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Structuring of Amazonian bat assemblages: the roles of flooding patterns and floodwater nutrient load

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Summary

1. River system dynamics results in ecological heterogeneities that play a central role in maintaining biodiversity in riverine regions. In central Amazonia, large expanses of forest are seasonally flooded by nutrient-rich water (várzea forests) or by nutrient-poor water (igapó forests). Inundation patterns and the nutrient load of floodwaters are perhaps the most important abiotic factors determining spatial ecological variations in lowland Amazonia, and so they are expected to strongly influence the structuring of animal communities.

2. We examined how inundation patterns and water-nutrient load influence the structure of neotropical assemblages of bats, one of the most diverse vertebrate groups in tropical forests. Bat assemblages were sampled with mist nets in central Brazilian Amazonia, across a mosaic of várzea, igapó, and non-flooding nutrient-poor terra firme forests in the low- and high-water seasons.

3. An ordination analysis clearly separated the assemblages of the three forest types, demonstrating the structural relevance of both flooding and floodwater-nutrient load. Flooded forests had lower species richness because of the absence or rarity of species that make roosts out of leaves of understorey plants, and of those that feed on fruits of shrubs. Gleaning insectivores, also partly dependent on the understorey, were less abundant in flooded forests, but aerial insectivores more abundant, presumably because they benefited from a less cluttered foraging environment. These differences suggest that flooding affects bat assemblages mostly because it reduces the availability of niches associated with understorey vegetation, which tends to be sparser in flooded forests.

4. Nutrient-rich várzea forests had a bat biomass twice that of nutrient-poor igapó and unflooded forests. This difference was not only mostly due to a greater overall abundance of bats, but also attributable to a disproportionate higher abundance of large-bodied bat species.

5. We concluded that both flooding and floodwater-nutrient load are very important in the structuring of lowland Amazonian bat assemblages, with inundation mostly constraining the species composition of the assemblages, and water-nutrient load mostly influencing the abundance of species. The distinctiveness of bat assemblages associated with flooding emphasizes the need to preserve inundated forests, which are under particular pressure in Amazonia.

Key-words: Brazil, Chiroptera, community, tropics

Introduction

At large biogeographical scales, the structure of vertebrate communities is mostly determined by climate (Gaston & Blackburn 1995; Brown & Gibson 1998; Hawkins *et al.* 2003), but many other factors can also play important roles, especially at regional scales (Brown & Gibson 1998). In the case of tropical rainforests, these include vegetation complexity and forest succession, competition and predation, seasonality and soil fertility (Eisenberg 1990). Neotropical forests hold extremely rich animal communities, but these ecosystems are still poorly studied, so the understanding of the factors that structure their animal communities remains very incomplete.

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In central lowland Amazonia, seasonal flooding is likely to play a role in shaping vertebrate assemblages. In fact, a substantial part of its forests consists of a natural mosaic of seasonally flooded and unflooded areas, following spatial patterns that result from ancient and ongoing geological and hydrological disturbances (Tuomisto *et al.* 1995). The diversity of this mosaic is increased by the different types of water involved in the seasonal inundations. Although the Amazon River receives turbid nutrient-rich water from the ice-melt and steep slopes of the Andes ('white waters'), some of its tributaries carry nutrient-poor water coming from the forest plains ('black waters', darkly stained by organic compounds), or drain predominantly pre-Cambrian rocky areas of the Brazilian and Guayanan shields ('clear waters'). The forests seasonally flooded by nutrient-rich waters are fertile and called várzea, whereas those inundated by nutrient-poor waters are oligotrophic and called igapó (Prance 1979; Ayres 1993). The areas of várzea and igapó are embedded in a matrix of terra firme forests, which develop in soils that never flood and are usually nutrient-poor (Irion, Junk & Mello 1997).

Inundation patterns of Amazonian forests, together with differences in the nutrient load of the flooding waters, influence forest structure, floristic composition and tree phenology (Kubitzki 1989; Junk 1993; Haugaasen & Peres 2005a), so they are also likely to play an important role in structuring animal communities, both at the local and landscape scales. Although some vertebrate species may thrive well in the various types of forest, those with narrower niches are likely to be constrained by the environmental differences between them. At the landscape scale, the forest mosaic created by inundation may contribute to the persistence of species that have home ranges large enough to allow individuals to take advantage of resources that became available in space and time (Renton 2002; Haugaasen & Peres 2007). Indeed, inundation patterns in Amazonia seem to have a strong influence in the structuring of assemblages of birds (Borges & Carvalhães 2000; Haugaasen & Peres 2007), and non-volant mammals (Haugaasen & Peres 2005b).

