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STRUCTURING OF A MEGADIVERSE MAMMALIAN COMMUNITY

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NOTA PRÉVIA

A presente tese apresenta resultados de trabalhos já publicados ou submetidos para publicação (capítulos 2 a 6), de acordo com o previsto no nº 1 do artigo 41º do Regulamento de Estudos Pós-Graduados da Universidade de Lisboa, publicado no Diário da República II série nº 209 de 30 de Outubro de 2006. Tendo os trabalhos sido realizados em colaboração, a candidata esclarece que liderou e participou integralmente na concepção dos trabalhos, obtenção dos dados, análise e discussão dos resultados, bem como na redacção dos manuscritos.

Lisboa, Fevereiro de 2010

Maria João Veloso da Costa Ramos Pereira

Ao Nuno

Aos meus pais

“..........*Our own experience provides the basic material for our imagination, whose range is therefore limited (…) In so far as I can imagine this (which is not very far), it tells me only what it would be like for me to behave as a bat behaves. But that is not the question. I want to know what it is like for a bat to be a bat. Yet if I try to imagine this, I am restricted to the resources of my own mind, and those resources are inadequate to the task. I cannot perform it either by imagining additions to my present experience, or by imagining segments gradually subtracted from it, or by imagining some combination of additions, subtractions, and modifications.*
To the extent that I could look and behave like a wasp or a bat without changing my fundamental structure, my experiences would not be anything like the experiences of those animals. On the other hand, it is doubtful that any meaning can be attached to the supposition that I should possess the internal neurophysiological constitution of a bat. Even if I could by gradual degrees be transformed into a bat, nothing in my present constitution enables me to imagine what the experiences of such a future stage of myself thus metamorphosed would be like. The best evidence would come from the experiences of bats, if we only knew what they were like.”

Thomas Nagel – What is like to be a bat?

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Resumo

Os morcegos, ordem Chiroptera, pela sua diversidade taxonómica e ecológica, constituem um excelente taxon para investigar como os factores bióticos e abióticos influenciam os padrões de distribuição, diversidade e abundância das espécies. É na região Neotropical que os morcegos atingem o seu pico de diversidade, podendo existir mais de 100 espécies simpátricas pertencentes a dez *guilds* tróficas distintas.

Nas últimas décadas temos assistido a avanços significativos no conhecimento dos processos e padrões associados à distribuição, abundância e diversidade das espécies nas comunidades biológicas. Actualmente, a estrutura dessas comunidades é considerada como sendo o produto de dois grandes factores: condições ambientais actuais e interacção entre espécies, como a competição, e variações ambientais históricas e processos bióticos associados, tais como eventos de especiação, dispersão e extinção.

Apesar da sua excepcional diversidade, vasta distribuição e abundância local em algumas regiões, os factores que influenciam a estruturação das comunidades de morcegos são ainda pouco conhecidos. No entanto, é já evidente que os processos e padrões observados localmente resultam não só de mecanismos locais, mas também de processos que actuam aos níveis regional, continental e global.

Assim, a presente dissertação teve como principal objectivo a análise de factores que afectam a distribuição, diversidade e abundância de morcegos a diferentes escalas espaciais e temporais. Para os estudos a nível local foram seleccionadas comunidades de morcegos de florestas da Amazónia Central, uma vez que estas estão sujeitas a uma elevada heterogeneidade espacial e ambiental. Ao nível regional foram seleccionadas as comunidades de morcegos das florestas da bacia Amazónica. Por último, foram descritos e analisados os gradientes latitudinais na riqueza e na idade dos taxa de morcegos do continente americano à luz da história evolutiva conhecida para o grupo.

Os morcegos são um dos grupos mais diversos e abundantes das florestas neotropicais, tendo papéis essenciais, e muitas vezes insubstituíveis, no funcionamento destes ecossistemas. Apesar da planície Amazónica ser uma das regiões climaticamente menos sazonais do planeta, muitas zonas de floresta são sazonalmente inundadas por água rica em nutrientes (florestas de várzea) ou por água pobre em nutrientes (florestas de igapó); a inundação resulta do efeito combinado da chuva e do degelo dos Andes. Nos capítulos 2, 3 e 4 desta dissertação são apresentados os resultados do estudo acerca do modo como a heterogeneidade espacial e a sazonalidade ambiental das florestas da planície central Amazónica afectam a estrutura das comunidades de morcegos na região. Para tal capturaram-se morcegos durante as épocas de água alta e água baixa utilizando redes de neblina colocadas quer ao nível do solo, quer ao nível da copa; avaliou-se ainda a disponibilidade de frutos, o principal recurso alimentar de uma grande percentagem dos morcegos neotropicais.

Os padrões de inundação e a carga de nutrientes da água são dois dos factores abióticos determinantes das variações ecológicas na planície Amazónica, com impacto a nível da complexidade e heterogeneidade da vegetação. É assim expectável que influenciem directa ou indirectamente a estrutura das comunidades animais. Assim, no capítulo 2 examinou-se o modo como estes factores influenciam os padrões de diversidade e abundância das comunidades de morcegos em três tipos de florestas: florestas de terra firme, que não sofrem inundação e que são, em geral, pobres em nutrientes, florestas de várzea e florestas de igapó. Tal como acontece noutros grupos animais com menor capacidade de deslocação, também os morcegos são claramente afectados pelos padrões de inundação e pelos nutrientes disponíveis. Com base na captura de 1242 morcegos de 60 espécies diferentes, foi possível encontrar diferenças significativas em termos de composição e abundância nas comunidades de morcegos dos três tipos de floresta amostrados. A inundação parece afectar as comunidades, ao reduzir a disponibilidade de nichos associados à vegetação do sub-coberto; assim, as comunidades mais ricas encontram-se em terra firme, já que aquele estrato é muito mais estruturado neste tipo de floresta do que nas florestas sazonalmente inundadas. Por outro lado, a elevada disponibilidade de nutrientes na várzea permite suportar uma grande abundância de algumas espécies, em particular de morcegos de grande porte, o que se reflecte nos níveis de biomassa.

No capítulo 3 foi investigado se a estratificação vertical das espécies de morcegos ocorre nos três tipos de floresta, incluindo naqueles que sofrem inundação sazonal (cuja altura da copa é significativamente mais baixa do que em terra firme). Para tal, compararam-se as capturas efectuadas nas redes colocadas no solo com as capturas efectuadas em redes de copa. Uma análise de ordenação separou claramente – e nos três tipos de floresta – as espécies de morcegos que utilizam preferencialmente o sub-coberto daquelas que utilizam preferencialmente a copa. Apesar da composição das comunidades nos dois estratos ser diferente, os níveis de diversidade demonstraram ser muito semelhantes. A consistência dos resultados em terra firme e nas duas florestas sazonalmente inundadas sugere que as diferentes espécies de morcegos escolhem o mesmo estrato, independentemente do tipo de floresta onde se encontram. A utilização dos estratos verticais parece estar fortemente associada à dieta, ecologia alimentar e selecção de abrigos das diferentes espécies.

O principal objectivo do capítulo 4 consistiu em determinar se as flutuações sazonais na disponibilidade de frutos em florestas neotropicais são suficientemente marcadas para afectar a ecologia e a fisiologia dos morcegos frugívoros. A disponibilidade de frutos demonstrou ser fortemente sazonal, verificando-se ser significativamente superior durante a época inundada, em particular nas florestas de várzea. A abundância de morcegos demonstrou estar positivamente correlacionada com a abundância de frutos. As consequências da variação da disponiblidade de alimento na condição corporal e na actividade reprodutora foram investigadas nas duas espécies mais abundantes: em *Artibeus planirostris* a condição corporal decresceu quando os frutos eram mais escassos; a actividade de alimentação e a actividade reprodutora em *Carollia perspicillata* e *A. planirostris* estiveram positivamente correlacionadas com a disponibilidade de frutos. Os resultados sugerem que existe uma sazonalidade nos recursos que é suficientemente marcada para afectar os morcegos frugívoros, forçando-os mesmo a fazer importantes ajustes eco-fisiológicos.

A energia disponível nos ecossistemas é reconhecida como sendo um dos factores primordiais na determinação dos padrões de diversidade das espécies. Contudo, enquanto alguns autores consideram que é a energia directamente disponível nos ecossistemas que limita essa riqueza, outros sugerem que é a transformação dessa energia em recursos, *i.e.*, a produtividade, que explica as variações nos padrões de riqueza. No capítulo 5 procurou-se determinar qual das duas versões – energia directa ou produtividade – explica melhor os padrões de riqueza de morcegos frugívoros das florestas da bacia Amazónica. Para tal compilaram-se os dados de 22 inventários de morcegos na região e foram seleccionadas quer variáveis climáticas, quer variáveis associadas à produtividade como potenciais preditoras dos padrões de riqueza de morcegos frugívoros. Através de regressões *stepwise* múltiplas determinou-se que é o valor máximo anual do índice de vegetação de diferença normalizada, uma variável associada à produtividade, que melhor explica a variação da riqueza de morcegos frugívoros nas florestas Amazónicas. Regiões mais produtivas estão associadas a regiões com maior biomassa e diversidade de plantas, permitindo quer a existência de populações com maior número de efectivos – o que reduz o risco de extinção –, quer a coexistência de um maior número de espécies através da disponibilização de mais nichos ecológicos para os morcegos.

A teoria de conservação do nicho procura explicar como a ecologia e o clima actuam sobre os processos evolutivos e biogeográficos, baseando-se na hipótese de que a maioria das componentes do nicho fundamental são conservadas ao longo da história evolutiva das espécies. No capítulo 6, à luz da história conhecida da especiação e dispersão das famílias extantes de morcegos que ocorrem no continente americano, procurou-se testar algumas predições ao abrigo desta teoria. Testou-se se, em média, a riqueza de morcegos e a riqueza

de taxa evolutivamente basais são maiores em regiões cujas condições ambientais são mais próximas daquelas que caracterizaram o nicho ancestral do grupo. Em seguida, comparou-se a correlação espacial entre a riqueza total e a riqueza dos taxa basais e derivados, já que, se a conservação do nicho determina o padrão latitudinal da riqueza, então este padrão deveria ser determinado pela distribuição dos taxa mais basais. Para tal, utilizaram-se mapas de distribuição de 305 espécies de morcegos que ocorrem no continente americano; a idade evolutiva foi calculada contando o número de nodos que separa uma espécie da raiz de uma filogenia molecular disponível na literatura e que engloba uma percentagem muito significativa das espécies de mamíferos extantes. Os padrões de riqueza e de idade descritos foram modelados com base em modelos aditivos generalizados. Tal como ocorre em muitos outros taxa, a riqueza de espécies de morcegos aumenta dos pólos para o equador, embora numa família, Vespertilionidae, o pico da riqueza se encontre na região temperada. Contudo, a teoria de conservação do nicho apenas explica parcialmente os padrões encontrados para a idade dos taxa, sendo necessária a inclusão de outros factores explicativos, tais como diferenças latitudinais na taxa de evolução molecular, competição, ou a existência de mais oportunidades ecológicas nos trópicos.

A informação recolhida para esta dissertação permitiu conhecer melhor os mecanismos que regulam os padrões de diversidade e abundância de morcegos a diferentes escalas e determinar as implicações para a conservação resultantes deste conhecimento. Alguns dos resultados e conclusões poderão ser extrapolados para outros grupos animais.

Palavras-chave: Amazónia, Chiroptera, diversidade, ecologia de comunidades, igapó, macroecologia, morcegos, neotrópicos, terra firme, várzea

Abstract

Bats are the second more diverse mammalian order, reaching their taxonomic and ecological diversity peak in the neotropics, where they play key ecological roles. In spite of this, the factors that affect the distribution, diversity and abundance of bats at different spatial and temporal scales are still poorly known. This dissertation focused on the analysis of such factors. For the study of factors acting at local scales the structuring of bat assemblages of Central Amazonian forests was analysed. These assemblages are subject to great spatial and temporal environmental heterogeneity, because some forests endure seasonal flooding by waters with distinct nutrient content. It was demonstrated that flooding and floodwater nutrient load are determinant in the structuring of bat assemblages, with inundation constraining species composition by affecting the availability of niches, and water nutrient load influencing species abundance. These assemblages show vertical stratification associated to the diet and foraging behaviour of the species, and this occurs even within forests with lower canopy heights. Resource seasonality forces bats to make important eco-physiological adjustments, affecting their activity levels, body condition and reproduction. The results underline the importance of maintaining the mosaic of natural habitats of lowland Amazonia. At a regional scale it was shown that the conversion of energy into food available, *i.e.* productivity, explains the patterns of frugivore bat richness in Amazonian forests. The applicability of obtaining correlates of bat species richness from multitemporal remote sensing was also demonstrated, which has a direct application in conservation planning. Finally, in a continental context, it was analysed if the latitudinal diversity patterns of New World bats are explained by the niche conservatism theory. It was shown that the geographical patterns in the evolutionary age of bat taxa are better explained by alternative theories, such as latitudinal differences in rates of molecular evolution or the existence of more diverse ecological opportunities in the tropics.

Key-words: Amazonia, bats, Chiroptera, community ecology, diversity, igapó, macroecology, neotropics, terra firme, várzea

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Chapter 1

General introduction

1 General introduction

1.1 Bat diversity and ecology

Bats, order Chiroptera, are a very good taxon for investigating how patterns in the distribution, abundance, and diversity of species are influenced by abiotic and biotic environments, a central problem in community ecology. This because bats are a very diverse group, comprising approximately 1100 extant species, which makes them second only to rodents in terms of mammalian diversity (Koopman 1993; Altringham 1996; Hutson *et al.* 2001; Wilson & Reeder 2003; Simmons 2005).

The Chiroptera are usually divided into two distinct suborders based on paleontological and morphological data: the Megachiroptera, with about 200 species of fruit- and nectar-feeding bats, commonly designated as flying foxes and restricted to tropical and sub-tropical areas of the Old World; and the Microchiroptera, comprising all the remaining species that include the echolocating and usually smaller bats occurring in both the Old and the New World. This traditional division has been somewhat contested by recent phylogenetic studies that place the Megachiroptera in the same group with the rhinolophid microbats, separated from all the remaining species (Springer *et al.* 2001; Hutcheon & Kirsch 2004; Van den Bussche & Hoofer 2004; Teeling *et al.* 2005).

Bats can reach high levels of local (alpha) diversity and, in tropical regions, more than 100 species may coexist in the same site (Voss & Emmons 1996). No other group of mammals has ever reached this level of alpha diversity (Patterson *et al.* 2003). This is partially possible because they show not only taxonomic diversity, but are also ecologically more diverse than any other group of terrestrial mammals (Patterson *et al.* 2003).

As the world's only true flying mammals, bats developed several morphological and sensory adaptations that allowed them to exploit a varied range of habitats and food resources (Kalko 1997). Consequently, they are widely distributed and found throughout the World, except in

Polar regions, some deserts and remote oceanic islands (Altringham 1996; Hutson *et al.* 2001).

Flight also seems to have contributed to their unusual life-histories. In fact, despite their small size, bats have life-history traits generally attributable to larger species: they develop and reproduce slowly and live extended lives (Barclay & Harder 2003). In fact, flight, together with nocturnality, may have allowed a reduction in the vulnerability to some environmental hazards and, consequently, in the mortality rates of bats (Partridge & Barton 1993; Holmes & Austad 1994).

1.1.1 New World bats: a specially diverse group

Bats reach their diversity peak in the New World, especially in the neotropics. Indeed, New World bats are highly specious with about 300 species belonging to nine of the 18 extant families of bats (Koopman 1993): Emballonuridae (20 species in the New World), Furipteridae (two species), Molossidae (29 species in the New World), Mormoopidae (eight species), Natalidae (five species), Noctilionidae (two species), Phyllostomidae (145 species), Thyropteridae (four species), and Vespertilionidae (70 species in the New World).

Prompted by the diversity of foraging habitats and feeding modes and/or diets of bats found in the neotropics, Kalko (1997) proposed a guild concept for all bat communities (Table 1.1). All these guilds can be found in the New World, though bats of the temperate and boreal zones feed mostly on arthropods.

The ecological diversity found in Neotropical bats alone is higher than that of any mammalian group. In the neotropics, bats play key roles in forest dynamics and regeneration (Whittaker & Jones 1994; Kelm *et al.* 2008) because they are key pollinators and seed dispersers (Medellin & Gaona 1999; Korine *et al.* 2000; Patterson *et al.* 2003), also controlling insect populations (Cleveland *et al.* 2006).

Most of the investigation included in this dissertation was done in Central Amazonian rainforests, home to over 100 species of bats (Marinho-Filho & Sazima 1998). A characterization of those rainforests will be provided in section 1.3 of this introduction. In figure 1.1 some examples of the highly diverse Neotropical bats are presented.

Table 1.1 Bat feeding-guilds (following Kalko 1997).

	Habitat	Feeding mode	Diet
I	Uncluttered space	Aerial	Insectivore
II	Background cluttered space	Aerial	Insectivore
III	Highly cluttered space	Aerial	Insectivore
IV	Highly cluttered space	Gleaning	Insectivore
V	Highly cluttered space	Gleaning	Carnivore
VI	Highly cluttered space	Gleaning	Piscivore
VII	Highly cluttered space	Gleaning	Sanguinivore
VIII	Highly cluttered space	Gleaning	Frugivore
IX	Highly cluttered space	Gleaning	Nectarivore
X	Highly cluttered space	Gleaning	Omnivore

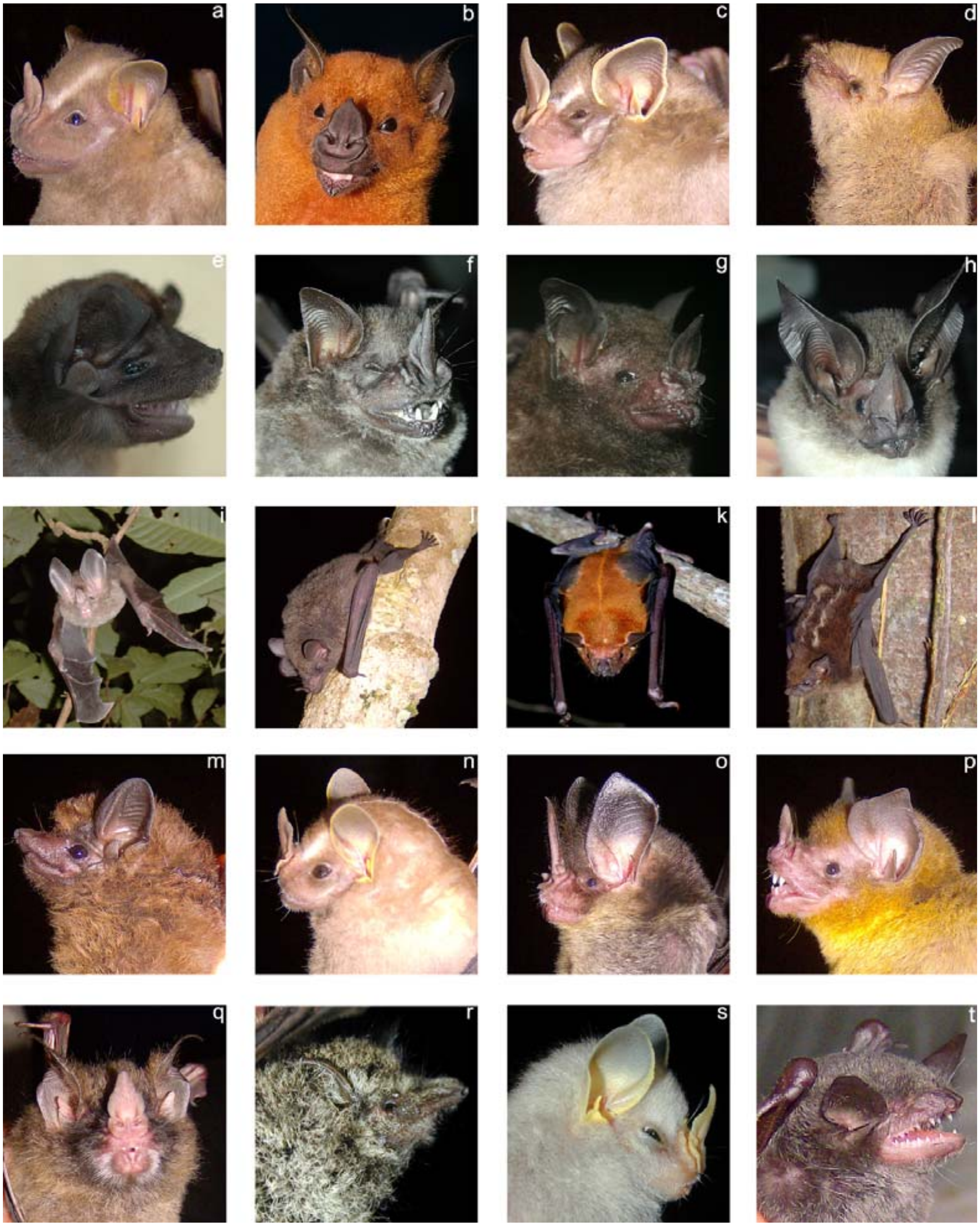

Figure 1.1 Some Neotropical bat species: a) *Artibeus lituratus,* b) *Phyllostomus hastatus,* c) *Artibeus gnomus,* d) *Centronycteris maximiliani,* e) *Molossus molossus,* f) *Artibeus obscurus,* g) *Carollia perspicillata,* h) *Lophostoma silvicola,* i) *Chrotopterus auritus,* j) *Glossophaga soricina,* k) *Noctilio leporinus,* l) *Saccopteryx bilineata,* m) *Peropteryx macrotis,* n) *Platyrrhinus helleri,* o) *Mimon crenulatum,* p) *Lampronycteris brachyotis,* q) *Glyphonycteris daviesi,* r) *Rhynchonycteris naso,* s) *Mesophylla macconnelli,* and t) *Myotis albescens.* All photos by Maria João Pereira / João Tiago Marques except *N. leporinus* from www.faune-guadeloupe.com.

