myrmotherula hauxwelli*	IAG	G	0	0	3	0	0	0
White-flanked Antwren	*Myrmotherula axillaris*	IAG	G	0	0	0	0	2	0
Long-winged Antwren	*Myrmotherula longipennis*	IAG	TF	6	4	0	0	0	0
Banded Antbird	*Dichrozona cincta*	ITG	TF	1	0	0	0	0	0
Guianan Warbling-Antbird	*Hypocnemis cantator*	IAG	G	0	0	1	1	3	0
Yellow-browed Antbird	*Hypocnemis hypoxantha*	IAG	TF	3	0	0	0	0	0
Black-faced Antbird	*Myrmoborus myotherinus*	ITG	TF	6	6	0	0	0	0
Black-chinned Antbird	*Hypocnemoides melanopogon*	IAG	VZ, IG	0	0	10	0	7	1
White-plumed Antbird	*Pithys albifrons*	IAF	TF	21	12	0	0	0	4
Bicoloured Antbird	*Gymnopithys leucaspis*	IAF	TF	15	10	0	0	0	1
Chestnut-crested Antbird	*Rhegmatorhina cristata*	IAF	TF	3	1	0	0	0	0
Spot-backed Antbird	*Hylophylax naevius*	IAG	TF	2	5	0	0	0	1
Dot-backed Antbird	*Hylophylax punctulatus*	IAG	VZ, IG	0	0	1	0	1	1
Scale-backed Antbird	*Willisornis poecilinotus*	IAF	TF	9	4	0	0	0	0
Reddish-winged Bare-eye	*Phlegopsis erythroptera*	IAF	TF	5	0	0	0	0	0
FORMICARIIDAE									
Rufous-capped Antthrush	*Formicarius colma*	ITG	TF	3	1	0	0	0	0
CONOPOPHAGIDAE									
Chestnut-belted gnateater	*Conopophaga aurita*	ITG	TF	8	2	0	0	0	0
TYRANNIDAE									
Ringed Antpipit	*Corythopis torquatus*	ITS	TF	0	1	0	0	0	0
Forest Elaenia	*Myiopagis gaimardii*	IAG	G	0	0	1	0	0	0
Yellow-crowned Elaenia	*Myiopagis flavivertex*	IAG	VZ	0	0	1	0	0	0
Ochre-bellied Flycatcher	*Mionectes oleagineus*	OA	G	4	3	0	0	0	2
McConnel's Flycatcher	*Mionectes macconnelli*	OA	TF	1	0	0	0	0	0
Snethlage's Tody-Tyrant	*Hemitriccus minor*	IAS	G	0	0	0	0	3	0

Table 5 continued

Common name	Species	Guilds[a]	Habitat[b]	Terra firme		Várzea		Igapó	
				Wet	Dry	Wet	Dry	Wet	Dry
Yellow-olive Flycatcher	*Tolmomyias sulphurescens*	IAS	G	1	0	3	0	0	0
Golden-crowned Spadebill	*Platyrinchus coronatus*	IAS	G	8	1	0	0	0	0
White-crested Spadebill	*Platyrinchus platyrhynchos*	IAS	TF	0	3	0	0	0	0
Royal Flycatcher	*Onychorhynchus coronatus*	IAS	G	0	1	1	3	2	0
Sulphur-rumped Flycatcher	*Myiobius barbatus*	IAS	G	0	0	2	0	0	0
Ruddy-tailed Flycatcher	*Terenotriccus erythrurus*	IAS	G	0	2	0	0	0	1
Euler's Flycatcher	*Lathrotriccus euleri*	IAS	G	0	0	1	1	3	1
Great Kiskadee	*Pitangus sulphuratus*	IAS	G	0	0	4	0	0	0
Dull-capped Attila	*Attila bolivianus*	IAS	VZ	0	0	1	0	0	0
Bright-rumped Attila	*Attila spadiceus*	IAS	TF	0	0	1	0	0	0
Unidentified Tyrannidae		IAS		0	0	0	0	1	0
COTINGIDAE									
Screaming Piha	*Lipaugus vociferans*	IAS	G	1	1	0	0	0	0
PIPRIDAE									
Blue-crowned Manakin	*Lepidothrix coronata*	FA	TF	24	15	0	0	2	2
Blue-backed Manakin	*Chiroxiphia pareola*	FA	TF	1	2	0	0	0	0
Wire-tailed Manakin	*Pipra filicauda*	FA	VZ, IG	0	0	1	5	0	0
Golden-headed Manakin	*Pipra erythrocephala*	FA	G	0	6	0	0	2	3
TITYRIDAE									
Varzea Schiffornis	*Schiffornis major*	IAS	VZ, IG	0	0	4	1	1	1
Thrush-like Schiffornis	*Schiffornis turdina*	IAS	TF	1	4	0	0	0	0
White-winged Becard	*Pachyramphus polychopterus*	IAS	G	0	0	1	0	0	0
VIREONIDAE									
Tawny-crowned Greenlet	*Hylophilus ochraceiceps*	IAG	TF	2	0	0	0	0	0
TROGLODYTIDAE									
Coraya Wren	*Thryothorus coraya*	IAG	G	0	0	0	0	0	1
Musician Wren	*Cyphorhinus arada*	IAG	G	2	3	0	0	0	0
POLIOPTILIDAE									
Collared Gnatwren	*Microbates collaris*	IAG	TF	6	4	0	0	0	0
TURDIDAE									
Swainson's Thrush	*Catharus ustulatus*	OA	G	0	0	0	2	0	0
Hauxwell's Thrush	*Turdus hauxwelli*	OA	G	0	0	0	3	2	5