Bats are one of the most abundant and diverse vertebrate groups in neotropical forests, contributing between 40% and 60% to their mammalian diversity (Brosset & Charles-Dominique 1990; Simmons & Voss 1998). Additionally, they play important roles in tropical forest ecosystems, acting as key pollinators, seed dispersers and predators (Patterson, Willig & Stevens 2003). Consequently, it is important to understand the structure of neotropical bat assemblages, and to identify the factors that shape them. As in other groups of organisms, inundation and floodwater-nutrient loads – and the different types of forest that result from them – are likely to influence the structure of bat assemblages in Amazonia. But this influence may be quite different from that on non-volant mammals, to which inundation may act as a barrier for accessing and using some resources, at least during a substantial part of the year. Inundation is likely to influence the composition of bat assemblages mostly through indirect mechanisms, such as the structure of vegetation. Bats are also more mobile than other mammals and can easily make regional movements in response to temporal changes of the environment, and this may result in seasonal changes in the structure of the species assemblages of the different forest types.

Although there is a fair number of studies on the structure of bat communities in neotropical terra firme rainforests (e.g. Lim & Engstrom 2001; Sampaio *et al.* 2003; Barnett *et al.* 2006), the information available about bat assemblages of flooded forests is very limited (Rex *et al.* 2008). In addition, as the available information on assemblages of different types of forest comes from regions far apart, it becomes difficult to separate the effect of flooding and nutrients from that of large-scale biogeographical factors (Tuomisto & Ruokolainen 1997). Our aim was then to determine the actual roles of inundation and of floodwater-nutrient loads in the structuring of Amazonian bat assemblages. In particular, we tested how these factors influence the abundance of bats, the species composition and diversity of the assemblages, and their guild-level structure. For this, we studied bat assemblages both during the inundation period and when the waters were low in a region where terra firme, várzea and igapó forests exist in adjacent areas.

Materials and methods

STUDY AREA

The study was carried out around lake Amanã (2°37′ S, 64°37′ W), in the South of the Amanã Sustainable Development Reserve (Amazonas, Brazil). This is one of the largest protected areas of tropical rainforest in South America, covering 2 350 000 ha, and is part of the Central Amazonian Ecological Corridor. Lake Amanã is mostly a black-water lake fed by streams draining catchments dominated by terra firme forests, although the south of the lake also receives some inflow of white-waters from the river Japurá (Fig. 1). Igapó forests occur mainly along the streams and margins of the lake, whereas most of the várzea forests are in the floodplain of the river Japurá. Population density is quite low, with only *c.* 4000 people living inside the reserve, and most of the area is relatively free of anthropogenic disturbance.

Average annual precipitation is 2500 mm, most of which falls in the wetter season (January–June). Usually, the waters are the lowest in September and October and highest in May and June (Ayres 1993). During the high-water season, large extensions of forest are inundated to depths of up to 10 m. Flowering and fruiting peaks mostly occur in the low-water and the high-water season respectively (Rankin-De-Merona *et al.* 1992; Ayres 1993; Haugaasen & Peres 2005a). The dominant trees belong to the families Sapotaceae, Lecythidaceae, Euphorbiaceae, Myristicaceae and Leguminosae, in particular Mimosidae, Caesalpinioideae and Faboideae (M.J.R. Pereira & J.T. Marques, personal observation; Ayres 1993; Souza 2006). Canopy height is between 15 and 35 m with emergent trees reaching at least 50 m high (M.J.R. Pereira & J.T. Marques, personal observation).

BAT SAMPLING

Bat assemblages were sampled in 2007 between April and June, when várzea and igapó forests are flooded, and between October and December, during the low-water season. Bats were captured in four stations of terra firme, three of várzea and three of igapó (Fig. 1).

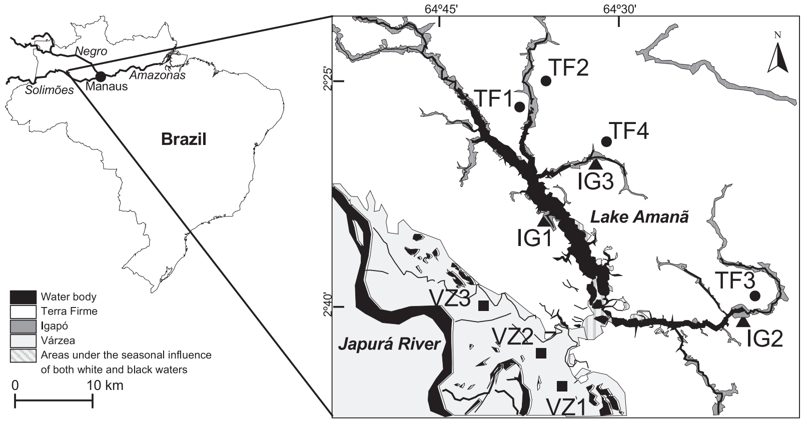

Fig. 1. Study area and location of sampling stations (TF, terra firme; VZ, várzea; IG, igapó). Lake Amanã has mostly black water, but in the south it can temporarily receive white waters, creating an ecological transition zone. The distribution of the forest types is based on cartography by the Mamirauá Sustainable Development Institute and on satellite imagery.