1.2 Factors affecting the distribution, diversity and abundance of bats: a matter of scale?

In recent years, there have been significant advances in the knowledge of both the patterns and processes related to the distribution, abundance, and diversity of species in biological communities (Gaston 2000; Gaston *et al.* 2008). Nowadays the structure of biological communities is considered as a product of factors that can be divided into two major groups: (i) contemporary environmental conditions, including local and regional physical conditions, and interactions among species, and (ii) historical variations in environmental conditions and associated processes such as dispersal, speciation, migrations, and extinction (Rosenzweig 1995; Whittaker *et al.* 2007).

Despite the great diversity of bats, their wide distribution and high abundance in some regions, the factors that influence bat community structure and biogeographical patterns are still poorly studied, but methodological advances, such as the development of more sensitive ultrasonic bat detectors and the miniaturization of radio tags, have promoted investigation on various new aspects of bat ecology (see Kunz & Parsons 2009 for a review). It is becoming increasingly clear that the patterns and processes observed in local bat communities result not only from local mechanisms – *e.g.* competition (Moreno *et al.* 2006) and vegetation structure (Mancina *et al.* 2007) – but also from processes operating at larger spatial scales – *e.g.* habitat fragmentation (Meyer & Kalko 2008).

On the other hand, the spatial structure of groups of communities within regions also seems to result from the union of local and regional processes. This is the basis for the metacommunity concept (Leibold *et al.* 2004; Leibold & Miller 2004; Holyoak *et al.* 2005); this paradigm integrates within-community phenomena, such as biotic interactions and environmental tolerances, with larger-scale phenomena, such as dispersal. Stevens *et al.* (2007) suggested that the spatial heterogeneity found in bat species composition among communities within Paraguay was the result of affinities between bats and habitat characteristics, regulated by the integration of sites via dispersal. Indeed, as bats are highly mobile, dispersion allows sites within regions to be integrated (Willig & Moulton 1989; Stevens & Willig 1999; Bernard & Fenton 2003).

So, when studying patterns in bat community structure, and in any biological taxa for that matter, is crucial to define the scale of analysis – local (within a site), regional (among sites in a region), or geographical (among regions) – because scale will have a strong influence on the determination of the explanatory factors (Begon *et al.* 2006). It should be noticed, however, that the question of scale is complex and that the limits of each class are not always obvious.

1.2.1 Local scale

Patterns of composition and diversity in bat communities have been associated with several biological and physical factors acting at local scales. Niche partitioning and competition are probably the best studied of these biological factors (*e.g.* Stevens & Willig 2000; Aguirre *et al.* 2002; Delaval *et al.* 2005). Moreno *et al.* (2006) demonstrated that species diversity in local communities is shaped by competition among ecomorphological similar species. They suggest that as bat species richness in Neotropical bat ensembles increases, the interspecific morphological distance decreases while the volume of the morphological spaces of the total set of species increases (the ‘‘volume-increasing mechanism’’, Ricklefs & Schluter 1993; Ricklefs & Miles 1994).

This pattern, in turn, relates to the simple model of species richness presented by Begon et al. (2006): for certain values of average niche breadth and niche overlap, a given community will contain more species the more the resources available for that community. The influence of vegetation complexity and habitat/resource diversity on bat species richness locally is then straightforward: spatially heterogeneous conditions will provide a greater diversity of potentially suitable niches for the array of species present. In fact, Aguirre (2002) found higher levels of bat diversity in Bolivian savannas’ forests than in grasslands because they provide more niches, both in terms of feeding areas and roosting sites; Zortea and Alho (2008) suggested that bat community composition mirrored the composition of local plant assemblages, again supporting the idea that the distributional patterns of resource diversity are an important factor shaping bat assemblages.

Other local processes, such as environmental variability, have been proven to affect the structure of bat communities, especially when related to resource productivity. At local scales, the species-energy hypothesis suggests that the amount of available solar energy and water determines the levels of productivity, setting the limits to the number of species present in a given system. It is generally accepted in the literature that there is an unimodal relationship between productivity and species diversity at local scales due to competitive exclusion (Grime 1973; Waide *et al.* 1999; Mittelbach *et al.* 2001; 2007). The explanation lays on the principle that species richness would increase with productivity at low levels, but then decrease at high levels of productivity because it would lead to high rates of population growth and, consequently, to competitive exclusion among similar species. However, a meta-analysis conducted by Mittelbach *et al.* (2001) based on 171 studies found positive and unimodal relationships between species richness and productivity in vascular plants, whereas in animals, positive, negative, and unimodal relationships were common at most geographical scales and no particular pattern predominated. In bats, Tschapka (2004) proposed energy density as a major niche dimension that influences the structure of nectar-feeding bat guilds by restricting the access of the species to given habitats.

In chapter 2 we revisit several of these questions by investigating the impact of environmental seasonality and nutrient availability on the structuring of bat communities in Amazonian forests under different seasonal flooding regimes; the relevance of maintaining a mosaic of natural habitats for the regional (gamma) diversity is also underlined.

Bats are also affected by another form of habitat heterogeneity that does not occur at ‘horizontal scales’. Indeed, vertical stratification has been considered an important characteristic of bat communities in tropical forests (Bernard 2001; Kalko & Handley 2001; Shanahan & Compton 2001; Henry *et al.* 2004; Hodgkison *et al.* 2004a). In general, the literature indicates that the composition of bat assemblages differs between understorey and canopy strata and that the differences in the spatial distribution of the species are explained by diet, foraging behaviour, roost-site selection, and wing morphology. In Central Amazonian floodplain forests, due to long lasting seasonal floods, the height of trees is usually lower than in the highly structured unflooded forest. Chapter 3 addresses how this affects the patterns of vertical stratification in bat assemblages.

The patterns of bat species abundance and distribution may also vary with the seasonality of food resources. Bat species richness and/or abundance may be higher at sites with high productivity, but what are the consequences if one site is very productive in some parts of the year but suffers seasonal drops in food availability? Flight ability gives bats additional routes to deal with food scarcity: searching for food within larger home-ranges (Hodgkison *et al.* 2004b; Chaverri *et al.* 2007), and migrating following peaks of food production. This seems to occur in the northern populations of nectar-feeding bat, *Leptonycteris curasoae*, that follow the flowering events of columnar cacti along Mexico (Fleming & Nassar 2002; Penalba *et al.* 2006), and with the straw-colored fruit bat, *Eidolon helvum*, that travels hundreds of kilometres in Austral Africa following peaks of fruit production (Richter & Cumming 2006). There are other probable physiological consequences of seasonal shifts in food availability: the reproduction cycle may adjust to the availability of food (Racey & Entwistle 2000), and there may be changes in corporal condition (Ceballos *et al.* 1997; Zahn *et al.* 2007). In chapter 4 the ecophysiological responses of frugivorous bats to the seasonality of fruit production in Central Amazonian forests are investigated.

Climatic variables, such as temperature and rainfall, topographic relief and geologic types, distance to rivers and occurrence of fire are other variables that can influence the structuring of bat communities (*e.g.* Lumsden & Bennett 1995; Ports & Bradley 1996; Holloway & Barclay 2000; Milne *et al.* 2005; Lloyd *et al.* 2006).

1.2.2 Regional and continental scales

At macro-scales, studies on the spatial and temporal variation in bat communities, and in biological communities in general, are often based on the number of species observed or estimated to occur in an area – species richness. This results from widespread recognition of the significance of the species as a biological unit, but mainly from the practical issues of the ease and magnitude of data acquisition (Gaston 2000). Because patterns of species richness are often well known, there have been some ambitious approaches to develop a single unifying theory that could relate local, regional and global patterns in species richness to one single explanatory factor, such as the species-energy hypothesis (Currie 1991) and the metabolic theory of ecology (Brown *et al.* 2004), but none is universally accepted.

The latitudinal diversity gradient is the largest scale known pattern in ecology (Hawkins *et al.* 2003). The decrease in the number of species from tropics to poles seems to be persistent along the history of biodiversity (Stehli *et al.* 1969; Crane & Lidgard 1989). Bats are no exception to this pattern (Fleming 1973; Kaufman 1995; Willig & Lyons 1998; Hutson *et al.* 2001). However, though latitude can be seen as a major explanatory factor of that global pattern in bat richness, it is surely only a surrogate for other environmental variables (Patten 2004).

It is now widely accepted that at larger spatial scales species richness is affected by contemporary factors, such as productivity and climate (Ruggiero & Kitzberger 2004; Whittaker *et al.* 2007). These interact with historical factors, such as environmental variations, glaciations, tectonic uplift, sea-level change (O'Brien 1993; 1998; McGlone 1996; Kerr & Packer 1997; Francis & Currie 2003; Hawkins *et al.* 2003; Whittaker *et al.* 2007), speciation rates (Cardillo 1999) and dispersal (Richter-Boix *et al.* 2007; Stevens *et al.* 2007).

Ulrich *et al.* (2007) indicated that a significant percentage of European bat species richness was explained by temperature. This links to a version of the species-energy theory relevant in regional and geographical scales, which is considered one of more parsimonious explanations for the latitudinal gradient in species diversity – the ambient-energy hypothesis (Turner *et al.* 1996; Hawkins *et al.* 2003). This hypothesis suggests that it is the amount of energy directly available in the systems together with the availability of water that limits species richness. It is suggested that high temperatures lead to faster individual growth rates and to shorter generation times, speeding the rate of molecular evolution (Rhode 1992; Allen *et al.* 2006; Wright *et al.* 2006).

Alternatively, the thermoregulatory load hypothesis states that high temperatures create better conditions for endotherms to develop larger populations that are less vulnerable to extinction because they can spare the investment of keeping warm to grow and reproduce (Turner *et al.* 1988). But high temperatures by itself are not enough; for instance, deserts have high levels of available energy, but low species richness, of bats and overall. Then, water is also a limiting factor.

The other version of the species-energy theory described for local scales – productivity – also applies to macro-scales. It suggests that the amount of available solar energy and water sets limits to the richness of a given system (Wright 1983; Hawkins *et al.* 2003; 2005) because high-productivity areas have more resources available and can sustain larger and more viable populations; this reduces the extinction risk, and allows species to specialize on few food types, narrowing the niche breadths and promoting the coexistence of more species (Vazquez & Stevens 2004; Evans *et al.* 2005). However, at macro-scales the productivity-richness relationship is usually described as increasing monotonically (Wright *et al.* 1993; Gaston 2000; Chase & Leibold 2003; Evans & Gaston 2005).

In a study with South American mammals, Ruggiero and Kitzberger (2004) found that bat species richness was more affected by direct energetic constraints (minimum temperatures) than by its transformation into available resources. These authors suggested that it is bat sensitivity to cold that controls the latitudinal gradient in species richness. However, should this relationship be the same in thermo-stable regions? Since temperatures are relatively stable and homogeneous within the Amazon river basin, in chapter 5 we investigate if, at the scale of that region, the ambient-energy hypothesis remains the best explanation for the variation in bat species richness, or if productivity variables describe better that variation.

Niche conservatism is a recently proposed hypothesis that provides an explanation of how ecology and climate act on evolutionary and biogeographical processes (*e.g.* speciation, dispersal, extinction) to determine patterns of species richness (Wiens 2004; Wiens & Donoghue 2004; Wiens & Graham 2005). This theory states that most of the aspects of the fundamental niche, which describes the abiotic conditions in which a species is able to persist (*sensu* Hutchinson 1957), are conserved over long evolutionary time scales. Species would then tend to retain their ancestral ecological characteristics because the rate of adaptation to conditions outside that fundamental niche is slower than the extinction process (Peterson *et al.* 1999). So, according to this theory the latitudinal gradient in species richness would be due to the fact that most species originated at a time when most of the globe had similar warm conditions, so they had more time to speciate under those conditions; today's pattern would reflect a contraction of the range of the species into regions where warmer climates persist (Hawkins *et al.* 2006). There are fewer species in temperate and boreal regions because they had less time to speciate, and they are in average more derived because they had to gain adaptations to survive colder temperatures.

According to Teeling *et al.* (2005), all bat lineages probably radiated within a narrow time frame between 52 to 50 million years ago (Mya), following the Paleocene-Eocene Thermal Maximum, a sudden global warming event resulting in a 7° C rise in mean annual temperature.

However, the colonization of the New World by bats seems to result from several radiation phenomena. The Emballonuroidea (family Emballonuridae) and Vespertilionoidea (families Vespertilionidae, Molossidae and Natalidae) are suggested to have a Laurasian origin. Teeling *et al.* (2005) suggested that the Emballonuroidea arrived to South America either via a 'vegetational raft' sailing from Gabon to Brazil or 'stepping-stones' spanning the Atlantic, occurring at about 30 Mya. The exact geographical origin of the Vespertilionidae lineage is still equivocal and so is its dispersal route in the New World. The Noctilionoidea (families Phyllostomidae, Mormoopidae, Noctilionidae, Furipteridae, and Thyropteridae), on the other hand, seem to have originated in Gondwana, most probably in South America, with clades originating between 47 and 37 Mya. So, the different origins of the lineages in the New World may have had consequences on the present distribution of species richness within the different families. In chapter 6 we describe the latitudinal patterns in species richness and in the age of the taxa of New World bat families and test if those patterns are consistently explained by the niche conservatism hypothesis.

There are several other theories to explain macro-scale variations in species-richness. Though they are not object of analysis in this dissertation, there are at least two theories that have been largely debated and, for that reason, deserve particular attention. They depend on spatial and areal features to explain the latitudinal gradient in species richness. The geographical area hypothesis (Terborgh 1973) advances area as the main cause of latitudinal gradients in species richness. The greater area of tropical zones would allow species to have larger ranges. This would promote larger population sizes, and consequently increased rates of allopatric speciation and lower extinction rates (Rosenzweig 2003), leading to an increased number of species. The main critique to this hypothesis is that ecogeographic tropical zones do not seem to be larger than the extra-tropical ones (Gaston & Blackburn 2000; Willig & Bloch 2006).

The mid-domain effect theory (Colwell & Hurtt 1994; Colwell & Lees 2000; Colwell *et al.* 2005) was based on simulation procedures which indicated that if the latitudinal ranges of species were shuffled within the geometric constraints of a bounded biogeographical domain, their ranges would show a tendency to overlap more toward the centre of the domain than towards the bordering areas, creating a mid-domain peak in species richness. Yet, this theory is highly controversial mainly because there is little correspondence between the predicted and the observed latitudinal richness of several taxa (Hawkins & Diniz-Filho 2002; Diniz-Filho *et al.* 2004; Kerr *et al.* 2006).

1.3 Rainforests of the Amazon basin

1.3.1 History and general characterization

The Amazon river basin is home to the largest rainforest on Earth covering about 40% of the South American continent. It comprises parts of Brazil, Bolivia, Colombia, Ecuador, French Guiana, Guyana, Peru, Suriname, and Venezuela. The Amazon river carries the world's largest volume of water, and in length is second only to the Nile. The river has approximately 1100 tributaries of which the Negro, Solimões and Madeira are some of the more important. The Amazon river basin is constituted by a mosaic of ecosystems that include rainforests, deciduous forests and savannas, but here we only characterize the Central Amazonian rainforests, which are the focus of most of our work.

The Amazon river system is the support of the rainforests and has been a key factor in their evolution and maintenance. The paleo-Amazon river probably formed about 200 Mya in Gondwana. At that time it flowed westwards to the Pacific. When Gondwana split about 140 Mya, South America separated from Africa (Dietz & Holden 1970) and eventually collided into the Nazca plate, causing the uprise of the Andes (Jordan *et al.* 2001). In the early Miocene, a large part of the drainage of Northwest Amazonia was directed northward along the paleo–Orinoco river system to a delta in Lake Maracaibo. The uplift of the Eastern Cordillera in the late middle Miocene probably resulted in the first development of the Amazon river, although still without a connection to the Atlantic (Hoorn *et al.* 1995). Probably in the Early Tertiary, the waters worked through the sandstone and much of the drainage systems was reversed, directing the river to flow eastwards (Sena Costa *et al.* 2001): the Amazon emerged as a transcontinental river some 11 Mya and developed into its current shape almost 2.4 Mya (Figueiredo *et al.* 2009).

After that the ocean level receded and exposed the Central American isthmus, facilitating the migration of terrestrial vertebrates between North and South America. Miocene Ice Ages caused a worldwide retreat in tropical forests (Servant *et al.* 1993); it is believed that ‘islands’ of forest were separated by savanna-like habitats and that this split promoted genetic differentiation between the species in different ‘island’ patches. When the ice ages ended, the forest patches joined and the area was then home for a great diversity of species. About 15000 years ago, sea level rose about 2 cm/year to at least 150 m (Haq *et al.* 1987; Irion *et al.* 1995; Hoorn 1996; Räsänen & Linna 1996). Again the Amazon valley was inundated because sedimentation rates in the riverbeds were not high enough to balance the rising water level, and a huge freshwater lake was probably formed; waters started to recede about 6000 years ago (Irion *et al.* 1995).

Today the Amazon river carries great loads of suspended sediment that give the water a muddy appearance, but its tributaries vary in terms of their sediment content, resulting in characteristic colours. Some, like the Solimões and the Madeira, receive turbid nutrient-rich water from the ice-melt and steep slopes of the Andes; these are known as white-water rivers. Others, like the Negro, carry nutrient-poor water coming from the forest plains; their water is darkly stained by organic compounds, and they are usually called black-water rivers. Finally, tributaries such as the Tapajós, Xingú and Branco, drain predominantly pre-Cambrian rocky areas of the highlands of Brazilian and Guayanan shield, where cloud forests may grow; these are called clear-water rivers because the water is crystal-clear most of the year.

In the Central Amazonian lowlands there are vast expanses of forest that remain flooded for much of the year. These flooded forests belong to two main types: the nutrient-rich várzea, seasonally flooded by white-water, and the oligotrophic igapó, seasonally flooded by nutrient-poor black-water (Prance 1979; Ayres 1993). These floodplain forests areas are embedded in a matrix of terra firme forests located in upland areas that never flood, and that are also nutrient-poor because they have long been deprived of alluvial sediments (Irion *et al.* 1997).

Central Amazonian forests, like most rainforests, are usually warm year round. According to Irion *et al.* (1997) the mean annual temperature is 26.6º C, the warmest months are from August to November while the coolest are from January to April, and daily variation in temperature is about 10º C, which is greater than the annual average variation. Once each year, in May or June, the temperature may fall below 20º C for a few days due to cold fronts coming from the Antarctic (Ayres 1993; Irion *et al.* 1997). Total annual rainfall averages 2100 mm but there is evidence for pronounced local differences in the distribution of the rainfall in the region (Irion *et al.* 1997). The precipitation is periodic with a rainy season from December to April and a dryer season from June to October (Irion *et al.* 1997). In the seasonally flooded forests, the high-water season usually coincides with the rainy season, though inundation is a consequence of both the rainfall and the ice-melt in the Andes. Seasonal water level fluctuates according to the location but usually is around 10 m, though in some years it may reach up to 30 m. Flowering and fruiting peaks generally occur in the low- and high-water season, respectively (Rankin-De-Merona *et al.* 1992; Ayres 1993; Haugaasen & Peres 2006). The inundation patterns of Amazonian forests and the existing differences in the nutrient load of the flooding waters influence forest structure, floristic composition and tree phenology (Kubitzki 1989; Haugaasen & Peres 2005a;b; c; 2006).

Rainforests are characterized by a vegetative structure that consists of several vertical layers, usually overstorey, canopy, understorey, and ground (Figure 1.2). The canopy is the dense ceiling of leaves and tree branches shaped by closely spaced forest trees. The upper canopy is 30-40 m above the forest floor, but a few emergent trees may be at least 50 m tall in what is known as the overstorey. Below the canopy is a multiple leaf and branch area known as the understorey, of which the lowest part is the shrub layer. Ground vegetation is usually minimal and made up of lianas and tree seedlings. Epiphytes are plants that search sunlight at the canopy by using host trees for support. They are well adapted to the aerial environment and possess ways to gather nutrients from their surroundings. The hemiepiphytes develop in the canopy but grow long roots that eventually reach the forest floor.