Table 5 continued

Common name	Species	Guilds[a]	Habitat[b]	Terra firme		Várzea		Igapó	
				Wet	Dry	Wet	Dry	Wet	Dry
White-necked Thrush	*Turdus albicollis*	OA	G	2	1	0	0	0	0
THRAUPIDAE									
Red-capped Cardinal	*Paroaria gularis*	GT	G	0	0	1	0	0	0
Grey-headed Tanager	*Eucometis penicillata*	IAG	VZ	3	0	1	1	0	0
Fulvous-crested Tanager	*Tachyphonus surinamus*	OA	G	1	2	0	0	0	0
Fulvous Shrike-Tanager	*Lanio fulvus*	IAS	TF	1	2	0	0	0	0
EMBERIZIDAE									
Chestnut-bellied Seed-Finch	*Oryzoborus angolensis*	GT	VZ	0	0	1	0	0	0
CARDINALIDAE									
Red-crowned Ant-Tanager	*Habia rubica*	IAG	TF	2	2	0	0	0	0
ICTERIDAE									
Velvet-fronted Grackle	*Lampropsar tanagrinus*	OA	VZ, IG	0	0	3	0	0	0

[a] Trophic and foraging guilds: *Aqu*, aquatic; *IAF*, ant-following insectivore; *IAG*, arboreal gleaning insectivore; *IAS*, arboreal sallying insectivore; *IBI*, bark-searching insectivore (internal); *IBS*, bark-searching insectivore (external); *IDL*, dead-leaf gleaning insectivore; *ITG*, terrestrial gleaning insectivore; *ITS*, terrestrial sallying insectivore; *FA*, arboreal frugivore; *GA*, arboreal granivore; *GT*, terrestrial granivore; *NA*, arboreal nectarivore; *OA*, arboreal omnivore; *OT*, terrestrial omnivore; *RNA*, nocturnal raptor (based in Terborgh et al. 1990; Barlow and Peres 2004; Barlow et al. 2007, and references therein)

[b] Main forest type associations: *G*, Generalist (occurring in floodplain and upland forests); *IG*, Igapó; *TF*, Terra Firme; *VZ*, Várzea (based in Remsen and Parker 1983, Ridgely and Tudor 1989, 1994; Terborgh et al. 1990, Borges et al. 2001; Restall et al. 2006)

References

Adis J, Junk WJ (2002) Terrestrial invertebrates inhabiting lowland river floodplains of Central Amazonia and Central Europe: a review. Freshw Biol 47:711–731

Ballinger A, Lake PS, Nally RM (2007) Do terrestrial invertebrates experience floodplains as landscape mosaics? Immediate and longer-term effects of flooding on ant assemblages in a floodplain forest. Oecologia 152:227–238

Barlow J, Peres CA (2004) Avifaunal responses to single and recurrent wildfires in Amazonian forests. Ecol Appl 14:1358–1373

Barlow J, Mestre LAM, Gardner TA, Peres CA (2007) The value of primary, secondary and plantation forests for Amazonian birds. Biol Conserv 136:212–231

Bissonette JA, Storch I (eds) (2007) Temporal dimensions of landscape ecology. Wildlife responses to variable resources. Springer, Heidelberg

Blake JG, Loiselle BA (2009) Species composition of neotropical understory bird communities: local versus regional perspectives based on capture data. Biotropica 41:85–94

Bodmer RE (1990) Responses of ungulates to seasonal inundations in the Amazon floodplain. J Trop Ecol 6:191–201