Each station was sampled during a period of four consecutive nights in both seasons. The types of forest sampled in consecutive sampling periods were alternated to avoid temporal biases. Bats were caught using three 3×12 m mist nets set at canopy level (17–35 m) and ten 12×3 m nets at ground level. During the high-water season, ground mist-nets were set above water in both várzea and igapó, but canopy nets were not used in these habitats because of the logistic difficulties of setting them in flooded areas. During floods, nets had to be set and checked using small boats and canoes. Nets remained open between 18h30min and 24 h, and were checked every 20 min. Each captured bat was identified, and weighted using a 20-, 50- or 100-g Pesola balance. Age was determined by the degree of ossification of the carpal joints and development of nipples and testis (Baagøe 1977). Individuals were marked in the patagium using a pen marker to allow recognition of recaptures during the same sampling period. Recaptures were very rare and were not included in the analyses. There are recognized biases in the results of mist-netting (e.g. Kalko & Handley 2001), as not all bat species are equally likely to be captured with them. However, it remains the single most informative method to sample bat assemblages in the neotropics and is the base of virtually all studies on these assemblages (e.g. Lim & Engstrom 2001; Rex *et al.* 2008).

DATA ANALYSIS

All bats captured were classified into guilds (Table S1) following Kalko (1997) and Schnitzler & Kalko (1998). As the flooded habitats were not sampled at the canopy level during the high-water season, canopy data were used just for inventorying. All subsequent analyses were conducted solely with understorey capture data. We estimated species richness with the nonparametric Jackknife2 estimator, using EstimateS (Colwell 2005). Jackknife2 is known to make a good correction for underestimation (Zahl 1977) and is the method that performed best in a recent study on neotropical phyllostomid bat assemblages (Rex *et al.* 2008). Species richness of the different habitats was compared using Coleman individual-based rarefaction curves (Coleman 1981; Gotelli & Colwell 2001), also computed using EstimateS. In contrary to the Jackknife2 (and other richness estimators), this method estimates species richness for a subsample of the pooled total species richness based on all species actually captured. The widely used Shannon diversity index was calculated to allow comparisons with the results of other studies. Equitability, the evenness with which the number of individuals is divided among the taxa present (Krebs 1999), was also calculated. Confidence intervals were obtained by bootstrap.

The effect of forest type and season on Shannon and equitability indices, capture rates, relative biomass, and the abundance of guilds, was tested with two-way analyses of variance (ANOVA), followed by Tukey HSD *post hoc* tests, all computed in R software (Ihaka & Gentleman 1996). Juveniles and females were excluded from biomass comparisons, to avoid biases due to incompletely grown or pregnant individuals.

A canonical correspondence analysis (CCA) was computed to get an ordination of the 10 sampling stations and to detect species-habitat relations. The logarithm of bat abundance was used to stabilize the variance, linearize increasing slopes and to normalize the distribution of that variable. Analysis of similarity (ANOSIM), a nonparametric permutations test analogous to an ANOVA for similarity matrices (Clarke & Gorley 2006), was used to test for significant differences in assemblage structure between the three forest types and the two seasons. The contribution of each bat species for differentiating assemblages was examined using percentage analysis SIMPER (Clarke & Warwick 2001). Data were normalized 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. Both ANOSIM and SIMPER were computed using Primer v6 (Clarke & Gorley 2006). The abundance of species with a contribution to the dissimilarity above 1·5% was compared using Pearson chi-square analysis.

Results

RICHNESS, DIVERSITY AND BIOMASS

During the 80 nights of mist-netting, a total of 1242 bats of 60 species and four families were captured (Table S1). Total capture effort was 5346 net hours (1 net hour corresponds to one 12 m mist-net opened for 1 h). We captured 56 species in terra firme, 43 in várzea and 36 in igapó.

Considering just understorey captures, 68% of the species were captured 10 times or less, whereas the five most abundant species (*Carollia perspicillata*, *Artibeus planirostris*, *Phyllostomus elongatus*, *Artibeus obscurus* and *Glossophaga soricina*) accounted for 59% of the total captures. Most of the species captured were insectivores (23 species) and frugivores (25 species), but although the former comprised only 12% of individuals, the latter reached 60%. Omnivores represented 15% of the captures, and carnivores and nectarivores 5% each. Species richness differed significantly between the three forest types, and was the highest in terra firme (Fig. 2). Jackknife2 yielded an estimate of 88

(SD = 4·60) species for terra firme, 66 (SD = 7·50) for várzea and 47 (SD = 5·26) for igapó.