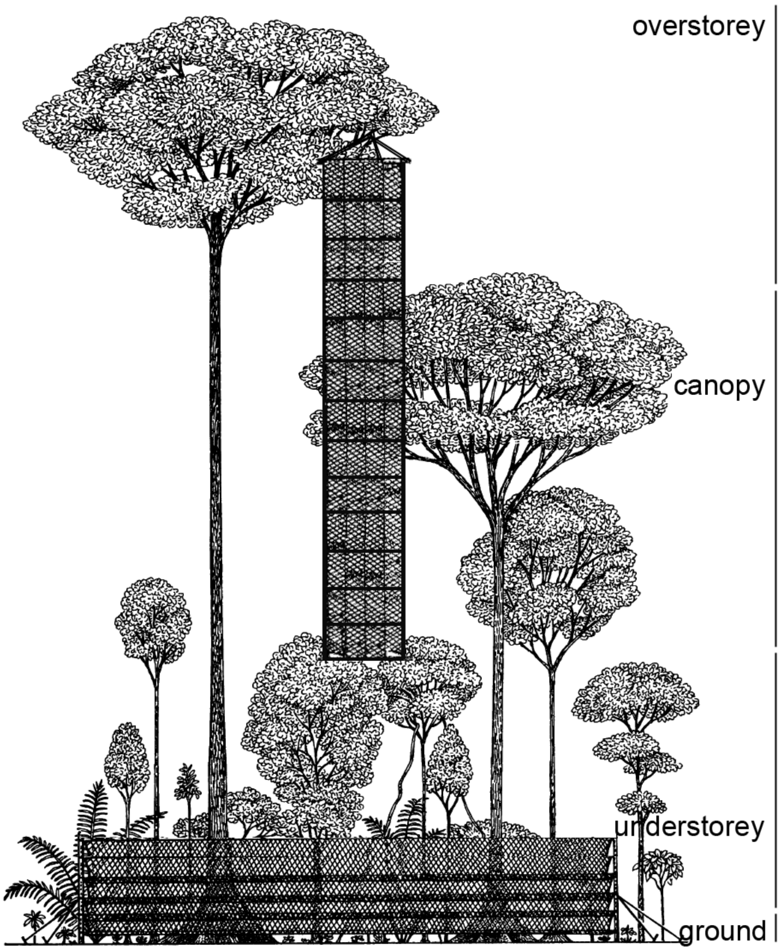

Figure 1.2. Vegetative structure of rainforests including the standard mist-net protocol used to capture bats in the canopy and understorey (adapted from Voss & Emmons 1996; vegetative profile after Duellman & Koechlin 1991).

1.3.2 Importance for bats

The Neotropical region is by far the most diverse region in the world for microchiroptera (Hutson *et al.* 2001). Amazonian rainforests may easily exceed 100 species on a regional scale (Marinho-Filho & Sazima 1998), while the highest number of species recorded locally is of 86 species in the Iwokrama Forest, in Central Guyana (Lim & Engstrom 2001a; b).

Due to the structural complexity of the rainforest vegetation, bats were able to occupy a large number of available niches. Different species and guilds use space differentially as already indicated in Table 1.1, and show patterns vertical stratification (Bernard 2001; Kalko & Handley 2001).

Studies done in several Amazonian rainforests (*e.g.* Bernard *et al.* 2001; Lim & Engstrom 2001a; Bernard & Fenton 2002; Sampaio *et al.* 2003; Barnett *et al.* 2006) indicate that the bulk of bat diversity is composed by species of the Phyllostomidae. This is indeed the most specious family in the region; however, this conclusion partly results from the fact that most of studies were based on mist-netting surveys, which underestimate the diversity of other bats groups, especially the open-space aerial insectivores. In fact, over 50% of all bats mist-netted in mature Neotropical forests may belong to just a few species (usually *Carollia perspicillata*, *Glossophaga soricina*, *Artibeus lituratus*, and *Artibeus planirostris*), which are easily captured with mist-nets.

1.4 Aims and outline of the dissertation

The overall objective of this dissertation is to analyse some of the factors that affect the distribution, diversity and abundance of bats at different spatial and temporal scales. In particular, at a local scale we chose the bat communities of Central Amazonian forests because they are subject to great spatial and temporal environmental heterogeneity and also because the local abundance of many species increases the power of statistical tests. When appropriate, the conservation implications of the findings are also described in each chapter.

The specific aims of each chapter are described below, along with the main methodological approaches followed.

In *Chapter 1* a general introduction to bat diversity and ecology is presented and the major factors that can affect the structure of bat communities in local and geographical scales are outlined, linking to the specific objectives of chapters 2 to 6. As most of our work was done in a Central Amazonian rainforest, a brief description of their history, climate and hydrology is also presented.

Chapter 2: Structuring of Amazonian bat assemblages: the roles of flooding patterns and floodwater nutrient load

Because bats are one of the most abundant and diverse vertebrate groups in Neotropical forests, playing key roles in tropical forest ecosystems, it is very important to understand the structure of Neotropical bat assemblages, and to determine the factors that shape them. The main aim of the study described in this chapter was to determine the roles of inundation and water nutrient load in the structuring of Amazonian bat assemblages. Bat assemblages were sampled with mist nets in central Brazilian Amazonia, across a mosaic of várzea, igapó, and terra firme forests in the low and high-water seasons, and it was investigated how the seasonality of flooding and the nutrient content of the water influence the abundance of bats, species composition, species diversity and their guild level structure.

The statistical analysis included a wide range of methods to examine how bat assemblages varied between seasons and forest types and to allow comparisons with previous studies. These included descriptive statistics, such as individual rarefaction curves and diversity indexes, ordination analyses to describe the overall assemblage patterns, and parametric and non-parametric tests to investigate the existence of significant differences in assemblage structure between seasons and forest types.

Chapter 3: Vertical stratification of bat assemblages in flooded and unflooded Amazonian forests

In this study the vertical stratification of bat assemblages in Neotropical flooded forests (igapó and várzea) and in adjacent terra firme forests was analysed. The main purpose was to test if the assemblages of bats using the understorey and canopy strata were different, and to determine which species tend to be associated with each stratum.

Species richness of the understorey and canopy was compared using individual rarefaction curves and an ordination analysis was used to create a graphical representation of the vertical stratification of the bat communities within each of the three forest types. The association to the canopy or understorey stratum was investigated in the more abundant species.

Chapter 4: Ecological responses of frugivorous bats to seasonal fluctuation in fruit availability in Amazonian forests

The main aim of this study was to determine if, in humid equatorial Amazonian flooded and unflooded forests, seasonal changes in fruit availability have eco-physiological impacts on frugivorous bats.

The low- and high-water seasons are known to correspond to periods of fruit abundance, so fruit abundance in terra firme, várzea and igapó forests in each season was measured, and it was investigated if bats shift habitats, change their activity levels, or suffer changes in reproductive activity and in body condition as a response to seasonal changes in food availability. A set of parametric and non-parametric approaches was used to examine those potential responses.

Chapter 5: Environmental correlates of bat species richness in Amazonian rainforests: the importance of primary productivity

The aim of this study was to determine which of the two versions of the energy hypothesis –

ambient-energy or productivity – better explains the patterns of frugivorous bat richness in the Amazon basin.

To achieve this objective, species richness was compiled for 22 lowland rainforest sites within the Amazon basin and 14 potential explanatory variables were extracted from high-resolution digital data. These included several climatic variables, such as temperature and precipitation, and also several productive-energy variables, such as net primary productivity, its correlates such as the Normalized Difference Vegetation Index (NDVI), or phenological variables extracted from NDVI time-series. The effects of environmental variables on bat species richness were investigated using multiple regression analyses; to avoid models with redundant and multicollinear data structures, we applied a forward stepwise selection procedure to the predictor variables.

Chapter 6: Niche conservatism and the latitudinal diversity gradient in New World bats

The aim of this study was to describe the latitudinal gradients in species richness and in the evolutionary age of the species of the nine extant families of New World bats, and to test if those latitudinal patterns, under the light of the known evolutionary history of the Chiroptera, can be explained by the niche conservatism hypothesis.

Maps of the ranges of New World bat species were obtained and rasterized to estimate the species richness in 1° grid cells. Each bat species was assigned to a root distance, a proxy of the age of the taxa, obtained from a published mammal phylogenetic tree resolved to the species level. The mean root distance for each cell of the grid was calculated and generalised additive models were used to determine the direction and the significance of the relationship between species richness and latitude, and the age of the taxa and latitude for the order Chiroptera and for each New World bat family. Spatial autocorrelation was also tested. The patterns found were then analysed under the niche conservatism hypothesis.

A general discussion is presented in *Chapter 7*, in which the most important results are discussed and integrated. The general conservation implications of the results obtained in the previous chapters are presented, and a prospect for future work is made. Finally, the major conclusions are outlined.

Chapter 2

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

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

2.1 Abstract

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. 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. 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. Nutrient-rich várzea forests had a bat biomass twice that of nutrient-poor igapó and unflooded forests. This difference was mostly due to a greater overall abundance of bats, but also attributable to a disproportionate higher abundance of large bodied bat species. 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.

2.2 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.

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. While 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 *et al.* 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 2005c), so they are also likely to play an important role in structuring animal communities, both at the local and landscape scales. While 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 2005a).

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 *et al.* 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.

While there is a fair number of studies on the structure of bat communities in Neotropical terra firme rainforests (*e.g.* Lim & Engstrom 2001a; 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.

2.3 Methods

Study area

The study was carried out around lake Amanã (2º37' S, 64º37 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 2350000 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 (Figure 2.1). Igapó forests occur mainly along the streams and margins of the lake, while most of the várzea forests are in the floodplain of the river Japurá.

Population density is quite low, with only about 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 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 meters. 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 2005c). The dominant trees belong to the families Sapotaceae, Lecythidaceae, Euphorbiaceae, Myristicaceae and Leguminosae, in particular Mimosidae, Caesalpinioideae and Faboideae, (pers. obs.; Ayres 1993; Souza 2006). Canopy height is between 15 m and 35 m with emergent trees reaching at least 50 m high (pers. obs.).

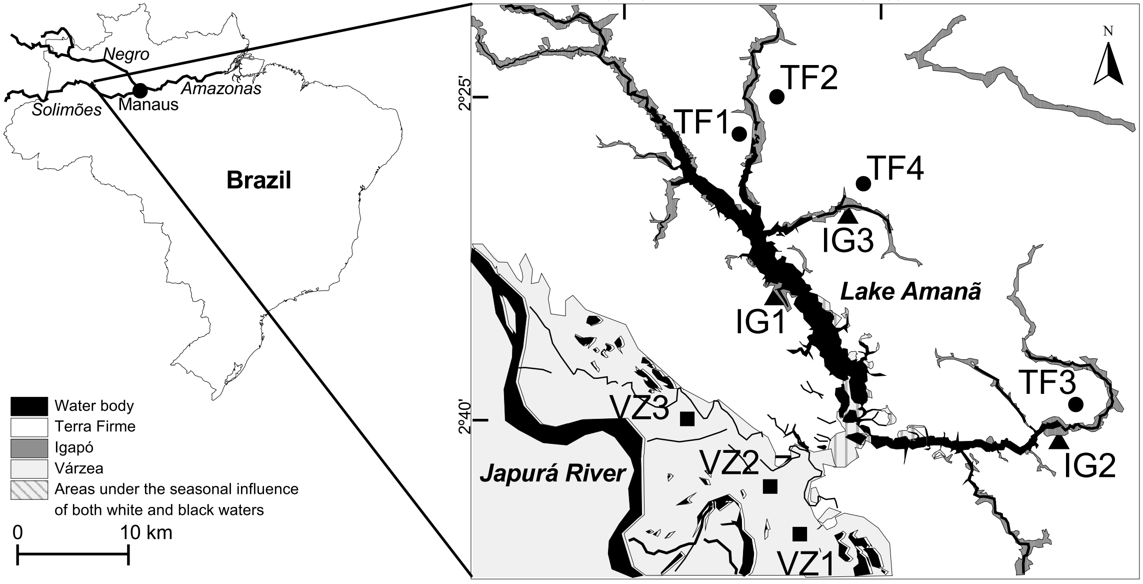

Figure 2.1 Study area and location of sampling stations (TF – terra firme, VZ – várzea, IG – igapó). Lake Amanã has mostly black water, but in the south it can temporarily receive white waters, creating an ecological transition zone. The distribution of the forest types is based on cartography by the Mamirauá Sustainable Development Institute and on satellite imagery.

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 (Figure 2.1). 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 x 12 m mist nets set at canopy level (17-35 m) and ten 12 x 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 18h and 24h, and were checked every 20 minutes. 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 2001a; Rex *et al.* 2008).

Data analysis

All bats captured were classified into guilds (Annex I) following Kalko (1997) and Schnitzler & Kalko (1998). Since the flooded habitats were not sampled at the canopy level during the high-water season, canopy data was used just for inventorying. All subsequent analyses were conducted solely with understorey capture data. We estimated species richness with the non-parametric 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. Contrarily to the Jackknife2 (and other richness estimators) this method estimates species richness for a sub-sample 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, 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 non-parametric 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 normalised per site in order 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 chi-square tests.

2.4 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 (Annex I). Total capture effort was 5346 net hours (1 net hour corresponds to one 12 m mist-net opened for 1 hour). 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, while 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 while 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 highest in terra firme (Figure 2.2). 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 < 0.001) (Figure 2.3). The *post-hoc* comparisons showed that it was higher in terra firme than in várzea and igapó (both P < 0.001), and higher in igapó than in várzea (P = 0.046).

Equitability also differed between habitats (P<0.001), and was significantly higher in both terra firme (P < 0.001) and igapó (P = 0.002) than in várzea. Capture rates and relative biomass were significantly different between habitats (both P < 0.001) (Figure 2.3).

Captures were higher in várzea than in terra firme and igapó (both $P < 0.001$). Biomass was also higher in várzea than in the two other forest types (both $P < 0.001$). In fact, the mean relative biomass in várzea was more than twice the value found for terra firme and igapó (Figure 2.3), 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 analyses of variance used in these comparisons.

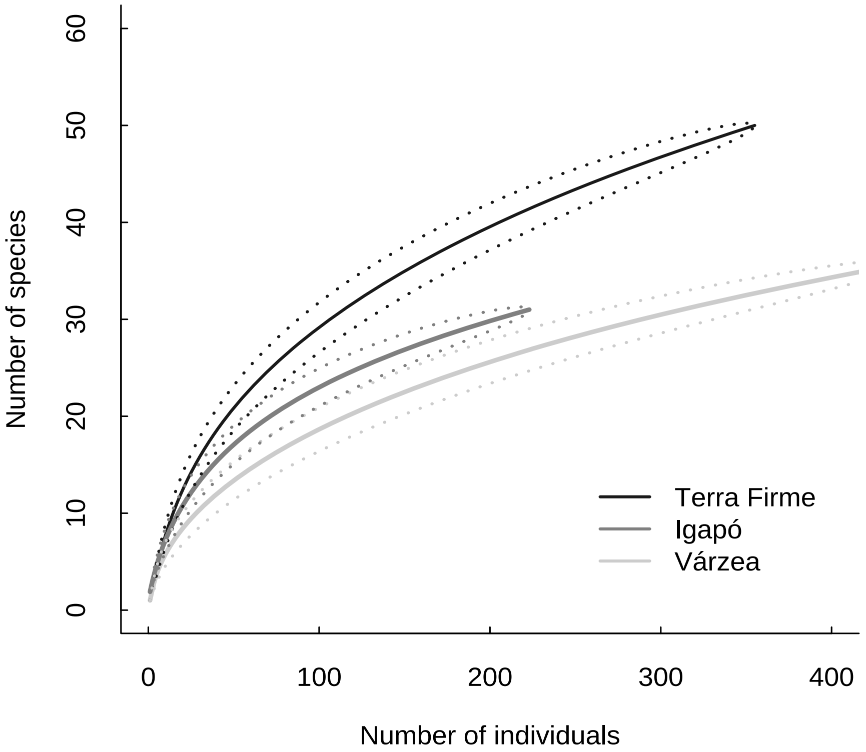

Figure 2.2 Individual-based Coleman species-rarefaction curves (solid lines) with 95% confidence intervals (dashed lines), based on mist-net captures for terra firme, várzea and igapó.

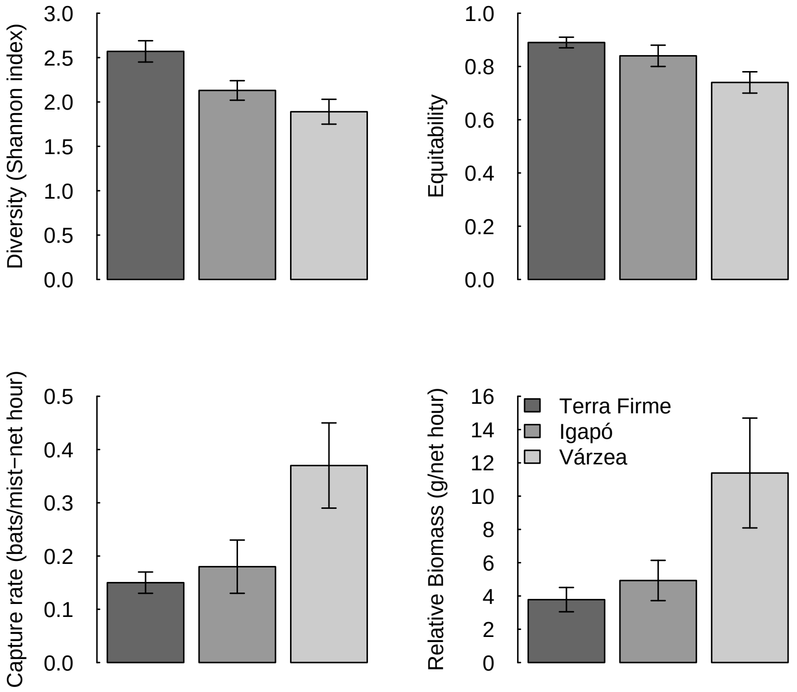

Figure 2.3 Diversity (Shannon index), equitability, capture rate and relative biomass by forest type (vertical lines correspond to 95% confidence intervals). Data was pooled among seasons because the patterns of between-habitat variation were consistent among seasons and there were no significant seasonal changes in the patterns of diversity, equitability, biomass and capture rates within forest types.

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 (Figure 2.4), in which forest sites were positioned according to their species composition. This underlines the strong influence of inundation distinguishing terra firme from both igapó and várzea, but also of the relevance of nutrient availability, which separates várzea from the nutrient-poor forest types. The ANOSIM confirmed that the difference between the assemblage structure of the three forest types was statistically significant, mainly due to differences between terra firme and the two seasonally flooded forests (Table 2.1).

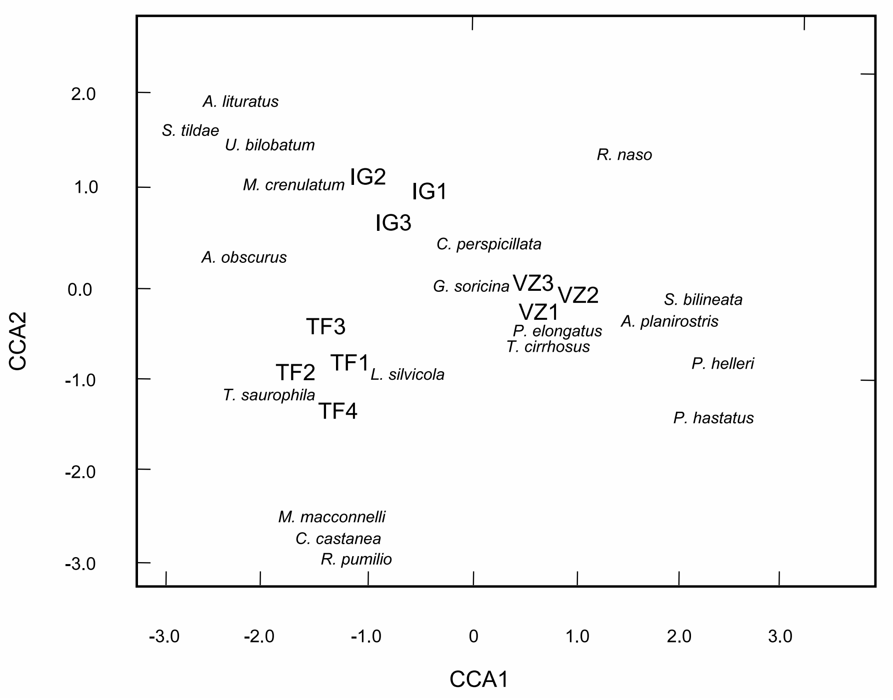

Figure 2.4 Biplot of the canonical correspondence analysis (sampling stations: TF – terra firme, VZ – várzea, IG – igapó). Total inertia=0.60; eigenvalues for constrained axes: CCA1: 0.19, CCA2: 0.04. Species matrix for species with total captures of 10 or more individuals. Since there was no significant seasonal variation in assemblage structure, data from both seasons were pooled.

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* = -0.19, *P* = 0.935) or within any of the forest types.

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 (Figure 2.5).

Table 2.1 Average dissimilarity values based on the Bray-Curtis similarity index on bat species and guilds between forest types.