Borges SH, Carvalhaes A (2000) Bird species of black water inundation forests in the Jaú National Park (Amazonas state, Brazil): their contribution to regional species richness. Biodivers Conserv 9:201–214

Borges SH, Cohn-Haft M, Carvalhaes AMP, Henriques LM, Pacheco JF, Whittaker A (2001) Birds of Jaú National Park, Brazilian Amazon: species check-list, biogeography and conservation. Ornitol Neotrop 12:109–140

Cadena CD, Londoño GA, Parra JL (2000) Nesting records of five antbird species from the Colombian Amazon. Wilson Bull 112:313–317

Castello L (2008) Lateral migration of *Arapaima gigas* in floodplains of the Amazon. Ecol Freshw Fish 17:38–46

Cintra R, Santos PMRS, Leite CB (2007) Composition and structure of the lacustrine bird communities of seasonally flooded wetlands of Western Brazilian Amazonia at high water. Waterbirds 30:521–540

Clarke KR, Gorley RN (2006) PRIMER v6: User manual/tutorial. PRIMER-E, Plymouth, p 192

Cotton PA (2007) Seasonal resource tracking by Amazonian hummingbirds. Ibis 149:135–142

Fearnside PM (2001) Environmental impacts of Brazil's Tucuruí dam: unlearned lessons for hydroelectric development in Amazonia. Environ Manage 27:377–396

Fearnside PM, Ferraz J (1995) A conservation gap analysis of Brazil's Amazonian vegetation. Conserv Biol 9:1134–1147

Gascon C, Malcolm JR, Patton JL, da Silva MNF, Bogart JP, Lougheed SC, Peres CA, Neckel S, Boag PT (2000) Riverine barriers and the geographic distribution of Amazonian species. Proc Natl Acad Sci 97:13672–13677

Gotelli NJ, Entsminger GL (2007) EcoSim: null models software for ecology. Version 7. Acquired Intelligence Inc. & Kesey-Bear

Gotelli NJ, Graves GR (1996) Null models in ecology. Smithsonian Institution Press, Washington

Haugaasen T, Peres CA (2005a) Mammal assemblage structure in Amazonian flooded and unflooded forests. J Trop Ecol 21:133–145

Haugaasen T, Peres CA (2005b) Tree phenology in adjacent Amazonian flooded and unflooded forests. Biotropica 37:620–630

Haugaasen T, Peres CA (2005c) Primate assemblage structure in Amazonian flooded and unflooded forests. Am J Primatol 67:243–258

Haugaasen T, Peres CA (2006) Floristic, edaphic and structural characteristics of flooded and unflooded forests in the lower Rio Purús region of central Amazonia, Brazil. Acta Amazon 36:25–36

Haugaasen T, Peres CA (2007) Vertebrate responses to fruit production in Amazonian flooded and unflooded forests. Biodivers Conserv 16:4165–4190

Haugaasen T, Peres CA (2008) Population abundance and biomass of large-bodied birds in Amazonian flooded and unflooded forests. Bird Conserv Int 18:87–101

Henderson PA, Crampton WGR (1997) A comparison of fish diversity and abundance between nutrient-rich and nutrient-poor lakes in the Upper Amazon. J Trop Ecol 13:175–198

Herrera CM (1998) Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. Ecol Monogr 68:511–538

Hess LL, Melack JM, Novo EMLM, Barbosa CCF, Gastil M (2003) Dual-season mapping of wetland inundation and vegetation for the central Amazon basin. Remote Sens Environ 87:404–428

Holbrook KM, Smith TB, Hardesty BD (2002) Implications of long-distance movements of frugivorous rain forest hornbills. Ecography 25:745–749

Junk WJ (1997) The central Amazon floodplain: ecology of a pulsing system. Springer, Heidelberg

Karr JR (1981) Surveying birds in the tropics. Studies in Avian Biology 6:548–553

Keuroghlian A, Eaton DP (2008) Importance of rare habitats and riparian zones in a tropical forest fragment: preferential use by *Tayassu pecari*, a wide-ranging frugivore. J Zool 275:283–293

Laurance WF, Cochrane MA, Bergen S, Fearnside PM, Delamonica P, Barber C, D'Angelo S, Fernandes T (2001) The future of the Brazilian Amazon. Science 291:438–439

Lees AC, Peres CA (2008) Conservation value of remnant riparian forest corridors of varying quality for Amazonian birds and mammals. Conserv Biol 22:439–449

Moore RP, Robinson WD, Lovette IJ, Robinson TR (2008) Experimental evidence for extreme dispersal limitation in tropical forest birds. Ecol Lett 11:960–968