The Shannon diversity index differed significantly between forest types ($P < 0{\cdot}001$; Fig. 3). The *post hoc* comparisons showed that it was higher in terra firme than in várzea and igapó (both $P < 0{\cdot}001$), and higher in igapó than in várzea ($P = 0{\cdot}046$). Equitability also differed between habitats ($P < 0{\cdot}001$), and was significantly higher in both terra firme ($P < 0{\cdot}001$) and igapó ($P = 0{\cdot}002$) than in várzea. Capture rates and relative biomass were significantly different between habitats (both $P < 0{\cdot}001$; Fig. 3). Captures were higher in várzea than in terra firme and igapó (both $P < 0{\cdot}001$). Biomass was also higher in várzea than in the two other forest types (both $P < 0{\cdot}001$). In fact, the mean relative biomass in várzea was more than twice the value found for terra firme and igapó (Fig. 3), and this was mainly due to the greater abundance of large-bodied species such as *Phyllostomus hastatus*, *Trachops cirrhosus*, *A. planirostris* and *P. elongatus* in várzea. The effect of season and interaction were not significant in any of the ANOVAS used in these comparisons.

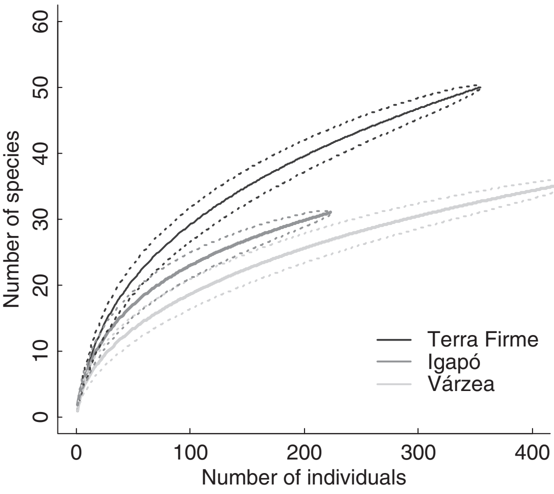

Fig. 2. Individual-based Coleman species-rarefaction curves (solid lines) with 95% confidence intervals (dashed lines), based on mist-net captures for terra firme, várzea and igapó.

SPECIES COMPOSITION

The most common species differed between habitats: in terra firme, the most abundant were *C. perspicillata* (16%) and *Rhinophylla pumilio* (10%); in várzea, *A. planirostris* (25%) and *C. perspicillata* (23%); and in igapó, *C. perpicillata* (26%) and *A. obscurus* (12%).

Terra Firme, várzea and igapó samples formed very distinct clusters in the CCA plot (Fig. 4), in which forest sites were positioned according to their species composition. This underlines not only the strong influence of inundation distinguishing terra firme from both igapó and várzea, but also the strong influence of the relevance of nutrient availability, which separates várzea from the nutrient-poor forest types. The ANOSIM confirmed that the difference between the assemblage structures of the three forest types was statistically significant, mainly due to differences between terra firme and the two seasonally flooded forests (Table 1). However, during the low-water season, only differences between terra firme and várzea remained significant. There was no significant seasonal variation in the overall community structure (two-way ANOSIM: global $R = -0{\cdot}19$, $P = 0{\cdot}935$) or within any of the forest types.

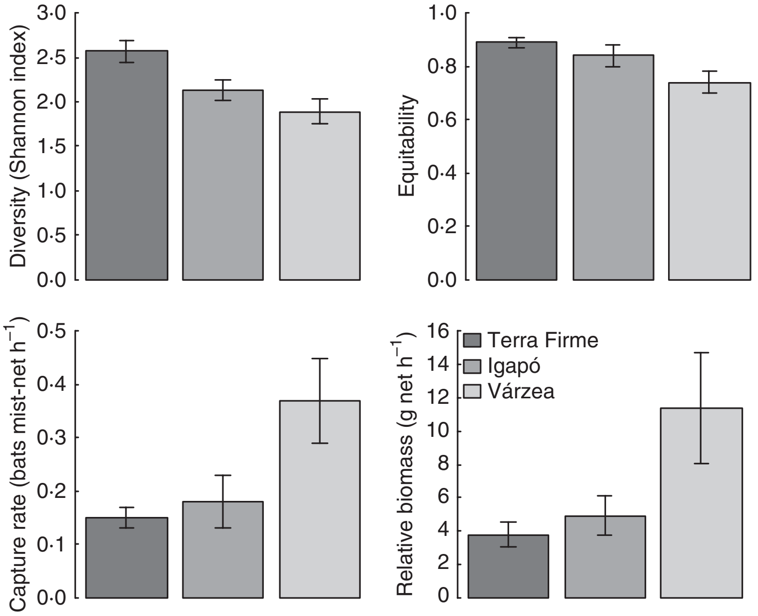

Fig. 3. Diversity (Shannon index), equitability, capture rate and relative biomass by forest type (vertical lines correspond to 95% confidence intervals). Data were pooled among seasons because the patterns of between-habitat variation were consistent among seasons and there were no significant seasonal changes in the patterns of diversity, equitability, biomass and capture rates within forest types.