Factor: Forest	Species			Feeding guilds		
	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^{ns}	0.21^{*}	0.35^{*}	0.22^{ns}
Terra firme and várzea	0.91^{**}	0.81^{*}	0.91^{*}	0.74^{**}	0.91^{*}	0.66^{*}
Igapó and várzea	0.06^{ns}	0.80^{ns}	0.85^{ns}	0.03^{ns}	0.81^{ns}	0.05^{ns}

**P < 0.01, *P < 0.05, ^{ns} P > 0.05

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. A. planirostris* had the strongest contribution to the dissimilarity between flooded and unflooded forests since 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 (Annex I). 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.

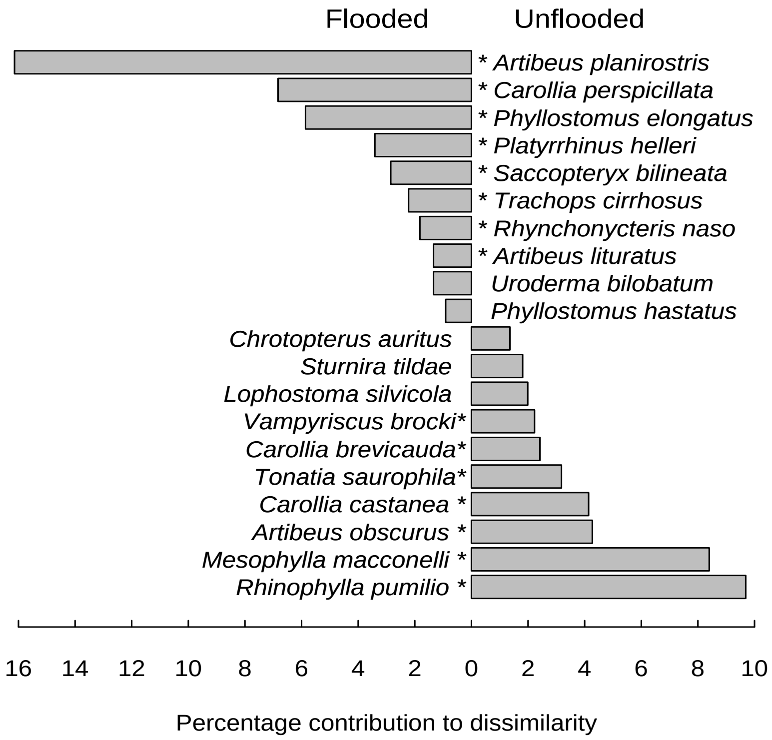

Figure 2.5 Species making the highest contributions (>1.5%) to assemblage dissimilarity between unflooded (terra firme) and flooded (várzea and igapó) forests. Asterisks indicate significant differences in the abundances between the habitats at α = 0.05.

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 2.1). This pattern was observed in both the low- and high-water seasons, though 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 (Figure 2.6): 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, while 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 analyses of variance used in these comparisons.

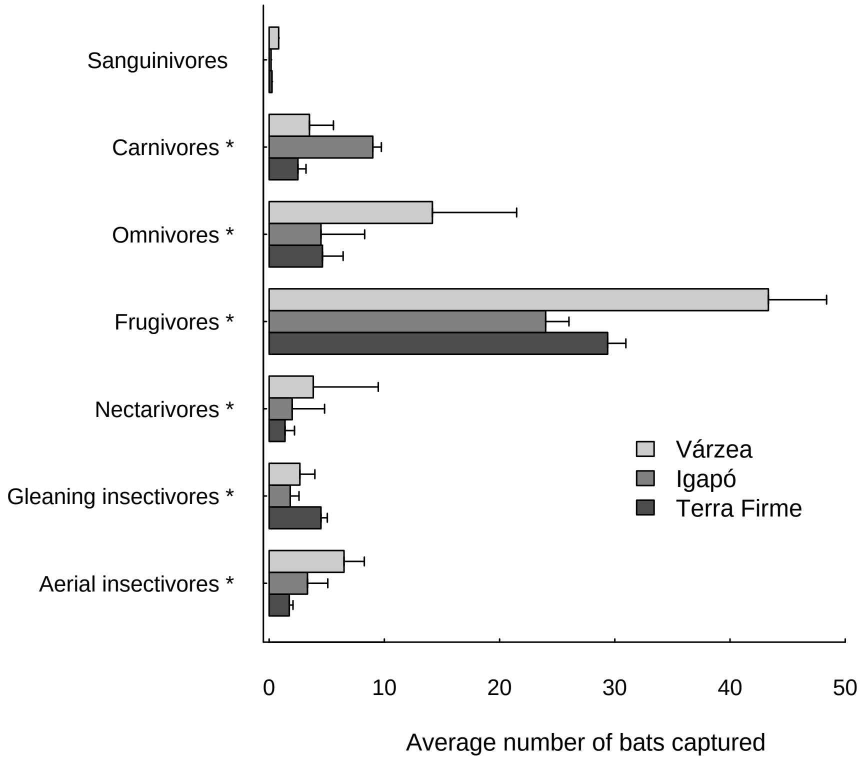

Figure 2.6 Average number of captures by feeding guilds in the three habitats. Lines represent 95% confidence intervals and asterisks significant differences between habitats at α = 0.05. The guilds of aerial insectivores were here clumped in just one group due to the low number of captures.

2.5 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 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 (Figure 2.1; 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 *et al.* 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 *et al.* 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 *et al.* 1989; Bernard 2001), which may be unavailable or scarce in seasonally flooded forests. *C. 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 1982; Geiselman *et al.* 2002). 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 (2005a) 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 can not 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 done 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 floodwater 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 the 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 *et al.* 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 2005a), 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 (2000) 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 (Henderson & Crampton 1997; Haugaasen & 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).

Chapter 3

Vertical stratification of bat communities in flooded and unflooded Amazonian forests

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3 Vertical stratification of bat communities in flooded and unflooded Amazonian forests

3.1 Abstract

Tropical rainforests usually have multiple strata which results in a vertical stratification of ecological opportunities for animals. We investigated if this stratification influences the way bats use the vertical space in flooded and unflooded forests of the Central Amazon. Using mist-nets set in the canopy (17 to 35 m high) and in the understorey (0 to 3 m high) we sampled four sites in upland unflooded forests (terra firme), three in forests seasonally flooded by nutrient-rich water (várzea), and three in forests seasonally flooded by nutrient-poor water (igapó). Using rarefaction curves we found that species richness in the understorey and canopy were very similar. An ordination analysis clearly separated the bat assemblages of the canopy from those of the understorey in both flooded and unflooded habitats. Some species had a strong and significant preference for either the canopy or understorey, but others used the two strata extensively. Gleaning carnivores were clearly associated to the understorey, whereas frugivores were abundant in both strata. Among the frugivores the Carollinae and some Stenodermatinae were understorey specialists, but several Stenodermatinae mostly used the canopy. The first group includes mainly species that in general feed on fruits of understorey shrubs, and the second species that feed on figs and other canopy fruits. We conclude that vertical stratification in bat communities occurs even within forests with lower canopy heights, such as Amazonian seasonally flooded forests, and that the vertical distribution of bat species is closely related to their diet and foraging behaviour.

3.2 Introduction

Tropical rainforests tend to have a marked vertical stratification, varying dramatically in physical and biological characteristics from the understorey to the canopy. Differences in factors like solar radiation and water availability result in a great contrast in plant life, and influence animal species assemblages. The resulting vertical pattern in the distribution of species is well documented for birds (*e.g.* Walther 2002; Jayson & Mathew 2003) primates (*e.g.* Buchanan-Smith *et al.* 2000; Heymann *et al.* 2002), and other non-volant mammals (*e.g.* Vieira & Monteiro 2003).

Mammal biomass in the canopy represents up to 70% of the total mammal biomass in tropical forests (Terborgh 1986a). Bats are a very important part of tropical mammalian faunas because they are usually abundant and species diverse, and play key ecological roles, such as the control of insect populations (Findley 1993; Fleming 1993), pollination, and seed dispersal (Medellin & Gaona 1999; Korine *et al.* 2000). The latter roles make bats determinant in forest dynamics and regeneration (Kelm *et al.* 2008).

Over the last decade, several studies documented vertical stratification of bat communities in Old World tropical forests (*e.g.* Francis 1994; Shanahan & Compton 2001; Henry *et al.* 2004; Hodgkison *et al.* 2004a; Fukuda *et al.* 2009), and a few investigated this phenomenon in the neotropics (*e.g.* Bernard 2001; Kalko & Handley 2001; Lim & Engstrom 2001a; Delaval *et al.* 2005). These latter studies revealed a well defined vertical stratification in the bat communities of primary forests of Amazonia, but it is still not clear how this factor influences the assemblages of bats in flooded forests, which are a significant part of the landscape.

In fact, flooded forests represent up to 10% of the forests in the Amazon basin (Ayres 1993), and in some regions they are intermixed with upland unflooded forests, forming a mosaic of different habitat types. Some of the seasonally flooded forests receive nutrient-rich water, which partly flows from the eastern slope of the Andes (várzea forests), whereas others receive only nutrient-poor water draining from the flat Amazon basin (igapó forests). These inundation patterns, and the nutrient load of floodwaters, are perhaps the most important abiotic factors influencing spatial ecological variations in lowland Amazonia (*e.g.* Francis 1994; Shanahan & Compton 2001; Henry *et al.* 2004; Hodgkison *et al.* 2004a; Fukuda *et al.* 2009).

Inundation, which usually lasts for several months in both igapó and várzea, causes several major structural changes in the forests. The height of the trees in Amazonian inundated forests is usually lower than in unflooded forest (terra firme). In terra firme canopy height easily reaches and exceeds 50 m (Ayres 1993) while in igapó canopy height rarely exceeds 25 m (Borges & Carvalhães 2000). We sampled bats in both low and high várzea areas, where the upper canopy may reach respectively 35m and 45m in climax stage (Wittmann *et al.* 2002). In flooded forests, canopy cover also tends to be lower and the vegetation below the canopy tends to be less dense, particularly near the ground (Borges & Carvalhães 2000; Haugaasen & Peres 2006).

Some of these structural differences, as well as other biological parameters, are likely to influence the vertical stratification of animal assemblages. However, the patterns of vertical stratification in bat communities in these flooded forests of Central Amazon, known to harbour bat species assemblages different from those of terra firme (Ramos Pereira *et al.* 2009), remain obscure. All the existing studies were done in terra firme forests, with the exception of Kalko and Handley (2001) who sampled both terra firme and flooded forests but made a global analysis, without testing the existence of vertical stratification in each of the forest types separately.

In this study we analysed the vertical stratification in the two main types of Neotropical flooded forests (igapó and várzea) and in adjacent terra firme forests. In particular we tested if the assemblages of bats using the understorey and canopy are different, and determined which species tend to be associated with each stratum.

3.3 Methods

Study area

The study was carried out in the Amanã Sustainable Development Reserve (Amazonas, Brazil; 23500 km^2) (Figure 3.1) which partly consists of a mosaic of várzea and igapó forests within a matrix of upland terra firme forest. Total annual rainfall is about 2500 mm, and although it rains throughout the year, the wettest months are from January to June. Average monthly temperatures are about 29.5ºC (Ayres 1993). The joint effect of seasonal variation in local rainfall and in the discharge of rivers resulting from the Andes ice-melt produces fluctuations of about 10 m in the water level of lake Amanã and the surrounding river systems, inundating vast expanses of forest, usually from April to July. Nutrient rich "white-water" flows out of the Japurá river, and the nutrient poor "black-water" is brought by the smaller streams that feed lake Amanã.

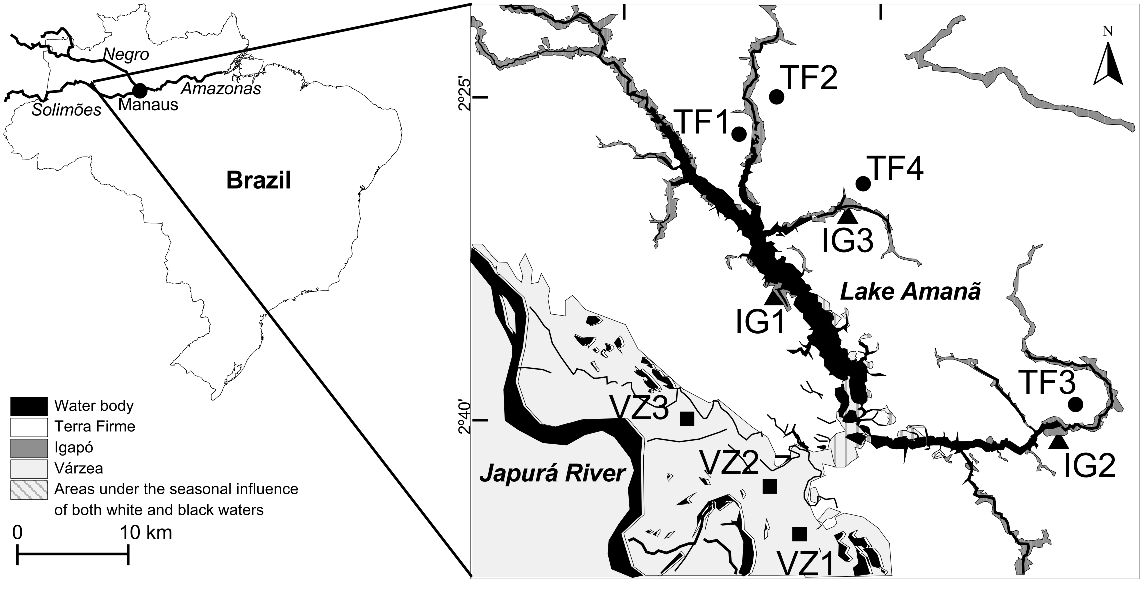


Figure 3.1 Study area and location of sampling stations (TF, terra firme; VZ, várzea; IG, igapó). The distribution of the forest types is based on cartography by the Mamirauá Sustainable Development Institute and on satellite imagery.

Bat sampling

We sampled bats at 10 sites (four in terra firme, three in várzea and three in igapó, Figure 3.1), using three 3 x 12 m canopy mist nets and ten 12 x 3 ground nets. The upper edge of the canopy nets was positioned at about 29 to 35 m. Each site was sampled for 4 consecutive nights, from 18:30 to 24:00 h. Sampling was done in the high-water season (from April to June 2007) and the low-water season (from October to December 2007). However, in várzea and igapó the canopy was only sampled during the low-water season due to the difficulty of setting canopy nets in the flooded areas. So, for these two habitats, the statistical analyses include solely the low-water season captures to allow comparisons between the understorey and canopy strata.

Statistical procedures

We compared species richness of the understorey and canopy using Coleman individual-based rarefaction curves (Coleman 1981; Gotelli & Colwell 2001). Capture data was standardized per mist-net effort, by dividing by the total number of mist-net hours per site, to account for differences in capture effort.

We used Non-Metric Multidimensional Scaling (NMMDS) and the Jaccard similarity index to reduce the matrix of species and sampling sites to fewer dimensions, thus allowing a graphical representation of the vertical stratification of the bat communities within each of the three forest types. We chose NMMDS because it is robust to nonlinear effects and is usually able to summarize more information in fewer axes than other ordination techniques (Zuur *et al.* 2007).

Following this ordination procedure we selected those species with sample size $n \geq 6$ and we did an Analysis of Similarity (ANOSIM), a non-parametric permutations test analogous to an ANOVA for similarity matrices (Clarke & Gorley 2006), to test for significant differences in bat assemblage structure between the canopy and the understorey in terra firme, várzea and igapó forests.

We used a methodology similar to that of Kalko and Handley (2001) to test the association of each species to the canopy or understorey strata, and like those authors we only applied it to species with $n \geq 6$. To normalize abundance values we used a log+1 transformation. We then used a paired *t*-test to compare the captures in the canopy and understorey. We chose the paired *t*-test to account for the correlation between the pairs sharing the same sampling site.

3.4 Results

A total of 260 bats were captured in the canopy: 137 bats were captured in terra firme (low and high water seasons), 72 in várzea (low water season) and 51 in igapó (low water season). A total of 645 bats were captured in the understorey: 318 in terra firme (low and high water seasons), 217 in várzea (low water season) and 110 in igapó (low water season). The list of captures per species in the three habitats and in both seasons is presented in Annex I. Despite the higher total capture effort made at the understorey level, the individual rarefaction curves indicated that a similar effort returns similar richness values in the two strata (Figure 3.2).

The NMMDS revealed a well-marked vertical stratification of the species assemblages (Figure 3.3), with a good separation between the species assemblages of the canopy and understorey. This separation is evident in terra firme and in the two flooded habitats. Twenty-five species had $n \geq 6$ captures, and the ANOSIM analyses revealed a significant overall dissimilarity between canopy and understorey assemblages of those species (*all forests*: R = 0.39, $P < 0.001$). The pattern was consistent within each forest type, although in várzea and igapó it was marginally non-significant (*terra firme*: R = 0.39, $P = 0.02$; *várzea*: R = 0.48, $P = 0.06$; *igapó*: R = 0.46, $P = 0.07$). Pooling the data from the two seasonally flooded habitats, the dissimilarity between canopy and understorey bat assemblages became highly significant (*várzea + igapó*: R = 0.39, $P = 0.01$).

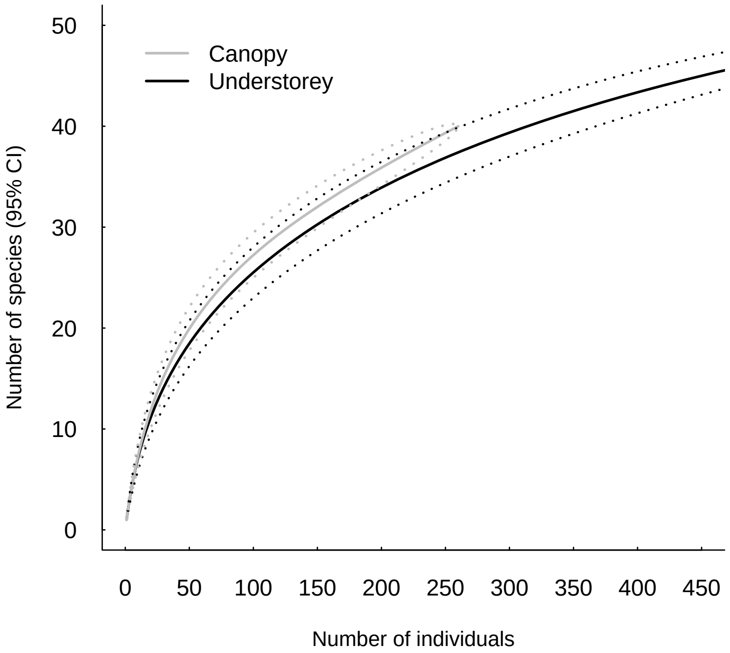


Figure 3.2 Individual-based Coleman species-rarefaction curves (solid lines) with 95% confidence intervals (dashed lines), based on mist-net captures in the understorey and canopy strata.

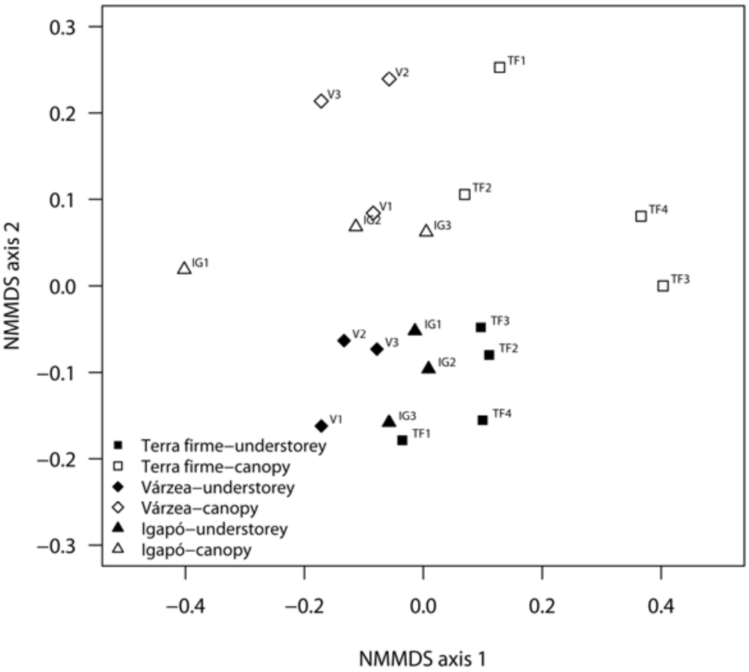


Figure 3.3 Non-metric multidimensional scaling (NMMDS) plot of bat assemblage variation among forest types and strata (understorey and canopy).

We found significant differences between understorey and canopy captures in nine of the 25 species with *n* ≥ 6. Capture frequency was significantly higher in the understorey in five species – *Chrotopterus auritus, Lophostoma silvicola, Phyllostomus elongatus*, *Trachops cirrhosus* and *Carollia perspicillata* – and in four species in the canopy – *Artibeus glaucus*, *Artibeus concolor*, *Uroderma bilobatum*, and *Platyrrhinus helleri* (Figure 3.4).