Noriega AJ, Botero JP, Viola M, Fagua G (2007) Dinámica estacional de la estructura trófica de un ensamblaje de Coleóptera en la Amazonia Colombiana. Rev Colomb Entomol 33:157–164

Pearson DL, Derr JA (1986) Seasonal patterns of lowland forest floor arthropod abundance in southeastern Peru. Biotropica 18:244–256

Pereira MJ, Marques JT, Santana J, Santos CD, Valsecchi J, Queiroz HL, Beja P, Palmeirim JM (2009) Structuring of Amazonian bat assemblages: the roles of flooding patterns and floodwater nutrient load. J Anim Ecol. doi:10.1111/j.1365-2656.2009.01591.x

Peres CA (2005) Why we need megareserves in Amazonia. Conserv Biol 19:728–733

Pierpont N (1986) Interspecific aggression and the ecology of woodcreepers (Aves: Dedrocolaptidae). PhD Dissertation, Princeton University, Princeton, NJ

Poff NLR (1997) Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. J North Am Benthol Soc 16:391–409

Pollock MG, Paxton EH (2006) Floating mist nets: a technique for capturing birds in flooded habitats. J Field Ornithol 77:335–338

Prance GT (1979) Notes on the vegetation of Amazonia III. The terminology of Amazonian forest types subject to inundation. Brittonia 31:26–38

Rasmussen PC, Collar NJ (2002) Family Bucconidae (Puffbirds). In: del Hoyo J, Elliot A, Sargatal J (eds) Handbook of the birds of the World, vol 7. Jacamar to Woodpeckers, Lynx Editions, pp 102–138

Remsen JV Jr, Good DA (1996) Misuse of data from mist-net captures to assess relative abundance in bird populations. Auk 113:381–398

Remsen JV Jr, Parker TA III (1983) Contribution of river-created habitats to bird species richness in Amazonia. Biotropica 15:223–231

Remsen JV, Cadena CD, Jaramillo A, Nores M, Pacheco JF, Robbins MB, Schulenberg TS, Stiles FG, Stotz DF, Zimmer KJ (2009) A classification of the bird species of South America. American Ornithologists' Union. http://www.museum.lsu.edu/~Remsen/SACCBaseline.html

Renton K (2001) Lilac-crowned parrot diet and food resource availability: resource tracking by a parrot seed predator. Condor 103:62–69

Renton K (2002) Seasonal variation in occurrence of macaws along a rainforest river. J Field Ornithol 73:15–19

Restall R, Rodner C, Lentino M (2006) Birds of Northern South America. An Identification Guide. Species Accounts. Helm Field Guides, London

Ridgely RS, Tudor G (1989) The birds of South America. Volume 1: The oscines passerines. University of Texas, Texas

Ridgely RS, Tudor G (1994) The birds of South America. Volume 2: The Suboscines Passerines. University of Texas, Texas

Saint-Paul U, Zuanon J, Correa MAV, García M, Fabré NN, Berger U, Junk WJ (2000) Fish communities in central Amazonian white- and blackwater floodplains. Environ Biol Fishes 57:235–250

Sick H (1997) Ornitologia brasileira. Ed. Nova Fronteira, Rio de Janeiro

Taylor BL, Gerrodette T (1993) The uses of statistical power in conservation biology–the Vaquita and Northern Spotted Owl. Conserv Biol 7:489–500

Tellería JL, Ramírez A, Pérez-Tris J (2008) Fruit tracking between sites and years by birds in Mediterranean wintering grounds. Ecography 31:381–388

Terborgh J, Robinson SK, Parker TA III, Munn CA, Pierpont N (1990) Structure and organization of an Amazonian forest bird community. Ecol Monogr 60:213–238

Thiollay JM (1994) Structure, density, and rarity in an Amazonian rain-forest bird community. J Trop Ecol 10:449–481

Vale MM, Cohn-haft M, Bergen S, Pimm SL (2008) Effects of future infrastructure development on threat status and occurrence of Amazonian birds. Conserv Biol 22:1006–1015

Van Bael SA, Bichier P, Ochoa I, Greenberg R (2007) Bird diversity in cacao farms and forest fragments of western Panama. Biodivers Conserv 16:2245–2256

Van Houtan KS, Pimm SL, Halley JM, Bierregaard RO, Lovejoy TE (2007) Dispersal of Amazonian birds in continuous and fragmented forest. Ecol Lett 10:219–229

Willis EO (1966) Interspecific competition and the foraging behavior of plain-brown woodcreepers. Ecology 47:667–672