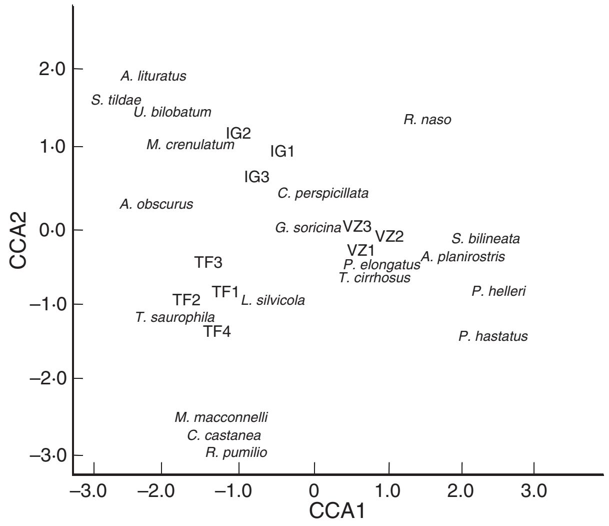

Fig. 4. Biplot of the canonical correspondence analysis (sampling stations: TF, terra firme; VZ, várzea; IG, igapó). Total inertia = 0·60; eigenvalues for constrained axes: CCA1: 0·19, CCA2: 0·04. Species matrix for species with total captures of 10 or more individuals. As there was no significant seasonal variation in assemblage structure, data from both seasons were pooled.

As the dissimilarities between terra firme and the two seasonally flooded habitats were statistically significant, a SIMPER analysis was conducted to determine which species contributed most to the difference between flooded and unflooded forests (Fig. 5). SIMPER analysis was consistent with the CCA results: *R. pumilio* presented a strong contribution because this moderately abundant species was almost exclusively captured in terra firme. Other species characterizing unflooded forests included *Carollia castanea* and *Mesophylla macconelli*. *Artibeus planirostris* had the strongest contribution to the dissimilarity between flooded and unflooded forests as it was captured in very high numbers in várzea forests. However, *Rhynchonycteris naso* was the only relatively common species clearly associated simultaneously with the two flooded forests, as it was never captured in terra firme (Table S1). A few other species tended to be more important in the assemblages of one or both types of flooded forest than in that of terra firme, such as *Saccopteryx bilineata*, and *Platyrrhinus helleri* in várzea or *Artibeus lituratus* and *Uroderma bilobatum* in igapó.

GUILD STRUCTURE

Guild structure in terra firme was significantly different from that in várzea and igapó, but there were no significant differences between the two seasonally flooded forests (Table 1). This pattern was observed in both the low- and high-water seasons, although there were no significant differences between terra firme and igapó during the low-water season. Guild structure did not change between these two seasons within any of the habitats, or in the study area as a whole (two-way ANOSIM: global R = 0·05, P = 0·34). Nonetheless, the pattern of relative abundance of feeding guilds was similar in the three habitats (Fig. 6): frugivores were by far the most numerous guild, followed by omnivores. The abundance of frugivores, omnivores and insectivores, both gleaning and aerial, differed statistically between forest types. The *post hoc* comparisons confirmed that frugivores and omnivores were significantly more abundant in várzea than in terra firme and igapó (all P < 0·05). Aerial insectivores were more abundant in the two seasonally flooded forests than in terra firme, whereas in the latter gleaning insectivores were in average more abundant than in várzea or igapó (all P < 0·05). The effect of season and interaction were not significant in any of the ANOVAS used in these comparisons.

Discussion

Inundation patterns and the geochemistry of floodwaters are perhaps the most important abiotic factors determining spatial variations in soil fertility, habitat structure and floristic composition in lowland Amazonian forests (Peres 1997). Consequently, understanding how these two factors influence the structure of species assemblages is an issue of paramount importance in the knowledge of the community ecology of Amazonian vertebrates. This study confirms this view, strongly suggesting that both flooding and floodwater-nutrient load play key roles in the structuring of the lowland Amazonian bat assemblages. However, the influence of these two factors seems to be quite distinct, with inundation constraining the species composition of the assemblages and water-nutrient load mostly determining the abundance of species.