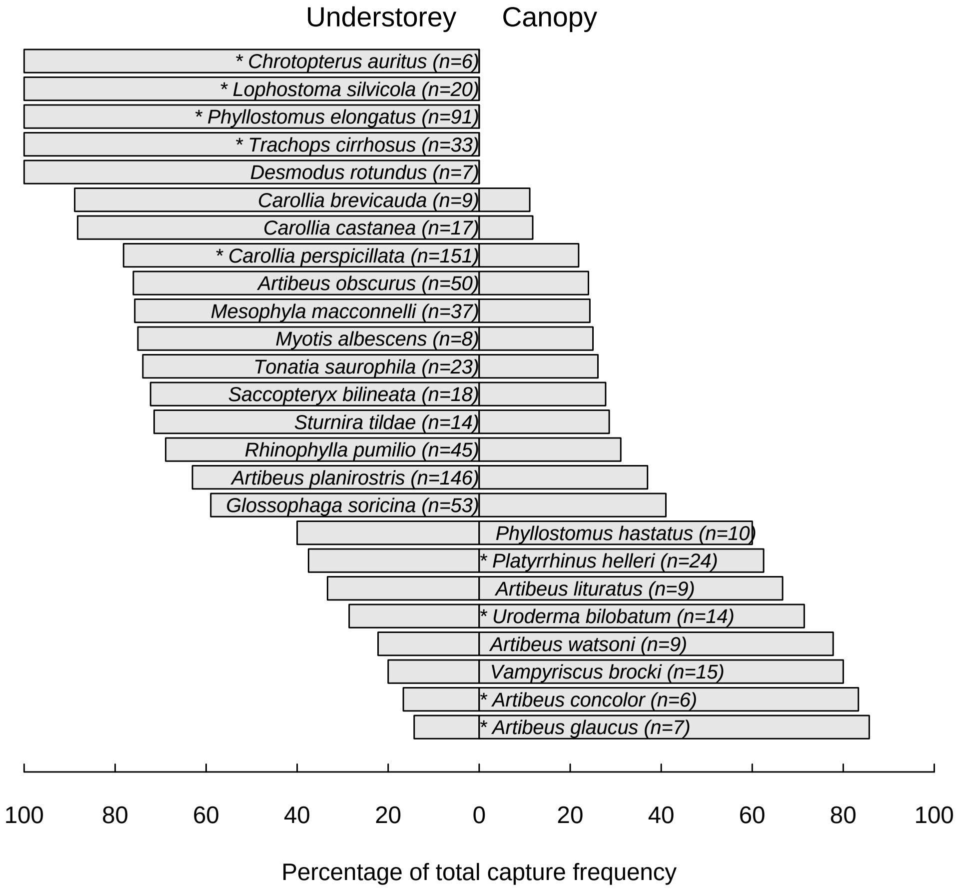


Figure 3.4 Percentage of total capture frequency in canopy or understorey levels of species with captures ≥ 6 individuals. Asterisks indicate significant differences in the abundances between the levels at α = 0.05.

3.5 Discussion

Vertical stratification

Our results indicate the existence of vertical stratification in the way bat species use space in Central Amazonian rainforests, as found before in other Neotropical rainforest areas (Bonaccorso 1979; Brosset & Charles-Dominique 1990; Cosson *et al.* 1999; Bernard 2001; Kalko & Handley 2001; Delaval *et al.* 2005). In addition, we have been able to demonstrate that this stratification also is evident in the two main types of Amazonian flooded forests (várzea and igapó).

The vertical stratification in our data is evident in the result of the NMMDS ordination (Figure 3.3), and the associated ANOSIM tests. The second axis of the ordination separates all samples of the understorey from those of the canopy, and the clarity of this separation underlines the importance of forest strata as an ecological factor for Amazonian bats.

Flooded Amazonian forests have a vertical structure that is quite different from that of terra firme forests, as described in the introduction, and they also harbor differently structured bat assemblages (Ramos Pereira *et al.* 2009). Consequently, the results of studies of vertical stratification of bat assemblages carried out in terra firme do not necessarily apply to flooded forests. However, in the ordination that we carried out, the canopy assemblages in the two types of flooded forest are just as distinct from those of the understorey as in terra firme, and they separate along the same axis. This congruence of the results in flooded and terra firme forest suggests that the various bat species make similar choices of strata, independently of the type of forest where they are.

The results of the ordination that we carried out are in line with that of bat assemblages from a French Guiana forest (Delaval *et al.* 2005), in which the first axis of the ordination represented the differences in use of vertical space. The first axis of our ordination separates the different types of flooded and unflooded forest, which is not surprising because inundation is known to be a key determinant of Amazonian vertebrate assemblages, including bats (Ramos Pereira *et al.* 2009), non-volant mammals (Haugaasen & Peres 2005a), and birds (Beja *et al.* 2010).

The ANOSIM tests confirmed the statistical significance of the vertical structuring in terra firme and in the flooded forests. When we separate the samples obtained in the two types of flooded forest we lose statistical power due to the decrease in sample sizes. However, in spite of this loss, the ANOSIM tests carried out separately for várzea and igapó are just marginally non-significant.

The distinctiveness between the assemblages evidenced by the ordination is confirmed by the species analysis (Fig 3.4). Indeed, we found significant differences in capture rates between understorey and canopy nets for nine species. In general, the strata associations in our data were similar to those of other studies. For example, Kalko and Handley (2001) and Bernard (2001) also captured more *T. cirrhosus*, *P. elongatus, L. silvicola* and *C. perspicillata* in the groundstorey, and in Kalko and Handley (2001) *U. bilobatum* was also significantly associated to the canopy. However, the comparisons with other studies are often made difficult by the small sample sizes for some species.

The data also revealed that there are some species that seem to be very flexible in the use of the vertical space. That is, for example, the case of *Glossophaga soricina* and *Artibeus planirostris*, which were represented by large numbers in our samples but seem to show no clear preference for either of the two strata (Figure 3.4).

Although the composition of the bat assemblages using the understorey and canopy strata is different, their levels of species diversity seem to be very similar. Neither the canopy nor the understorey species-rarefaction curves reached an asymptote, demonstrating that our species lists are incomplete, but the curves show that the same sampling effort would return comparable species richness values in the two strata. This suggestion that bat species richness is evenly distributed among the two strata, together with the demonstrated preference of some species for one of them, emphasizes the need for sampling both strata when conducting bat inventories in forests, in particular in highly diverse tropical regions.

Finally, it is important to note that the distinctiveness of the assemblages of bats feeding in the canopy and in the understorey is probably even more marked than evidenced by our data, or by those of other studies that focused this issue. This is because forest bats tend to commute along defined routes that take advantage of openings in the vegetation, such as man-made trails (Palmeirim & Etheridge 1985). Even fruit-eating bats that feed on the canopy may fly within the forest to avoid predation (Bonaccorso 1979) or to detect fruiting trees, as odoriferous cues may be easier to detect within the forest than above the canopy (Kalko & Handley 2001). It is possible that the trails where we set most of our mist nets are used by species that forage in both strata, and this may artificially dilute the difference between them.

We should point out that we only have one full vertical sample in one season during a single year. Because the canopy in várzea and igapó was only sampled during the low-water season, it is impossible to infer from our data what happens to the ‘understorey specialists’ when their habitats are below water. In fact, canopy samples from flooded forest during the high-water season may show a much stronger congruence with understorey samples at this time of year.

Relationship between trophic guilds and vertical stratification

An interpretation of our results in the light of the diet of bats and their foraging behaviour suggests that both are key determinants of the way bats use the vertical strata in the study area.

Gleaning bats that prey on small vertebrates seem to be strongly associated to the understorey, as they were absent or rare in the canopy captures. That is the case of *C. auritus,* which eats lizards, mice, shrews and birds (Peracchi & Albuquerque 1976; Medellin 1988), and of *T. cirrhosus,* known to consume insects, lizards, geckos, anoles and frogs (Bonaccorso 1979; Whitaker & Findley 1980; Kalko *et al.* 1996b). *L. silvicola* and *P. elongatus* are also large bats that in addition to arthropods prey on vertebrates such as lizards or geckos (Bonaccorso 1979), and they were also captured exclusively in the understorey. This rarity or absence of carnivorous gleaners from the canopy, corroborated by the captures in other studies (Bernard 2001; Kalko & Handley 2001; Lim & Engstrom 2001a) is somewhat surprising because some of the types of vertebrates that they feed on are also available in the canopies of Neotropical rain forests. Presumably, such potential prey are either less abundant or less easily available than at ground level.

Phyllostomus hastatus can also eat vertebrates, in addition to its more common diet of insects and fruit (Gardner 1977b), and our data and the literature show that it uses both the understorey and the canopy (Bernard 2001; Kalko & Handley 2001; Lim & Engstrom 2001a). However, there is no evidence that it captures vertebrates in the canopy, and the use of this stratum is parsimoniously explained by its substantial consumption of fruits of *Ficus* and of other canopy plants.

Delaval et al. (2005) suggest that gleaning insectivory tends to be associated with the understorey, and indeed some of the species that we just referred also consume arthropods. However, this tendency seems to be less marked than in the case of carnivory because, like other authors (*e.g.* Bernard 2001; Sampaio *et al.* 2003), we captured a number of *T. saurophila,* an insectivorous gleaner, in the canopy. In any case, these results suggest that, overall, animalivorous gleaning is a strategy far more used by bats in the understorey than in the canopy.

The situation with gleaning frugivory is quite different, because this foraging strategy was common among both canopy and understorey frugivores. *C. perspicillata* was the only frugivore that showed a significant preference for foraging in the understorey, but the other two

Carollinae, *Carollia castanea* and *Carollia brevicauda*, were also caught almost exclusively there. The three feed mostly on fruits of understorey plants of the genera *Piper, Vismia* and the epyphite *Philodendron* (Palmeirim *et al.* 1989; Thies & Kalko 2004; Delaval *et al.* 2005, pers. obs.). However, *C. perspicillata* is a very flexible species and occasionally feeds on canopy fruits (Bonaccorso 1979), which explains why we also captured quite a few individuals in canopy nets.

Stenodermatinae fruit gleaners are divided between the understorey and the canopy. Several species appear to be associated to the understorey, although samples sizes were insufficient to demonstrate significant associations for any species. In any case, the data suggests that in general these species of Stenodermatidae have a greater flexibility in the use of vertical space than the Carollinae. The canopy frugivory niche is virtually dominated by Stenodermatinae fruit gleaners, such as *A. glaucus*, *A. concolor*, *U. bilobatum*, and *P. helleri*, which were significantly associated to the canopy stratum. Other species of Stenodermatinae, such as *Vampyriscus brocki*, and the large-bodied *Artibeus lituratus*, were also captured mainly in the canopy but our data had no statistical power to demonstrate significance. In general these species depend heavily on figs, which are mostly in the canopy (Bonaccorso 1979; Bernard 2002; Giannini & Kalko 2004).

Desmodus rotundus, the only representative of the guild of sanguinivores in our sampling was only captured in the understorey, but the sample size was insufficient to detect a significant preference. Other studies (Bernard 2001; Lim & Engstrom 2001a; Sampaio *et al.* 2003; Delaval *et al.* 2005) also found it mostly in the understorey, presumably because it feeds on medium and large mammals that are usually on the ground (Turner 1975).

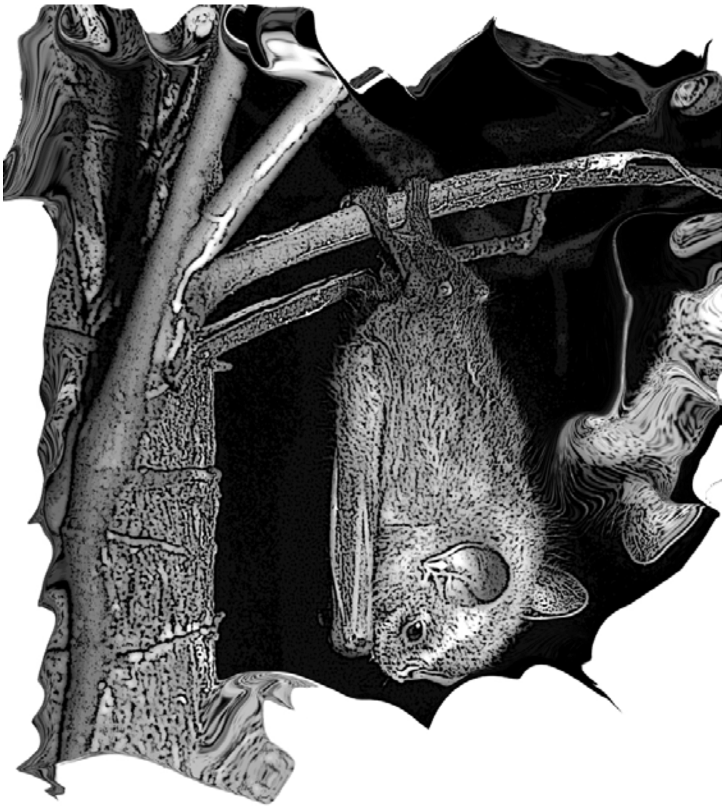
As expected from a sampling based on mist-nettting (Kalko & Handley 2001), captures of aerial insectivores were low when compared to those of the various groups of the Phyllostomidae, and we feel that we have too little data to make generalizations. The only nongleaner insectivorous that we captured frequently was *Saccopteryx bilineata* which made extensive use of both strata, as reported also in Lim and Engstrom (2001a).

Foraging ecology may not be the only element determining the use of forest strata by bats, and roosting preferences are also likely to be important. However, the direction of the influence of this factor is not necessarily the same as that of foraging ecology. In fact, whereas some species, like those of the genus *Carollia*, tend to roost in the same stratum where they feed, there are also species, like *U. bilobatum*, that usually roost in the understorey but feed mostly in the canopy (Kalko & Handley 2001).

It seems clear that, at least in the case of frugivorous bats, vertical stratification in the way different species use Neotropical forests is related to the consumption of different food resources. This segregation should be effective in maintaining high levels of diversity because it allows the coexistence of a larger number of species in the same geographical area. Lim and Engstrom (2001a) and Delaval et al. (2005) have made similar suggestions for other Neotropical bat assemblages, and the role of vertical stratification as a mechanism to minimize interspecific competition in tropical rainforests has been suggested for other groups of mammals (Meserve 1977; Vieira & Monteiro 2003). It follows from this situation that the preservation of rich and complete bat assemblages in Neotropical forests is dependent on maintaining the integrity of the vertical stratification of the forest. This is also true in flooded forests, which are underrepresented in protected areas networks (Fearnside & Ferraz 1995), and are more susceptible to human occupation, deforestation, agricultural conversion, and the construction of hydroelectric dams due to their accessibility from large river systems (Fearnside & Ferraz 1995; Vale *et al.* 2008).

Chapter 4

Ecological responses of frugivorous bats to seasonal fluctuation in fruit availability in Amazonian forests



Ramos Pereira M.J., Marques J.T, Palmeirim J.M. 2010. Biotropica, *in press*.

4 Ecological responses of frugivorous bats to seasonal fluctuation in fruit availability in Amazonian forests

4.1 Abstract

Lowland Amazon is climatically one of the least seasonal regions on the planet, but little is known about how this is reflected in ecological seasonality. The central objective of this study was to determine if seasonal fluctuations in the availability of fruit resources in Neotropical forests are sufficiently marked to affect the ecology and physiology of frugivorous bats. Seasonal variations in overall bat abundance and in captures, body condition and reproductive activity of the two most abundant species, *Carollia perspicillata* and *Artibeus planirostris*, were studied within a region of central Brazilian Amazonia dominated by a mosaic of non-flooded (terra firme) and seasonally flooded forests (várzea and igapó). Concurrent seasonal changes in fruit availability were measured. The abundance of fruits was markedly seasonal, with far fewer resources available during the low-water season. There was a positive correlation between fruit and bat abundance. Overall, bats did not increase the consumption of arthropods during the period of fruit shortage. In *A. planirostris* the body condition dropped when fruits were scarcer. In both *C. perspicillata* and *A. planirostris* foraging and reproductive activity were positively correlated with fruit availability. Consequently, the results suggest that resource seasonality is sufficiently marked to affect frugivorous bats and force them to make important eco-physiological adjustments.

4.2 Introduction

Most phenological observations in Neotropical forest areas show that fruiting is episodic (Foster 1982; Terborgh 1983; Haugaasen & Peres 2005c). Indeed, ripe fleshy fruits are ephemeral in nature, patchily distributed, fluctuate seasonally in abundance, and are scarce relative to other dietary constituents, like foliage or insects (Leigh & Windsor 1982; Howe

1984). Seasonal shifts in fruit abundance may result in periods of food scarcity, which potentially drive a variety of eco-physiological responses in frugivorous bats, such as changes in body condition (Fleming 1988), activity rates (Aguiar & Marinho-Filho 2004), diet (Fleming *et al.* 1972; Kunz & Ingalls 1994; Kunz & Diaz 1995), and timing of reproduction (Fleming *et al.* 1972; Bonaccorso 1979; Racey & Entwistle 2000).

Lowland Amazonia is characterized by a mosaic of flooded and unflooded forests. This mosaic is dominated by terra firme, upland forests that never flood and that tend to be nutrient-poor (Haugaasen & Peres 2006). Within this large matrix of terra firme are forest areas that are flooded seasonally. The most extensive type among these floodplain forests is várzea, which suffers seasonal inundation by nutrient-rich ‘white- waters’ that originate partly in the Andes ice-melt. Another important floodplain forest type is igapó, seasonally inundated by oligotrophic ‘black-waters’ that originate mostly in the Tertiary Amazonian lowlands. These contrasting inundation regimes and nutrient contents of floodwaters result in distinct tree phenological responses (Haugaasen & Peres 2005c).

Little is known about how seasonal changes in fruit availability affect aspects of the population dynamics and life history of bats, particularly in lowland Amazonian areas comprised of this mosaic of forests under distinct flooding regimes. Due to plant diversity and fruiting asynchrony, it is possible that fruit resources are plentiful throughout the yearly cycle, and may never reach levels of scarcity that affect frugivorous bats. The central objective of this project was to determine if, in humid equatorial Amazonian forests comprised of a mosaic of flooded and unflooded habitats, fruit availability is ever sufficiently low to affect frugivorous bats. We explored the following possible responses of bats to such periods of fruit scarcity: (1) bats may lower their level of activity to save energy, as some tropical bats appear to have the capacity to adjust their activity levels in response to food availability (Aguiar & Marinho-Filho 2004); (2) if fruit production is not synchronous across the different forest types, then bats may respond to fruit shortages by shifting between them; (3) predominantly frugivorous species may increase the consumption of arthropods during times of lower fruit availability; (4) pregnant and lactating females have great energy requirements (Speakman & Racey 1987; Kurta *et al.* 1989), so frugivorous bats could avoid reproducing during times of fruit scarcity; and finally (5) if fruit scarcity is severe, bats may be unable to maintain their optimal body condition, in which case we would expect measurable declines in their body condition that are coincident with low fruit abundance. To achieve our objectives we studied seasonal variations in the overall bat captures and their diet. Additionally, we looked for seasonal changes in the reproductive activity and body mass of the most abundant species, *Carollia perspicillata* (Linnaeus) and *Artibeus planirostris* (Spix). This was done within a region in central Brazilian Amazonia dominated by a mosaic of terra firme, várzea and igapó forest, where we also measured the concurrent seasonal changes in fruit availability in these three habitats. We focused on the dry and rainy seasons, which are known to correspond to periods of low and high fruit abundance, respectively (Ayres 1993; Haugaasen & Peres 2005c).

4.3 Methods

Study area

Field work took place around Lake Amanã, within the Amanã Sustainable Development Reserve (1º35' – 3º16' S, 62º44' – 65º23' W; Amazonas, Brazil) which encompasses large extensions of flooded forests, in a matrix of terra firme forests (Figure 4.1). Inundation is a consequence of both the ice-melt in the Andes, brought in by the Japurá River, and of rainfall over the region. Lake Amanã is a mostly black-water lake fed primarily by streams draining catchments dominated by terra firme forests. However, during seasonal floods, the south of the lake also receives some inflow of white-water. Daily variation in temperature (*ca* 10ºC) is greater than the annual average variation (Ayres 1993). In middle of June the temperature may fall to *ca* 18ºC due to cold fronts coming from the Antartic, but average monthly temperatures are about 29.5ºC. The area receives *ca* 2500 mm of annual precipitation, two thirds of which comes during the rainy season, which usually lasts from January to June. The dry season typically spans between July and December. Seasonal water level variation may reach up to 10 m. Flowering and fruiting peaks generally occur in the dry and rainy season, respectively (Rankin-De-Merona *et al.* 1992; Ayres 1993; Haugaasen & Peres 2005c).

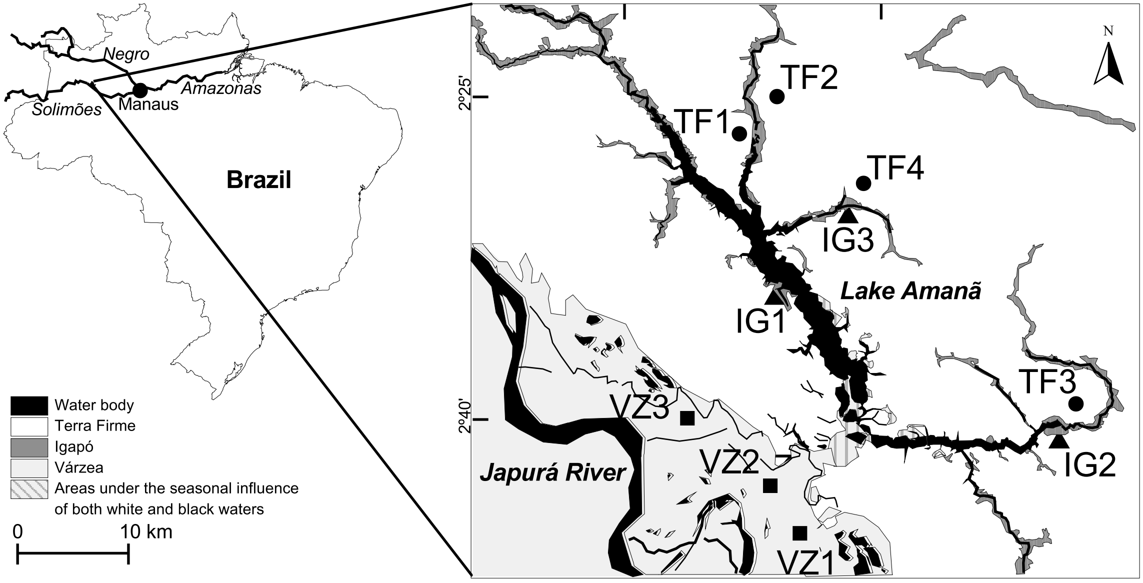


Figure 4.1 Main habitats in the study area and at sampling stations (TF – terra firme, VZ – várzea, IG – igapó; the southern part of Lake Amanã usually has black water, but can receive white water temporarily. The distribution of habitats is based upon cartography of the Mamirauá Sustainable Development Institute, and upon satellite imagery.

Plant phenology and food availability

We established a total of 10 sampling stations, of which four were in terra firme, three in várzea, and three in igapó. At each of these stations, we set up a 2-km line transect (divided into 100 sectors of 20 m) along which we made an inventory of trees and shrubs. With the help of a local field assistant with previous extensive experience in the collection of plant phenology data, we located all fruiting trees with canopies intersecting the transect line. We visually estimated the number of ripe and unripe fruits in each of these trees, often using binoculars. In some situations we estimated the number of fruits in a section of the canopy and then used this as a reference to make an estimate for the full canopy. All fruiting shrubs within 2 m from the transect line were also located, and the number of ripe and unripe fruits on them was estimated. The ripeness of fruits was determined with the help of the field assistant, using his extensive knowledge of the morphology and color of the fruits of each species. The results of these methods are approximate, and should not be interpreted as unbiased estimates of fruit abundance. As we used the same methodology in both seasons and in the three habitats, however, they are suitable for the types of comparisons made in this study. The estimates of fruit availability were done once in the high-water season and repeated in the low-water season, during the same periods used for bat sampling. At all sampling stations, a part of the plant phenology transect coincided with the location of mist-nets that were used to capture bats.

We estimated the approximate availability of fruiting resources to bats by pooling all detected fruits, mostly to increase the stability of the estimates. This is possible because the phenology of the fruits consumed by bats tends to be coincident with that of the generality of Neotropical rain forest fruits. This coincidence is evident when comparing the phenology of 'bat-fruits' (*e.g.*, Parolin *et al.* 2002; Mello *et al.* 2004; Thies & Kalko 2004) with that of the generality of fruits (Kubitzki & Ziburski 1994; Wallace & Painter 2002; Haugaasen & Peres 2005c; Ferreira & Parolin 2007). In both wet and dry Neotropical forests, maximum fruit production tends to occur early in the wet season, probably because germination conditions are best then (Garwood 1983). The general fruiting pattern may also be a good representation of the full range of fruits consumed by bats. In fact, although phyllostomid frugivores focus their diet on some core plant species, they supplement this core with a large variety of other plant resources (Fleming 1988; Lobova *et al.* 2009).

Bat sampling

We sampled the bat community between April and June 2007, when várzea and igapó forests are fully inundated, and again between October and December, in the low-water season, when all the forests are dry. Bats were captured at the 10 above-noted sampling stations. The type of forest sampled in consecutive sessions was changed, so there was a temporarily balanced sampling of the three types of forest. Each station was sampled over four consecutive nights. Bats were caught using ten 12 × 3 m mist-nets, for a total trapping effort of 4800 net hours (1 net hour corresponds to one 12-m net opened for 1 h). During the high-water season, mist nets were set immediately above water in both várzea and igapó. The nets remained open during 1800–2400 h, during which time they were checked every 20 min. Bat sampling during full moon was generally avoided. Each captured bat was identified and weighed using a 20, 50 or 100 g Pesola® spring balance. Bats were classified as adults or juveniles according to the degree of ossification of the carpal joints and the development of nipples or testes (Baagøe 1977). All individuals were marked temporarily in the patagium using a pen marker, to allow for recognition of recaptures over the same sampling period, but there were only four recaptures and these were not included in the analyses. We collected fecal pellets of the mist-netted bats to analyze their diet. Each animal was kept in a separate cotton bag for about 30 min to collect its individual pellets. Fecal content, usually seeds, fruit pulp or arthropod parts, were identified using a stereo-microscope. The presence of these items in the feces was quantified using the frequency of occurrence in the droppings of individual bats.

Data analysis

To test for differences in the number of frugivore bats captured between seasons and between habitats within each season, we applied one-way ANOVA, using each site as a sample. The same approach was used to compare the number of ripe fruits available within different habitat types and seasons. Tukey's HSD *post-hoc* tests were used to detect significant differences between pairs of habitats. To test for seasonal differences within each habitat, we used Pearson chi-square analysis.

The significance of differences in the structure of frugivore assemblages between habitats and seasons was assessed by means of Analysis of Similarity (ANOSIM), a non-parametric permutation test that is analogous to an ANOVA for similarity matrices (Clarke & Gorley 2006). Data were normalized per site to account for differences in total abundance, and then square-root-transformed to reduce the influence of the most abundant species, and to overcome the unity-sum constraint. Seasonal changes differences in captures, body mass and in the proportion of pregnant and lactating females were studied in the most abundant species: *C. perspicillata* and *A. planirostris*. To avoid biases due to incompletely grown individuals or pregnant females, comparisons of body mass excluded juveniles and females. Differences were detected using *t*-tests and Fisher exact tests. Changes in the frequency of occurrence of fruit and arthropods in the diet of bats between seasons were analyzed using generalized binomial linear regression models; due to small sample sizes, diet data were pooled across all captured species.

4.4 Results

Variation in fruit availability

Overall, we identified plants belonging to 46 families. The most abundant taxa were Sapotaceae, Caesalpinioideae, Mimosoideae and Lecythidaceae. In igapó, we identified 26 tree families, the lowest number among the three sampled habitats: Sapotaceae were the most abundant family, though subfamilies Mimosoideae and Caesalpinioideae were also common. In várzea, we identified 33 plant families, with families Euphorbiaceae, Sapotaceae and subfamilies Caesalpinioideae and Lecythidaceae the most represented. Terra firme was the most diverse of the studied habitats: we recorded 40 plant families, usually represented by a few individuals per family. Here, Lecythidaceae, Myristicaceae, Caesalpinioideae and Sapotaceae were the most represented taxa.

Ripe fruits were more abundant during the high-water than during the low-water season (Table 4.1) and this happened in the two sampled strata, understorey and canopy (Figure 4.2). There were significant differences in the abundance of ripe fruits between habitats in each of the seasons. In the high-water season, the abundance of ripe fruits was greater in várzea than in either terra firme or igapó. Ripe fruits were scarce during the low-water season in all habitats, but igapó had slightly more ripe fruits than várzea.

Table 4.1 Test statistics for comparisons of number of fruit eating bats and ripe fruits between seasons and habitats (ANOVA F), between pairs of habitats (Tukey's HSD) and for seasonal differences within each habitat (Pearson chi-square). P-values are given in parentheses.

Between seasons	Bats	*C. perspicillata*	*A. planirostris*	Ripe fruits
All habitats (F)	4.45 (0.02)	0.52 (0.48)	0.98 (0.33)	19.01 (0.00)
Terra Firme (χ^2)	15.12 (0.04)	6.00 (0.42)	2.03 (0.73)	5.10 (0.06)
Igapó (χ^2)	4.35 (0.53)	9.56 (0.04)	10.12 (0.03)	9.26 (0.06)
Várzea (χ^2)	12.71 (0.02)	12.63 (0.04)	6.84 (0.41)	14.13 (0.03)

	Bats		*C. perspicillata*		*A. planirostris*		Ripe fruits	
Between Forests	High water	Low water	High water	Low water	High water	Low water	High water	Low water
All forests (F)	6.01 (0.03)	0.51 (0.49)	5.59 (0.04)	5.75 (0.04)	5.35 (0.04)	5.11 (0.06)	9.20 (0.01)	5.34 (0.04)
Terra firme and igapó (HSD)	(0.03)	-	(0.40)	(0.04)	(0.95)	-	(0.34)	(0.68)
Terra firme and várzea (HSD)	(0.63)	-	(0.04)	(0.98)	(0.23)	-	(0.01)	(0.29)
Igapó and várzea (HSD)	(0.04)	-	0.03	(0.04)	(0.02)	-	(0.04)	(0.07)

Variation in bat captures

During the 80 nights of mist-netting, we captured 650 bats representing 27 frugivore or partial-frugivore species (Table 4.2). These included species of nectarivores also known to consume fruits, in particular those of the genera *Glossophaga*. The most frequently captured species were *C. perspicillata*, *A. planirostris*, *Artibeus obscurus*, and *Glossophaga soricina*. *C. perspicillata* and *A. planirostris* represented 55 percent of the frugivores captured.

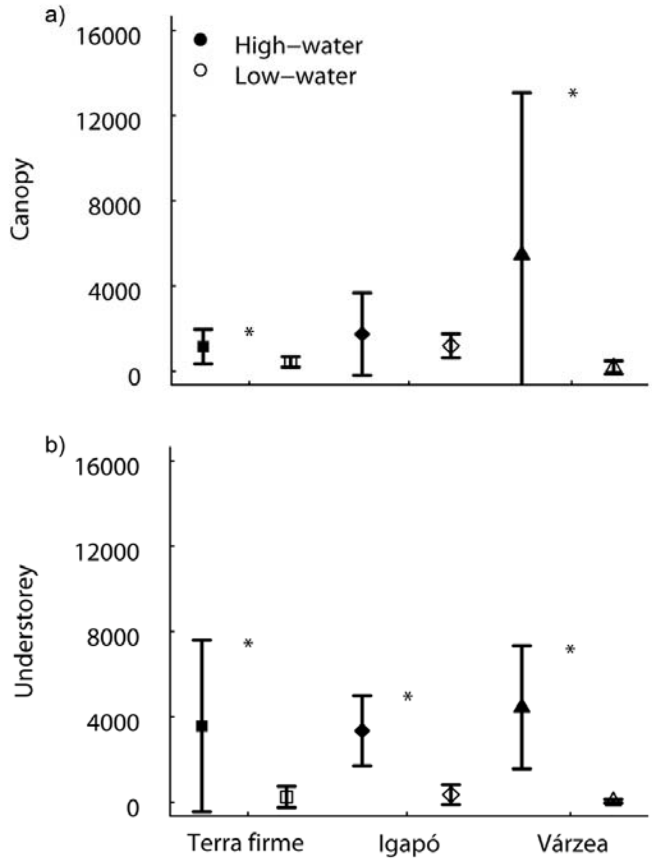


Figure 4.2 Mean fruit availability in the canopy (a) and understorey (b) in each habitat during the low and high-water seasons. Error bars represent 95% CI. Asterisks represent statistically significant differences between seasons (**P* < 0.05).

Total captures of frugivorous bats were greater during the high-water season (Table 4.1; Figure 4.3). Captures were higher in várzea and terra firme than in igapó during the high-water season. During the low-water season, there were no significant differences between the three habitats.

Table 4.2 List of fruit eating bats and number of captures of each species captured in each habitat and season.

Taxon	Guild*	Terra firme		Igapó		Várzea	
		High-water	Low-water	High-water	Low-water	High-water	Low-water
Phylloderma stenops	F	2	1	0	1	1	0
Glossophaga comissarisi	N	0	0	1	1	0	0
Glossophaga longirostris	N	0	0	1	0	0	0
Glossophaga soricina	N	7	3	4	5	8	15
Carollia brevicauda	F	3	5	0	0	0	0
Carollia castanea	F	8	7	1	0	1	0
Carollia perspicillata	F	28	30	21	37	81	23
Rhinophylla pumilio	F	14	17	1	0	0	0
Artibeus cinereus	F	0	0	1	0	0	0
Artibeus concolor	F	0	1	1	0	0	0
Artibeus glaucus	F	0	1	0	0	0	0
Artibeus gnomus	F	1	0	0	0	1	0
Artibeus phaeotis	F	0	1	0	0	0	0
Artibeus watsoni	F	1	1	0	0	1	0
Artibeus obscurus	F	19	10	8	9	2	0
Artibeus lituratus	F	1	1	7	1	3	0
Artibeus planirostris	F	5	5	7	8	40	74
Chiroderma trinitatum	F	0	0	0	0	1	0
Chiroderma villosum	F	0	0	0	0	2	1
Mesophyla macconnelli	F	21	7	3	0	2	0
Platyrrhinus helleri	F	0	1	0	2	17	6
Sturnira lilium	F	0	0	0	0	1	0
Sturnira tildae	F	1	7	12	2	0	0
Uroderma bilobatum	F	1	2	3	1	3	0
Vampyressa pusila	F	1	2	0	0	0	0
Vampyriscus bidens	F	0	0	1	0	0	0
Vampyriscus brocki	F	1	2	1	0	0	0

* Feeding-guilds following Kalko (1997) and Schnitzler & Kalko (1998): F - Highly cluttered space gleaning frugivores, N - Highly cluttered space gleaning nectarivores.

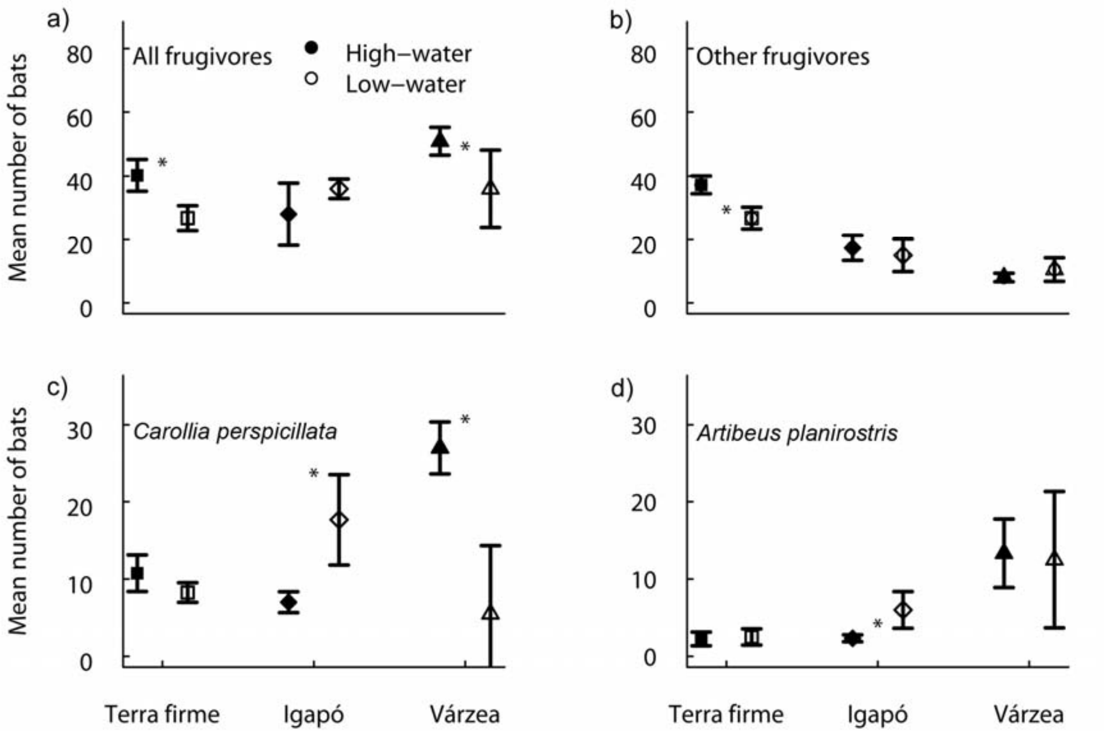


Figure 4.3 (a) Frugivorous bats captured in each habitat; (b) captures excluding *C. perspicillata* and *A. planirostris*; (c) and (d) captures of *C. perspicillata* and *A. planirostris,* respectively. Error bars represent 95% CI. Asterisks represent statistically significant differences between seasons (*$P < 0.05$).

The number of frugivorous bats captured was positively correlated with the abundance of ripe fruits ($R = 0.47$, $P = 0.03$). The patterns found suggest that bats are more abundant, or at least more active, when ripe fruits are more available (Figure 4.4). There was no evidence of seasonal movements across habitats. In fact, there were no significant changes in the assemblage structure across seasons within each forest type (average seasonal dissimilarity according to ANOSIM: terra firme $R = –0.24$, $P = 0.95$; várzea $R = 0.11$, $P = 0.30$; igapó $R = –0.33$, $P = 0.99$). Although seasonal habitat shifts were not sufficiently general to result in significant seasonal changes in the composition of bat assemblages in the three habitats, we did find evidence that the two most abundant species may partly shift habitats between seasons.

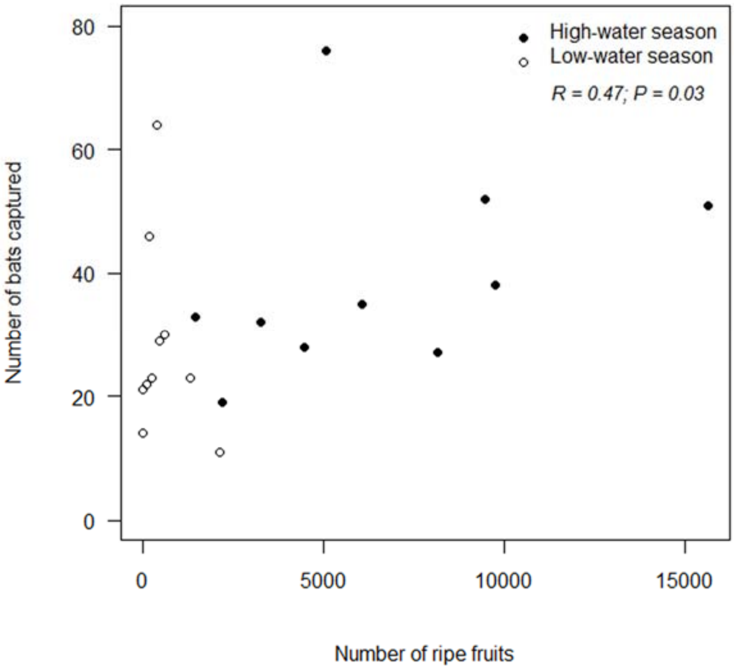


Figure 4.4 Relationship between ripe fruit abundance and the number of frugivorous bat captures in the two seasons.

Inspecting the patterns of abundance in *C. perspicillata* and *A. planirostris* there was evidence of variation in their abundance within and between habitats (Table 4.1; Figure 4.3). There were differences in the number of captures of *C. perspicillata* between habitats during each season. During the high-water season, this species was captured in higher numbers in várzea than in either terra firme or igapó. This pattern changed during the low-water season, with igapó presenting significantly more captures than either terra firme or várzea.

There were no significant changes, however, in the number of captures of *C. perspicillata* between seasons, probably because the higher number of captured bats in várzea during the high-water season was offset by the inverse pattern detected in igapó. Similarly, there was some variation in the number of captures of *A. planirostris* between seasons, with a slight decrease in várzea and a simultaneous increase in igapó towards the low-water season, but these differences were not statistically significant. During the high-water season, there were differences in the number of captures of *A. planirostris* between habitats, and these were greater in várzea than in either terra firme or igapó.

Changes in diet, body condition and reproductive activity

We examined if bats, overall, increased the consumption of arthropods during the period of fruit shortage, the low-water season, but there were no significant differences between the two seasons (F = 0.15, P = 0.89). The frequency of occurrence of fruits in the pellets (seeds or pulp) also showed no differences between the high-water and the low-water season (F = 0.31, P = 0.75). The mean weight in *A. planirostris* was higher during the high-water season (*i.e.*, the peak of fruit abundance), but there were no detectable differences in *C. perspicillata* (Figure 4.5). Each species exhibited significantly more pregnant and lactating females during the high-water season (Figure 4.5).