Season, on the other hand, does not seem to substantially influence the general parameters or the composition of bat

Table 1. Average dissimilarity values based on the Bray–Curtis similarity index on bat species and guilds between forest types

	Species			Feeding guilds		
Factor: Forest	Both seasons	High water	Low water	Both seasons	High water	Low water
Between all forests	0·63**	0·67**	0·67**	0·44**	0·63*	0·35*
Terra firme and igapó	0·40**	0·26*	0·27$^{\text{ns}}$	0·21*	0·35*	0·22$^{\text{ns}}$
Terra firme and várzea	0·91**	0·81*	0·91*	0·74**	0·91*	0·66*
Igapó and várzea	0·06$^{\text{ns}}$	0·80$^{\text{ns}}$	0·85$^{\text{ns}}$	0·03$^{\text{ns}}$	0·81$^{\text{ns}}$	0·05$^{\text{ns}}$

**P < 0·01, *P < 0·05, $^{\text{ns}}P$ > 0·05.

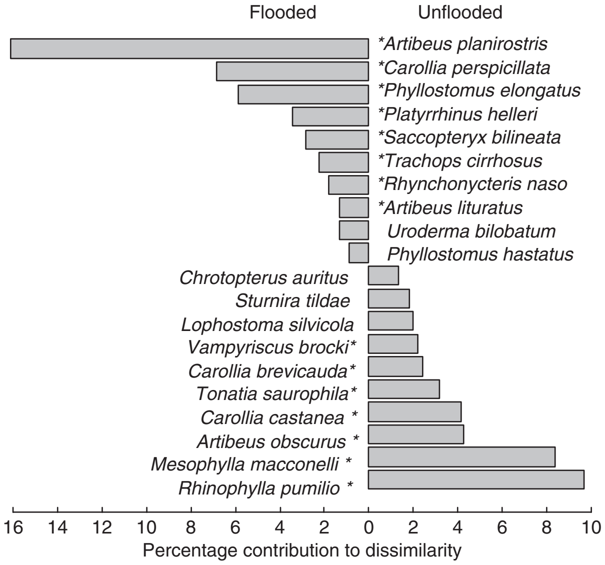

Fig. 5. Species making the highest contributions (> 1·5%) to assemblage dissimilarity between unflooded (terra firme) and flooded (várzea and igapó) forests. Asterisks indicate significant differences in the abundances between the habitats at $\alpha = 0{\cdot}05$.

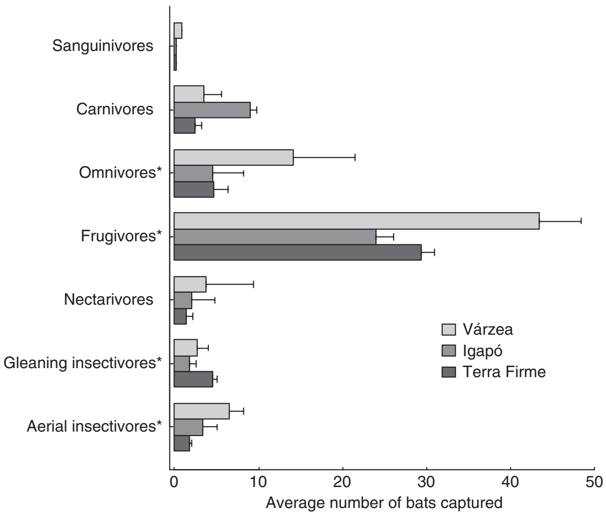

Fig. 6. Average number of captures by feeding guilds in the three habitats. Lines represent 95% confidence intervals and asterisks significant differences between habitats at $\alpha = 0{\cdot}05$. The three guilds of aerial insectivores were here clumped in just one group due to the low number of captures.

assemblages within forest types. So, although bats are able to fly large distances, our results suggest a lack of intense seasonal movements between habitats.

INFLUENCE OF FLOODING

In our study area, seasonal flooding appeared to be a fundamental factor in the structuring of bat assemblages. Although both types of flooded forest differed from terra firme, the differences were less marked in the case of igapó. The explanation for this may lie in the fact that most areas of igapó are not extensive, and usually located adjacent to terra firme, along forest streams (Fig. 1; Haugaasen & Peres 2006). As bats can move considerably during their foraging trips, it is likely that some individuals mostly dependent on terra firme visit sources of food in igapó, or simply cross it while commuting to foraging sites. Most of our nets were placed along trails, and bats are known to use trails as commuting flyways (Palmeirim & Etheridge 1985). This may substantially reduce the dissimilarity between the assemblages of the two habitats, especially in the areas of igapó closest to terra firme.

Differences between the assemblages of terra firme and várzea were marked, possibly due to the cumulative effects of inundation and of the greater productivity of várzea, as a result of the nutrients brought in by floodwater. In addition, the interchange of bats with terra firme is probably low, because várzea, unlike igapó, occupies large contiguous areas that, in our study region, are well separated from terra firme.