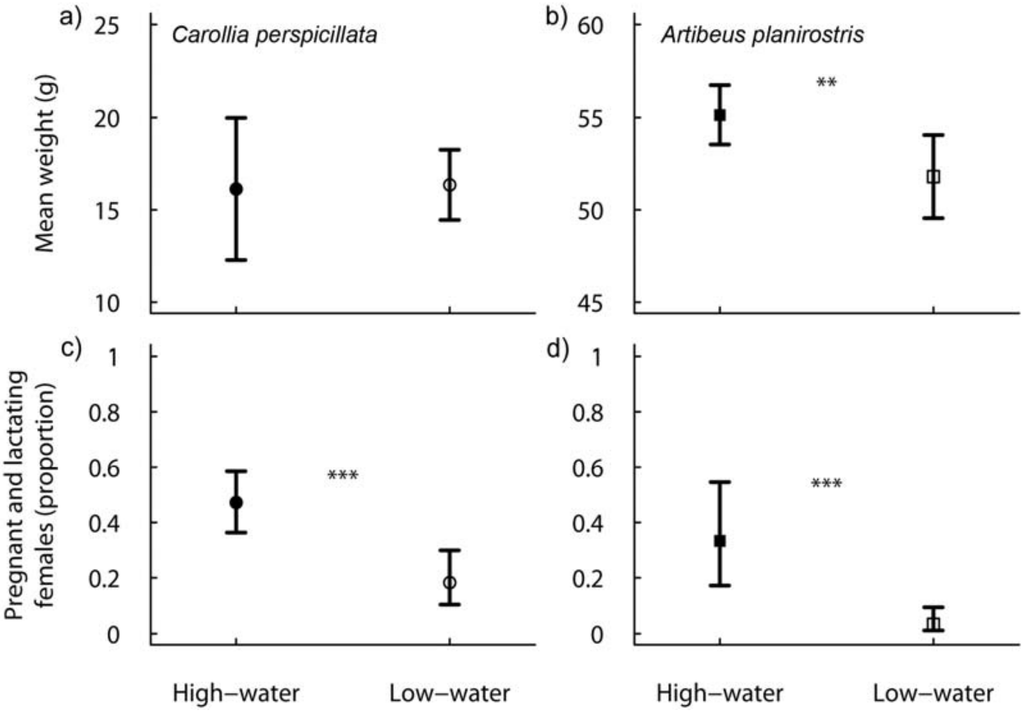


Figure 4.5 Weight and proportion of pregnant and lactating females among *C. perspicillata* (a and c) and *A. planirostris* (b and d). Error bars represent 95% CI. Asterisks represent statistically significant differences between seasons (**P < 0.01, ***P < 0.001).

4.5 Discussion

Spatio-temporal differences in fruit availability

Fruiting was a highly seasonal event in all three forest types. There were far more fruits during the high-water season in all habitats, but they were particularly abundant in várzea. During the low-water season, ripe fruits were much less abundant in all forests, but slightly more abundant in igapó. These results should be interpreted with care, as we sampled fruit abundance at a relatively small number of sites and do not have replicates across years. Nevertheless, this pattern of greater fruit availability during the high-water season has been observed in other Amazonian floodplain forests (Parolin *et al.* 2002; Haugaasen & Peres 2005c). In addition, fruiting peaks during the onset of the high-water season in terra firme have been reported (Janzen 1967; Foster 1982; ter Steege & Persaud 1991; Haugaasen & Peres 2005c), but our data did not have the temporal resolution to test for that pattern in the study area. However, a seasonal variation in the availability of fruits does not necessarily imply that food is limiting for frugivorous bats during part of the year. Food may be plentiful throughout the year, and during the peak of fruiting there may be a surplus of food that is not consumed.

Changes in activity levels

We captured 20 percent fewer frugivorous bats during the low-water season. The fact that the drop in captures was observed across all the major habitats in the region suggests that it was not mostly due to switches between habitats within the region in search for food. The drop in the captures is more parsimoniously explained by an overall decrease in flying activity.

Flight is an energy-demanding activity for bats (Speakman & Thomas 2003), and the greatest energy demand bats have is collecting enough food to provide the energy they need to get through the next night (Altringham 1996), so a reduction in foraging activity may allow tropical bats to preserve energy during times of food shortage. Seasonal variations in the capture rates of tropical bats associated with food availability have been reported (Aguiar & Marinho-Filho 2004; Hodgkison *et al.* 2004b) and greater temporal differences in activity are expected in frugivorous species that depend upon plants that experience peak fruit production during particular seasons (Presley *et al.* 2009). However, it is important to note that our bat sampling was limited in time and was not replicated across years, so further work is desirable to confirm the existence of temporal changes in activity due to changes in food availability.

Movement between habitats

The study area is a mosaic of different types of forest, so shifting habitats or commuting daily to foraging areas in habitats where resources are more abundant is a potential strategy by which to respond to periods of fruit shortage.

Only radiotracking of animals or a high number of inter-habitat captures of marked animals could determine with confidence if there are movements between habitats. However, the pattern of abundance of *C. perspicillata* may be partly explained by such seasonal inter-habitat movements. Its peak abundance was recorded in várzea during the high-water season, when this habitat provided more abundant fruit resources than the other two types of forest. The situation changed in the low-water season, as the greatest abundances of both ripe fruit and *C. perspicillata* shifted to igapó. Still, the drop in the number of captures of these bats in both terra firme and várzea was not totally compensated for by the observed increase in igapó. It is also possible that inter-habitat movements driven by the abundance of fruit resources are more common in some age guilds such as juveniles and/or non-dominant adults (Cosson 1994). Interestingly, the data for *A. planirostris* suggest a pattern similar to that of *C. perspicillata,* but changes were insufficient to demonstrate statistical significance.

Some phyllostomids have the capacity to commute long distances (Morrison 1978). *A. jamaicensis*, a sibling species to *A. planirostris,* is known to commute up to 10 km between roosts and feeding areas (Morrison 1978). However, the much smaller *C. perspicillata* usually forages within 1 to 3 km of its daily roosts (Fleming & Heithaus 1986; Bernard & Fenton 2003), but Fleming and Heithaus (1986) refer that site fidelity depends on the existence of enough food supply in the foraging areas. So why inter-habitat seasonal shifts in abundance are not more pronounced in our study area? Presumably, this is because there is a partial synchrony in the periods of fruit abundance and scarcity within the three habitats, so there is little advantage in seasonally shifting one’s foraging habitat. However, our terra firme and igapó sampling stations are quite far from várzea forest, and habitat shifts could be more common in areas closer to várzea.

Dietary shifts

Many frugivorous phyllostomid bats, most of which are predominantly frugivorous, are known to consume arthropods, so one possible strategy they might use to cope with periods of fruit scarcity would be to increase their consumption of arthropods. However, we failed to detect any significant increase in the frequency of arthropods in the pellets during the period of fruit scarcity. This suggests that, in general, it is more efficient for the studied bats to search for the few ripe fruits available, using their acute sense of smell (Laska 1990 a,b; Korine & Kalko 2005), than to shift towards the capture of arthropods.

Seasonal changes in reproductive activity

Seasonal bimodal polyoestry is a common reproductive pattern among frugivorous phyllostomids (Gardner 1977a; Fleming 1988), including *C. perspicillata* and *A. planirostris.* However, we found seasonal changes in the reproductive activity in both *C. perspicillata* and *A. planirostris,* with far more pregnant and lactating females captured during the high-water season, coinciding with the period of greater fruit abundance.

Reproduction is energetically expensive, because its costs include not only growth of the foetus and milk production, but also the increased costs of flight during pregnancy, and maternal care (Racey & Entwistle 2000). Consequently, if resources are strongly seasonal, bats adjust their reproductive cycles so that births and lactation occur during periods of food abundance (Bonaccorso 1979; Fleming 1988; Ramirez Pulido *et al.* 1993).

Seasonal changes in body condition

In bats, the optimal body condition should be a balance between the bat's requirement to satisfy its short- and long-term energy needs and the added energy costs and mortality risks of flying with energy reserves (Hamilton & Barclay 1998). A low condition indicates that bats are unable to consume enough food to maintain such an optimal body mass, and fruit shortages may lead to decreased body mass in frugivorous bats (Smythe 1986; Charles-Dominique 1991). Body mass may also be affected by reproductive activities, such as lactation, courtship, or territorial defense.

Our results reveal seasonal changes in body condition in *A. planirostris*, but not in *C. perspicillata*, and this difference may be related to their distinct diets and foraging strategies. Large *Artibeus* generally are fig-eaters; meanwhile, *C. perspicillata* feeds largely on *Piper* and *Vismia* fruits in rainforest areas, but it has generalist feeding habits (Palmeirim *et al.* 1989; Geiselman *et al.* 2002; Giannini & Kalko 2004). In general, in Amazonia fig fruits are available throughout the year, and may even represent a keystone species during resource bottlenecks (Terborgh 1986b; Kalko *et al.* 1996a). Still, our data suggests that figs are less abundant during the low-water season. When figs are scarcer, *A. planirostris* may have to use complementary food resources, which may be sub-optimal for this large-bodied species, and this could explain the drop in body condition during the low-water season. The diverse diet of *C. perspicillata* may minimize the impact of the drop in fruit availability in the low-water season, allowing it to maintain a relatively stable body condition.

In conclusion, although the climatic conditions of lowland Amazonia are relatively stable throughout the year, the availability of fruit resources varies seasonally. Overall, our results suggest that this variation is sufficiently marked to influence the ecology and physiology of frugivorous bats, forcing them to make adjustments in their yearly cycle to cope with periods of relative food shortage.

Chapter 5

Environmental correlates of bat species richness in Amazonian rainforests: the importance of primary productivity

Ramos Pereira M.J., Palmeirim J.M. *in prep.*

5 Environmental correlates of bat species richness in Amazonian rainforests: the importance of primary productivity

5.1 Abstract

The available energy in an ecosystem is recognized as one of the most important factors promoting spatial variation in species richness. However, it remains controversial if it is the direct amount of energy available or its transformation into resources that explains the geographical patterns in species richness. Here we aimed to determine which of those two versions of the energy hypothesis – ambient-energy or productivity – is the best in explaining the patterns of frugivore bat richness in Amazonian rainforests. Data on frugivore bat richness was compiled for 22 well-sampled rainforest sites within the Amazon basin and, as potential correlates of bat richness, we selected seven climatic variables and seven productive-energy variables. We calculated the variance inflation factor of each variable to quantify the severity of multicollinearity and to reduce the number of potential predictors. The effects of the predictor variables on frugivore bat richness were examined using multiple regression analyses by applying a forward stepwise selection procedure. Annual maximum Normalized Difference Vegetation Index (MaxNDVI) was the best predictor of the variation of frugivore bat richness, supporting the hypothesis that it is the conversion of energy into food available that explains the geographical patterns of bat richness in Amazonian forests. We suggest that sites with higher NDVI values are more productive, supporting higher abundance and diversity of plants. This creates the conditions to sustain larger and more viable bat populations and to allow the coexistence of many species without intense competition. Our results suggest that satellite remote sensing can be used for estimating spatial variation in bat richness, having a direct application in conservation planning.

5.2 Introduction

During the last decades, macroecologists have addressed the question of geographical patterns in species diversity, and it is generally accepted that the correlates of species richness can be divided in two major groups: contemporary environmental conditions and historical variations in those conditions (Whittaker *et al.* 2007).

A prominent pattern in species richness worldwide is its decrease from tropics to poles and bats are no exception to that pattern (Kaufman & Willig 1998; Horáček *et al.* 2000; Proches 2005). According to Willig & Selcer (1989) latitude is the best predictor of bat species richness in North and South America. However, even if latitude can be seen as a major explanatory variable in bat species diversity, it is only a surrogate for other environmental variables. Indeed, Patten (2004) found that contemporary temperature and precipitation were good correlates for species richness in North America, while Ulrich *et al.* (2007) suggested temperature as a major determinant of species richness in European bats.

However, at smaller spatial scales, or within climatically homogeneous regions, these two variables may not affect the diversity of bats. The Amazon basin is quite uniform in terms of temperature and precipitation. Consequently, at a macro-scale, the landscape is also quite homogeneous, with most of the basin classified as tropical moist semi-deciduous forest (Stone *et al.* 1994).

Amazonian bat faunas have been inventoried thoroughly in several locations in Brazil, Peru, Venezuela, Guyana, French Guiana, Bolivia and Ecuador. The Neotropical region is by far the most diverse region in the world for microchiroptera (Hutson *et al.* 2001) and some of the inventoried areas in Northern South America show an impressively high bat species richness, with an expected total number of species easily exceeding 100 on a regional scale (Marinho-Filho & Sazima 1998).

Currently, the highest number of species recorded locally in those areas encompasses 86 species at Iwokrama Forest in Central Guyana (Lim & Engstrom 2001a) while the lowest includes 49 species at Ilha de Maracá in Brazil (Robinson 1998). Even assuming that none of those inventories is complete, and that some may present sampling biases, it is evident that there is a significant variation in the number of bat species potentially found within sites in the region.

There are several theories to explain the geographical patterns in species richness and some have tried to relate these patterns to a single explanatory factor. One of these theories is the species-energy hypothesis (Currie 1991). It suggests that the amount of available energy sets limits to the richness of ecosystems. However, that energy may be either directly or indirectly available to the species, leading to the formulation of two possible versions of this hypothesis.

One is the ambient-energy version and suggests that it is the amount of energy directly available in the systems that limits animal species richness (Turner *et al.* 1996; Hawkins *et al.* 2003). In fact, Rohde (1992) proposed that high temperatures may lead to faster individual growth rates and to shorter generation times which could speed the rate of molecular evolution. Turner *et al.* (1988) also suggested that high temperatures may create better conditions for endotherms – such as bats – to develop larger populations that are less vulnerable to extinction because they can spare the investment of keeping warm to grow and reproduce, in what is known as the thermoregulatory load hypothesis.

The other version, the productivity hypothesis, suggests that it is not the direct energy but its transformation into different levels of resources that regulates the species-energy relationship (Wright 1983; Hawkins *et al.* 2003). In fact, plant productivity has been recognized as a major correlate of species richness (*e.g.* Oberdorff *et al.* 1995; Ruggiero & Kitzberger 2004; Tognelli & Kelt 2004; Ramos Pereira *et al.* 2009). It is hypothesized that in high-productivity areas there are more resources available in order to sustain larger and more viable populations, thus reducing the extinction risk, and/or species can specialize on few food types, narrowing the niche breadths and promoting the coexistence of more species (Vazquez & Stevens 2004; Evans *et al.* 2005).

Assuming that energy availability can explain much of the regional variation in bat species richness, our aim was to determine the measures of the availability of energy that best explain the variation of frugivore bat richness in the Amazon region. To achieve this aim, as potential correlates of frugivore bat richness in the Amazon basin, we selected several climatic variables, such as measures of temperature and precipitation and productive-energy variables, such as net primary productivity (NPP), its correlates such as the Normalized Difference Vegetation Index (NDVI), or phenological variables extracted from NDVI time-series.

5.3 Methods

Data on bat species richness in the Amazon basin

Frugivore bat richness was compiled for 22 well-sampled rainforest sites within the Amazon basin (Figure 5.1): Brazil (n = 8) – Serra do Divisor (Nogueira *et al.* 1998), Jaú (Barnett *et al.* 2006), Ilha de Maracá (Robinson 1998), Manaus (Sampaio *et al.* 2003), Alter do Chão (Bernard *et al.* 2001; Bernard & Fenton 2007), Rio Xingu (Voss & Emmons 1996), Belém (Kalko & Handley 2001), and Amanã (Ramos Pereira *et al.* 2009); Peru (n = 5) – Jenaro Herrera (Ascorra *et al.* 1993), Cosha Cachu and Pakitza (Voss & Emmons 1996), Balta (Voss & Emmons 1996), Cuzco (Voss & Emmons 1996), and Allpahuayo-Mishana (Hice *et al.* 2004); French Guiana (n = 3) – Saül (Simmons *et al.* 2000), Arataye (including Les Nourages and Saint Pararé, Voss and Emmons 1996), and Paracou (Simmons & Voss 1998); Guyana (n = 2) – Iwokrama forest (Lim & Engstrom 2001a) and Kanunu mountains (Parker *et al.* 1993); Venezuela (n = 3) – Imataca (Ochoa 1995), Canaima (Ochoa *et al.* 1993), Cunucunuma (including Culebra and Acanama, Voss and Emmons 1996); and Ecuador (n = 1) – Yasuni National Park (Reid *et al.* 2000).

Some bat guilds, in particular open space and gleaning insectivores, are difficult to capture using mist-nets. For this reason, and in order to use data comparable among inventories, we restricted our analysis to the guild of frugivores. In fact, most inventories rely solely on mist-netting and the richness of frugivores is usually well assessed using this method.

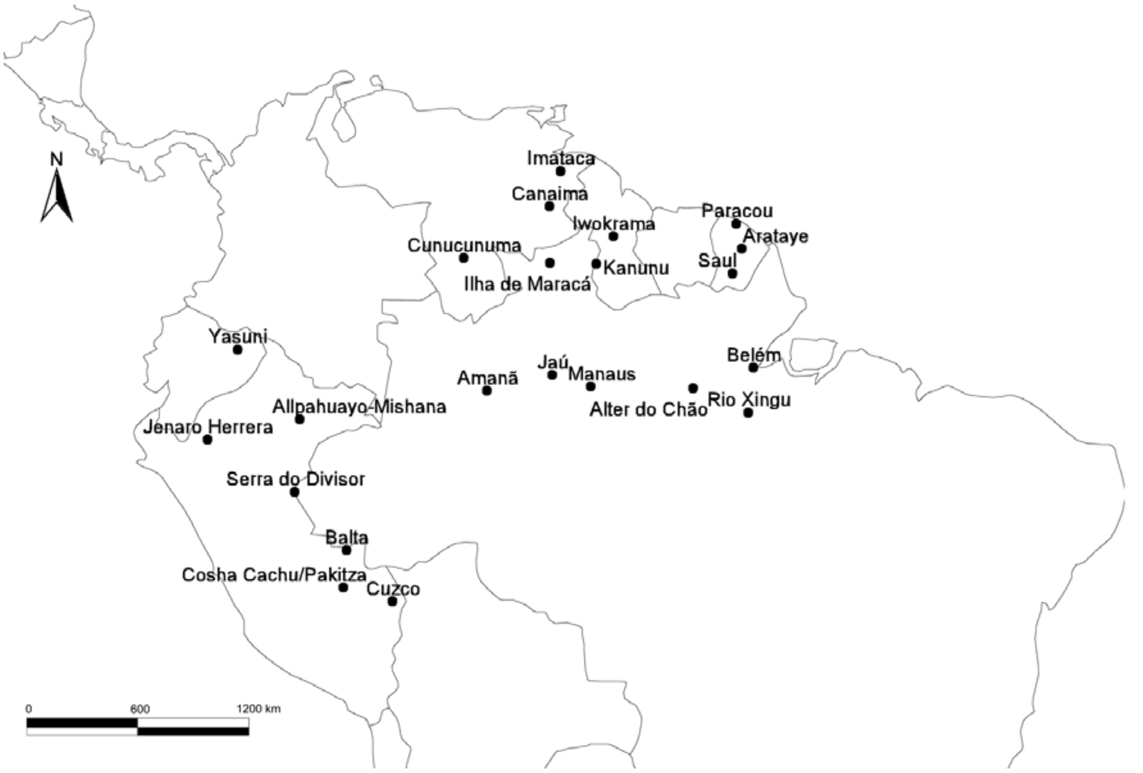


Figure 5.1 Location of the 22 rainforest study sites.

Environmental variables

We selected 14 potential explanatory variables extracted from high-resolution digital data (Table 5.1). The six climatic variables were extracted from WorldClim (Hijmans *et al.* 2005, http://www.worldclim.org). Net primary production (NPP) derived from the Ecosystem Demography Model (Hurtt *et al.* 1998; Moorcroft *et al.* 2001) was obtained from EOS-WEBSTER (http://eos-webster.sr.unh.edu/home.jsp). NDVI (monthly values from 1982 to 1993) were obtained from the same source. This NDVI time-series was then used to extract maximum and minimum annual values and to obtain information on seasonal vegetation development variables using the program TIMESAT (Jonsson & Eklundh 2002;2004). TIMESAT implements different statistical methods for extracting seasonality information from time-series of satellite sensor data; we chose the asymmetric Gaussian fitting function because it works properly for time-series that are quasi-periodical and shows less sensitivity to noise in the satellite images (Jonsson & Eklundh 2004). As the region analysed presented bimodal seasonality, indicating the existence of two annual growing seasons, we extracted the duration and amplitude of the first and the second growing seasons. All variables were re-sampled at 1º resolution in IDRISI (v.14.02).

Though the 22 inventories were based on robust sampling protocols, the sampling effort was distinct between the studies. To detect the potential influence of the sampling effort on the value of frugivore richness, we included surrogate measures of sampling effort as potential explanatory variables. These measures were the total number of bats captured and the use of canopy mist-netting (included as a binary variable).

Multicollinearity among predictor variables may introduce serious bias in these types of analyses, and that may complicate the selection of the best environmental predictors. As we had 16 explanatory variables for 22 values of richness, to avoid models with redundant and multicollinear data structures, we calculated the variance inflation factor (VIF) of each variable to quantify the severity of multicollinearity. A common rule of thumb is that if VIF > 5 then multicollinearity is considered high (Zuur *et al.* 2007). Through sequential least squares regressions analyses we eliminated all variables with VIF > 5 and reduced the list of potential explanatory variables to nine: TS, MinTCM, PS, MaxNDVI, DGS1, DGS2, AGS1, AGS2, and canopy sampling.