Because bats can fly, inundation of the forest floor is not likely to be an important direct determinant of the composition of bat species assemblages, but it may shape them through the influence on vegetation. Indeed, seasonal flooding affects both the structure and floristic diversity of the forest. Species richness of terra firme forest is higher than that of flooded forests (Campbell *et al.* 1986; Ayres 1993; Nebel, Dragsted & Vanclay 2001; Haugaasen & Peres 2006), mainly due to the persistent flood pulses, the anoxic or hypoxic conditions and the interruption of photosynthesis in várzea and igapó (Kubitzki 1989). At the level of vegetation structure, inundation has a particularly marked effect on the understorey, which is underwater for several months of the year, and during the low-water season tends to be more open in igapó and in várzea than in terra firme (Haugaasen & Peres 2006).

The species assemblages of the two-flooded forest types differed from the assemblage of terra firme. This was mainly due to the rarity, or absence, of some bat species in the flooded habitats. A clear pattern emerges from the analysis of the species that are rare in inundated forests, and therefore appear most associated with terra firme in the analyses: they are usually dependent on understorey plants to feed or roost. Two of them, *M. macconelli* and *R. pumilio*, are known to roost in tents made of large understorey leaves, such as those of palms (Kunz *et al.* 1994), which tend to be associated with non-flooding forests (Vormisto, Tuomisto & Oksaken 2004). Another species, *Vampyriscus brocki*, is also likely to use such roosts, as this behaviour has been described for other related species (Kunz *et al.* 1994). Consequently, our data support the suggestion of Findley (1993) that, in the Neotropics, the absence of suitable roosts may be a limiting factor for the occurrence of some bat species, especially of the Stenodermatinae. Two other species that are associated with terra firme, *C. castanea* and *C. brevicauda*, are probably limited in the flooded areas by the lack of food resources. They mostly eat fruits of undergrowth plants, such as *Piper*, *Solanum* and *Vismia* (e.g. Bonaccorso & Gush 1987; Palmeirim, Gorchov & Stoleson 1989; Bernand 2001), which may be unavailable or scarce in seasonally flooded forests. *Carollia perspicillata* also consumes these fruits, but it is abundant not only in terra firme but also in flooded forests, presumably because it has a more diverse diet (Fleming 1988; Geiselman, Mori & Blanchard 2002 onwards). Only one bat species seems to be clearly associated simultaneously with the two flooded forests, the insectivorous *R. naso*, which was captured in both várzea and igapó, but not in terra firme. This close association to inundated forests is presumably due to the type of roosts that it usually selects, stems of small trees overhanging water (Findley 1993), but may also be influenced by the structure of the vegetation, as discussed below.

Guild composition was also distinct between the three types of forest. In the case of insectivorous bats these differences seem to be related to inundation and its impacts on the structure of the understorey vegetation. Indeed, the greater overall abundance of aerial insectivores in both várzea and igapó than in terra firme may be explained by the greater availability of relatively open foraging volume at understorey level in the flooded forests. The highly cluttered space at this level in terra firme is possibly less suitable for several aerial insectivorous bats (Schnitzler & Kalko 1998). This interpretation naturally does not apply to fast-flying aerial insectivores known to forage above the canopy, such as the Molossidae, which are surely underrepresented in our mist-netting sampling (Kalko & Handley 2001). Contrasting with the situation of aerial insectivores, gleaning insectivores were more abundant in terra firme, presumably because they can take advantage of the greater availability of gleaning surfaces in this type of forest.

In a comparison between terra firme and várzea forests, Haugaasen & Peres (2005b) also showed that inundation had a major impact in the structuring of the assemblages of non-flying mammals. They concluded that the lower species richness found in the inundated forest could be due to the fact that prolonged seasonal inundation prevents terrestrial and understorey species from using these habitats. The reduction of richness that we observed in bats cannot be attributed to the exact same causes, and seems to be due mostly to a reduction in the availability of niches, particularly those for leaf roosting species and understorey foraging frugivores. It is important to point out that these conclusions apply mostly to frugivorous bats, which dominated our samples. A study focused on insectivorous bats is not possible using data collected with mist nets alone. However, such a study eventually carried out with ultra-sound sampling may reveal that inundation affects assemblages of insectivorous bats differently. Indeed, our limited results already point in that direction.

INFLUENCE OF NUTRIENT LOAD

Nutrient availability also appears to play an important role in the structuring of Amazonian bat assemblages, as suggested by the observed differences between igapó and várzea, which remain flooded during the same period of the year, but with floodwater with very distinct nutrient loads (Junk 1993; Irion *et al.* 1997). However, these differences were mostly at the level of the abundance of the various species and guilds, rather than on the species composition of the assemblages. There were no statistical differences between the assemblages of várzea and igapó, suggesting that, at least at the level of the species of high abundance, they showed no major differences in species composition.

Despite the overall similarity between the assemblages of várzea and igapó, there were less-abundant species that tended to be caught in just one of these habitats. There were more of such species in várzea, which consequently had a higher richness, suggesting that in Amazonia bat richness increases with ecosystem productivity. This increase in richness in the presence of both a greater productivity and higher density is compatible with the 'sampling hypothesis' (Evans *et al.* 2008): a random allocation of individuals from the regional bat assemblage results in a richer local assemblage in areas of várzea, because they hold larger populations. However, although species richness was greater in várzea than in igapó, the Shannon diversity index was higher in the latter. This happens because the index is a measure of diversity that combines species richness and equitability (i.e. the evenness with which the number of individuals is distributed among species), and equitability is higher in igapó. This is in line with the general observation that naturally nutrient-depleted habitats tend to harbour assemblages with more evenness among the species present (Tilman 1982). The influence of the nutrient load of flood water on the bat community seemed to be particularly important at the level of its total biomass, which is twice as high in várzea as in igapó. Terra firme, which is also poorer in nutrients than várzea, had a bat biomass just as low as that of igapó. The larger bat biomass of várzea was due to a greater overall abundance of bats and to a disproportionate higher abundance of large-bodied bat species in the assemblage.

Most guilds reached their abundance peaks in várzea, but frugivores, such as *A. planirostris*, and omnivores, such as *P. hastatus* and *P. elongatus*, which also eat a lot of fruit, were responsible for a great majority of the increase of bat biomass, suggesting that this increase is mostly explained by a greater availability of fruits. The high nutrient load of white water creates fertile soils (Furch 1997), which allows a greater productivity of fruits (Haugaasen & Peres 2007), and in turn a greater biomass of consumers. Indeed, chemical nutrients are the building blocks of biomass; as nutrients are absorbed by plants, primary productivity, which is the rate at which plant biomass is produced by unit area, increases and so does the potential for supporting more biomass at the higher levels of the food chain (Begon, Townsend & Harper 2006). It is worth noting that the observed amount of increase of bat biomass in várzea in relation to igapó is similar to that reported for primates, which are also strongly represented by frugivore species (Peres 1997; Haugaasen & Peres 2005b), possibly indicating that the greater availability of nutrients impacts various groups of Amazonian vertebrates in a similar way.

CONSERVATION IMPLICATIONS

The conclusions that bat assemblages of the three types of forest are distinct, and that the ecological optimum of some species is influenced by flooding and floodwater geochemistry, has important implications for the conservation of bats in neotropical forests.

Terra firme, the most species-rich assemblage, makes the largest contribution to the diversity of the bat fauna of the mosaic of flooded and non-flooded neotropical forests. Regional (gamma) diversity depends largely on the species richness of the historically dominant assemblage (Arellano & Halffter 2003), in this case terra firme, but has a mutual correlation with both local diversity (alpha diversity) and species turnover (beta diversity) (Whittaker 1972). Consequently, the existence of associations between some species of bats and a particular type of forest suggests that várzea and igapó are important contributors to the overall gamma diversity. A similar situation has been described for the bats of another neotropical region: Moreno & Halffter (2001) found that of the 20 bat species that comprised the gamma diversity in Veracruz, Mexico, 18 were found in the richest assemblage (subdeciduous tropical forest) but that alpha diversity in all vegetation assemblages was lower than the gamma diversity, suggesting that species richness is related to environmental heterogeneity.

The importance of várzea forests for several animal and plant groups has already been recognized because, as in the case of bats, the abundance of nutrients promote higher densities of some species in this habitat (e.g. Henderson & Crampton 1997; Haugaasen and Peres 2005a, b). The recognition of the particular value of igapó forests is more recent, but in the last few years, several studies demonstrated that it can support distinct assemblages of plants (Rodrigues *et al.* 2004), fish (Henderson & Crampton 1997) and birds (Borges & Carvalhães 2000).

The observed differences in the bat assemblages of terra firme, várzea and igapó, underline the importance of maintaining the mosaic of these natural habitats that characterizes much of the lowland Amazon. As in the case of other groups of organisms, this mosaic seems to contribute to the persistence of rich regional communities of bats. Consequently, our observations support that Amazonian nature reserves are most efficient when they combine forests under different flooding regimes, as it has been suggested by studies on other organisms (Haugaasen & Peres 2007). This requires a special focus on the protection of flooded forests that, due to their greater accessibility from rivers, are under the pressure of intense human occupation, and are often affected by the construction of hydroelectric dams (Borges & Carvalhães 2000; Fearnside 2001; Bernardes *et al.* 2004).

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Supporting Information

Additional supporting information may be found in the online version of this article

Table S1. Species list and number of bats captured with ground and canopy mist-nets in the three habitats and in both seasons