Table 5.1 Explanatory variables extracted from high-resolution digital data used in the regression analyses.

Explanatory variables	Abbreviation
Annual average potential net primary productivity	ANPP
Temperature Seasonality (standard deviation *100)	TS
Max Temperature of Warmest Month	MaxTWM
Min Temperature of Coldest Month	MinTCM
Annual Precipitation	AP
Precipitation of Wettest Month	PWeM
Precipitation of Driest Month	PDM
Precipitation Seasonality (Coefficient of Variation)	PS
Annual Maximum NDVI	MaxNDVI
Annual Minimum NDVI	MinNDVI
Duration of season (seasons 1 and 2)	DGS1 and DGS2
Amplitude of season (seasons 1 and 2)	AGS1 and AGS2

We then examined the effects of these environmental variables on frugivore bat species richness by means of multiple regression analyses by applying a forward stepwise selection procedure to the predictor variables. The best model was determined by the Akaike information criterion (AIC). After determining the best predictor variables we did a redundancy analysis to determine the variation explained by the environmental variables after removing the effect of spatial structuring. All statistical analyses were done in R (v. 2.8.0).

5.4 Results

At $\alpha = 0.05$, the best model included only MaxNDVI as an explanatory variable of the variation of frugivore bat richness in the rainforests of the Amazon basin. None of the sampling effort or climatic variables was significant at $\alpha = 0.05$ indicating that the 22 locations were well-sampled for frugivore bats and, answering our main question, the productivity hypothesis best explains the variation in frugivore species richness in the region. MaxNDVI had a strong and positive relation with frugivore bat richness ($\beta_{MaxNDVI}$ = 62.95; F = 4.78, P = 0.04). This variable accounted for 30% of the variance in frugivore bat species richness. Even when removing the effect of the spatial structure of the environmental variables, MaxNDVI still explained 22% of the variation in frugivore species richness.

The spatial pattern of frugivore richness predicted by this model estimates very high species richness in the Guyana shield region, showing a few hotspots where over 31 species of frugivores are expected to occur sympatrically (Figure 5.2). Most of the areas within the central Amazon basin are also expected to have high bat richness with most of the region easily reaching between 27 and 30 frugivore species. The model predicted lower richness of bats in the South and Southeast Amazonia.

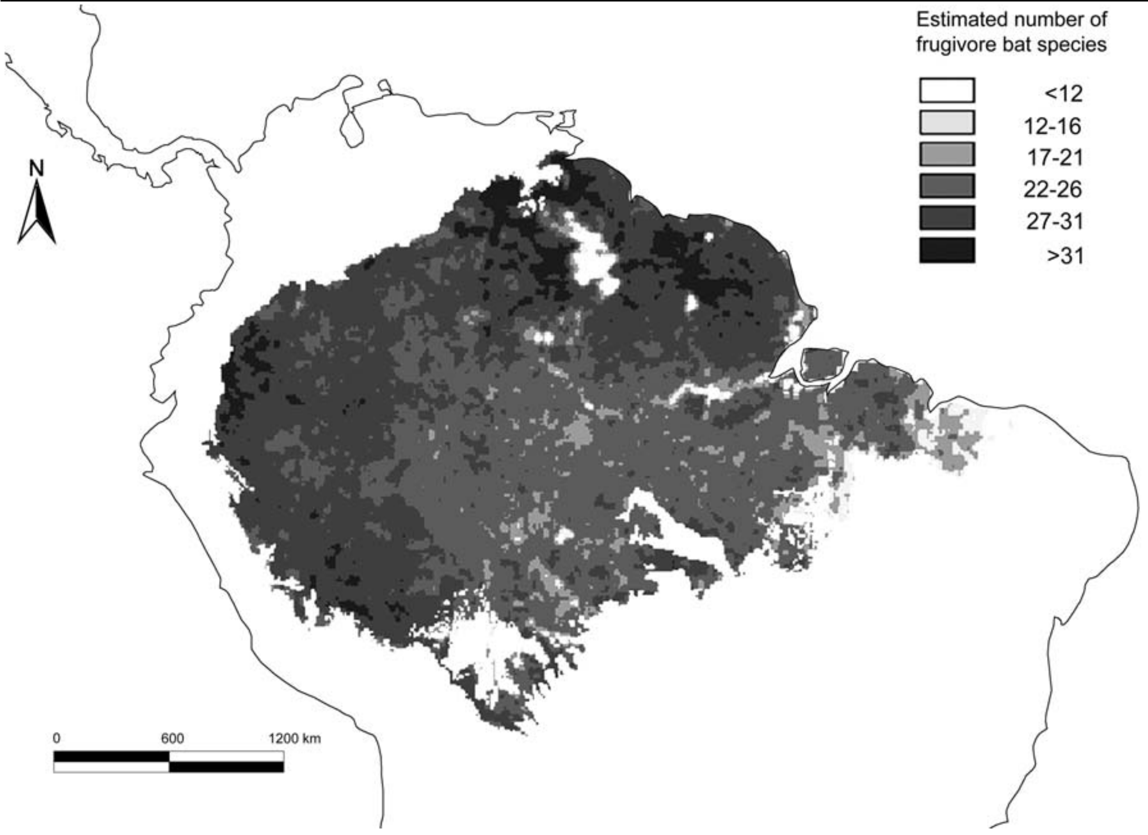


Figure 5.2 Geographical pattern of estimated frugivore bat species richness.

5.5 Discussion

The simultaneous analysis of several potential environmental predictors allowed us to determine which of the two versions of the energy hypothesis – ambient-energy or productivity – is the best in explaining the patterns of bat richness in the Amazon basin. Our results support the hypothesis that it is not the direct amount of energy available in the system but its conversion into food available (*sensu* Wright 1983) that seems to explain the pattern of frugivore bat richness. In fact, maximum annual NDVI, a productive-energy variable seems to be the best predictor of the patterns of frugivore bat richness in the studied region. Additionally, none of the climatic variables entered the multiple regression models indicating that, in Neotropical rainforests, the direct amount of available energy is a weaker predictor of bat richness than productivity. Indeed, while temperature may be an important predictor of bat richness in temperate and subtropical areas (Patten 2004; Ulrich *et al.* 2007), it does not seem to be as important within the study region, where temperature is always high and daily and seasonal fluctuations are small.

Our results suggest that the maximum annual NDVI value is the best indicator of the energy converted into food available for frugivore bats. Maximum annual NDVI was significantly and positively correlated with frugivore bat richness: our model predicted higher frugivore bat richness in the Guyana region followed by central Amazonia, where maximum annual NDVI values are higher and lower frugivore bat richness in South and Southeast Amazonia, where NDVI values are lower than in the former regions.

NDVI has been shown to be related to aboveground net primary production for different geographic areas and ecosystems (Goward *et al.* 1985; Diallo *et al.* 1991; Chong *et al.* 1993; Hobbs 1995), including the Amazon (Prince & Steininger 1999). In our modelling procedures ANPP was removed from the analyses because it showed strong collinearity with the other variables, in particular a correlation of about 0.3 with MaxNDVI.

The relationship between energy and diversity has received considerable attention (for a review see Mittelbach *et al.* 2001; Field *et al.* 2009). Overall, the existing studies suggest that globally NDVI/productivity is positively correlated to species richness, even though correlations are weak in several cases (Gould 2000; Tuomisto *et al.* 2003; Fairbanks & McGwire 2004; Gillespie 2005; Rocchini *et al.* 2005). Our study further confirms the positive relationship between productivity and diversity at a regional scale. In fact, at macro-scales the productivity-richness relationship is usually described as increasing monotonically (Wright *et al.* 1993; Gaston 2000; Chase & Leibold 2003; Evans & Gaston 2005), what seems to be confirmed by our results.

NDVI variables have been shown to be good predictors of species richness in a wide variety of landscapes and groups. These include small mammals at multiple spatial scales in arid and semi-arid grasslands of northern China (Wang *et al.* 1999), and plants of the vegetation communities of California (Fairbanks & McGwire 2004), just to name a few. Interestingly, Bailey *et al.* (2004) also found a strong linear relationship between species richness of Neotropical migrant birds and maximum NDVI suggesting that this guild has specific habitat requirements, relying more strongly on structurally complex vegetation. Similarly, the richness of frugivore bats may also be positively related with the availability of feeding and roosting niches promoted by a high degree of complexity of the vegetation.

Sites with high NDVI values are suggested to support more plants (or are at least representative of plant biomass concentration, *e.g.* Loveland *et al.* 1991; Groten 1993), and eventually more plant species (Gillespie 2005; Gillespie *et al.* 2009). It is then likely that in areas characterized by high NDVI values not only the abundance of fruits available to bats is higher, but also the diversity of their food items. This creates the conditions for the presence of rich frugivore communities because food is abundant and diverse, allowing the coexistence of many species without intense competition. In fact, high-productivity areas have more resources available and can sustain larger and more viable populations because, as suggested by Begon *et al.* (2006), for given values of average niche breadth and niche overlap, a given assemblage will contain more species the more the resources available for that assemblage.

The predicted pattern of higher bat richness in the Guyana region followed by central Amazonia, and lower richness in South and Southeast Amazonia is similar to the richness pattern found by Rahbek and Graves (2001) for breeding birds of South America. They described similar peaks in the richness of birds in the Guyana region, followed by Central Amazonia, while richness decreased in the Southeastern Amazonian region. However, Rahbek and Graves (2001) attributed the avian pattern to a synergism between climate and coarse-scale topographic heterogeneity.

Regardless of the historical productivity or climatic conditions that explain the patterns found for bats and birds, the lower richness predicted or found in Southern Amazonian areas is probably also related to the rapid rate of deforestation in the region in the last decades. In fact, the Amazonian Deforestation Monitoring Project (PRODES) showed that deforested area increased from 10 million hectares in the 1970s to 67 million hectares in 2005, and this was especially intense in the Southern parts of the region (Nogueira *et al.* 2008), affecting mostly Rondônia, Mato Grosso and Pará Brazilian states. On the contrary, the majority of Central and Northern Amazonia did not seem to have suffered extensive deforestation in the last decades. Ultimately, the reduction in forest cover, reflected by changes in vegetation indices (Ichii *et al.* 2003), implies a drop in productivity and has significant impacts on the hydrological cycle, explaining the lower richness values of bats and birds.

We should point out that there were different time scales for the richness and remote sensing datasets. At a time of fast landscape transformation, the integration of species records collected over different years with satellite imagery acquired at different dates is a potential source of error that could not be accounted for in the present study.

Conclusions

We have demonstrated the applicability of multitemporal remote sensing in analysing Neotropical bat species richness and found strong support for productivity as a factor indicative of frugivore bat richness in the Amazon basin. As suggested by Evans *et al.* (2005), the strength of the species–energy relationship is dependent on the energy metric used, implying the usefulness of including several currencies of energy availability in the modelling procedures. Still, as referred above, we believe that the exclusion of ANPP from the model is mostly due to its correlation with MaxNDVI.

Within this highly diverse region we identified hotspot areas where at least 31 frugivore bat species may coexist, and this pattern may be similar for other bats guilds. However, it is possible that some guilds show different strength of the species-energy relationship. Because they are primary consumers, frugivorous species may be the ones more critically affected by variations in productivity. Indeed, Evans *et al.* (2005) found that, within British avifauna, the richness of herbivores and omnivores exhibited a stronger relationship with productivity than that of invertebrate and vertebrate predators, while Bailey *et al.*(2004) found different strengths of the relation between NDVI and the richness of different bird guilds in the Great Basin area. We emphasize that the validation of productivity as a predictor of species richness would possibly be achieved by doing additional inventories, especially in the predicted hotspot areas. Our results suggest that satellite remote sensing can be used for estimating spatial variation in bat richness. This may have a direct application in conservation planning, as the selection of areas that support more species diversity per unit area may yield a large return for conservation efforts. This selection of areas is important in Neotropical rainforests because of the growing human pressure affecting them. In fact, this technique has the advantage of highlighting areas of potentially high species richness across large regions that would require substantial investments of time and money to survey directly. It may also allow the detection of trends studied over time, and the identification and subsequent management of areas that are consistently productive.

Chapter 6

Niche conservatism and the latitudinal diversity gradient in New World bats

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6 Niche conservatism and the latitudinal diversity gradient in New World bats

6.1 Abstract

The aim of this study was to: (i) describe the latitudinal gradients in species richness and in the evolutionary age of the species of the nine extant families of New World bats, and (ii) to test if those latitudinal patterns, under the light of the known evolutionary history of the Chiroptera, may be explained by the niche conservatism hypothesis. Maps of species ranges were used to estimate species richness within families in grids of 1º. A molecular phylogeny resolved to the species level were used to determine the root distance of each species, used as proxy of the age of the taxa. Generalised additive models (GAM) were used to determine the relationship between species richness and latitude, and mean root distance (MRD) and latitude for each of the three most specious New World bat families. Spatial autocorrelation was tested using Moran's *I*. Species richness was correlated with latitude, increasing towards the equator in the whole of the Chiroptera and in the Phyllostomidae and Molossidae, but not in the Vespertilionidae that presented its richness peak in temperate North America. In the whole of the Chiroptera, and in the three main families, the MRD latitudinal pattern was the same, with more basal species in the higher latitudes, and more derived species in tropical areas; the overall richness pattern was not more correlated with the basal species richness pattern than with the derived species richness pattern, as would be expected under a niche conservatism scenario. In general, our results were not consistent with the predictions of niche conservatism. In conclusion, niche conservatism only partly explains the latitudinal diversity patterns of New World bats. It does seem to explain the absence of many bat clades of tropical origin in the temperate zone, as they are unable to survive cold winters. In addition to this factor, the richness gradient is consistently explained by the global climatic conditions under which the different families possibly radiated, together with biotic factors such as competition. The patterns in MRD generally do not respect the predictions under the niche

conservatism hypothesis and are better explained by alternative theories such as latitudinal differences in rates of molecular evolution or the existence of more diverse ecological opportunities in the tropics.

6.2 Introduction

The dramatic increase in species diversity from the Poles to the Equator is one of the most obvious biogeographic patterns, but the mechanisms underlying it remain quite obscure. The relevance of contemporary ecological mechanisms, such as climate, to the development of this pattern is widely recognized, but since it developed over evolutionary time scales it is likely that historical factors played an important role in its formation. The relative importance of the contributions of contemporary and historical factors to the formation of latitudinal patterns in species richness is currently an active area of research (Ricklefs 2007).

Niche conservatism is one of the hypothesis that has been suggested to explain how ecology and climate act on evolutionary and biogeographic processes (*e.g.* speciation, dispersal, extinction) to determine large scale patterns of species richness (Ricklefs & Latham 1992; Peterson *et al.* 1999; Wiens 2004; Wiens & Donoghue 2004). This hypothesis is based on evidence that most of the components of the fundamental niche, which describes the set of abiotic conditions in which a species is able to persist (*sensu* Hutchinson 1957), are conserved over long evolutionary time scales. Such phylogenetic conservatism may constrain the geographic range of species (Wiens & Donoghue 2004), and consequently influence latitudinal biogeographic patterns.

The relevance of niche conservatism has received increasing support from ecologists (Wiens & Graham 2005; Crisp *et al.* 2009), but recent reviews by Pearman *et al.* (2008) and Losos (2008) suggested that the universality of niche conservatism may have been overstated. Analysing studies done during the last decade they found that phylogenetic niche conservatism seems to occur in some clades for some traits, but not in others, and that frequently niches exhibit great evolutionary lability. For this reason, more empirical studies are needed to address the theoretical predictions of niche conservatism.

The consequences of niche conservatism on species richness allow the formulation of testable predictions (Wiens & Donoghue 2004; Hawkins *et al.* 2005; 2006). First, if species tend to be unable to persist outside the conditions of their fundamental niche, then higher species richness is expected in regions with environmental conditions closer to the ones that characterized the ancestral niches of the clades. Second, if the ecological characteristics of basal clades are closely linked to climatic conditions, then basal taxa should be mostly confined to regions with climatic conditions similar to the ones prevailing where the group originated; conversely, more derived taxa are expected in regions with different conditions because they had more time to evolve and adapt to those conditions. Finally, if niche conservatism drives the latitudinal richness pattern, then this pattern should be mostly determined by the distribution of basal taxa. Consequently, the spatial correlation between the total richness and the richness of basal taxa should be higher than that between total richness and the richness of derived taxa.

New World bats are a particularly good group to test the niche conservatism hypothesis for a variety of reasons. First, they are a highly specious group with more than 300 species belonging to nine of the 18 extant families of bats (Simmons 2005). Second, at the ordinal level, New World bats are known to follow the typical latitudinal increase in species richness towards the tropics (Simpson 1964; Fleming 1973; Kaufman 1995; Patten 2004; Stevens 2004), but with apparent contrasting patterns at the family level. And third, recent studies based on molecular, morphological, and fossil data have shed additional light on the evolutionary history of the Chiroptera (*e.g.* Sears *et al.* 2005; Teeling *et al.* 2005; Sears 2008) making available useful information on the radiation of New World bats (Simmons 2008). This information, together with the availability of phylogenetic trees and of distribution datasets covering most of the New World bat species, allows us to investigate if the pattern of bat species richness in the New World can be explained by the niche conservatism hypothesis.

The overall objective of this paper is to contribute to the clarification of the potential role of niche conservatism in the establishment of latitudinal diversity trends in New World bats. To do this we (1) described the latitudinal gradients in both species richness and evolutionary age for New World bats as a whole, and individually for its three largest families, and (2) tested if the observed latitudinal diversity patterns, under the light of the known evolutionary history of the Chiroptera, are compatible with the predictions of the niche conservatism hypothesis. We based these tests on predictions analogous to those used for birds by Hawkins *et al.* (2006; 2007).

If niche conservatism is a dominant mechanism underlining the latitudinal diversity gradient in New World bats then more species and, in average, older (evolutionary more basal) species should occur in areas that retain climatic conditions similar to those found during the radiation of the group. In addition, the spatial correlation between the total species richness and the species richness of basal taxa should be higher than that between the species richness of the group and the species richness of derived taxa. We tested these predictions not only for New World bats in general, but also separately for each of the three most specious families - Phyllostomidae, Vespertilionidae, and Molossidae.

6.3 Methods

Maps of species ranges of New World bat species were obtained from NatureServe (Patterson *et al.* 2005). This dataset is the most comprehensive database of distribution ranges available and at the time of this study included 305 of the New World bat species.These maps were rasterized into grids of 1º (generating 5634 cells) in ArcView 3.2 and species richness was estimated for all grids. Each species was assigned to a root distance (RD), representing the number of nodes separating a species from the base of a phylogenetic tree (Hawkins *et al.* 2005; 2006; 2007). The RD was used as a proxy of the age of the species: a higher number of nodes reflect a more recent speciation event. The RD values were obtained from the mammal phylogenetic tree resolved to the species level presented by Bininda-Emonds *et al.* (2007), which integrates the Jones *et al.* (2002) pre-existing supertree for the Chiroptera. A mean root distance (MRD) for each cell of the grid was then calculated for each of the nine New World bat families, and for all the families combined. For 56 of the 305 species in the NatureServe dataset it was not possible to attribute a RD because they were not included in the phylogenetic tree; these species were removed from further analyses related to the age of the clades.

To determine the direction and the significance of the relationship between (1) species richness and latitude, and (2) MRD and latitude we used generalised additive models (GAM) because they allow for including non-linear terms in the linear predictor term (Hastie & Tibshirani 1990). The models were calculated using the package mgcv (Wood 2001) implemented in R software (Ihaka & Gentleman 1996). Spatial autocorrelation may inflate estimates of statistical significance, so we tested it using Moran's *I* values obtained at 10 different distance classes to create correlograms of the residuals of the initial models, using SAM software (Rangel *et al.* 2006). The statistical significance of Moran’s *I* ($P < 0.05$) is based on distances by randomization (using a Monte Carlo procedure; 200 permutations).

To test the prediction that total species richness follows the richness pattern of basal taxa, we calculated Pearson correlation coefficients between total richness and both basal and derived richness. To estimate these two types of richness we first ranked all the species from most basal to most derived and then defined as basal and derived the species in the 25% and 75% quartiles, respectively. Species richness was then calculated separately for each of these quartiles. As basal and derived groups are constrained to be correlated to the total data set (from which they were extracted), the spatial structure of total, basal and derived data sets was examined using Moran’s I autocorrelation coefficients obtained at 10 distance classes. Moran’s I coefficients for basal and derived taxa were then correlated against the Moran’s I of all taxa to assess the similarity of the spatial pattern of each of the subgroups with the pattern of the whole of the taxa using a major-axis model II regression implemented in RMA (http://www.bio.sdsu.edu/pub/andy/RMA.html); slope, R^2 and associated standard errors estimates were calculated using one-delete jacknife procedure (Weir 1990).

6.4 Results

Latitudinal patterns of richness and mean root distance

Both species richness and MRD were highly correlated with latitude in the Chiroptera (Figure 6.1).

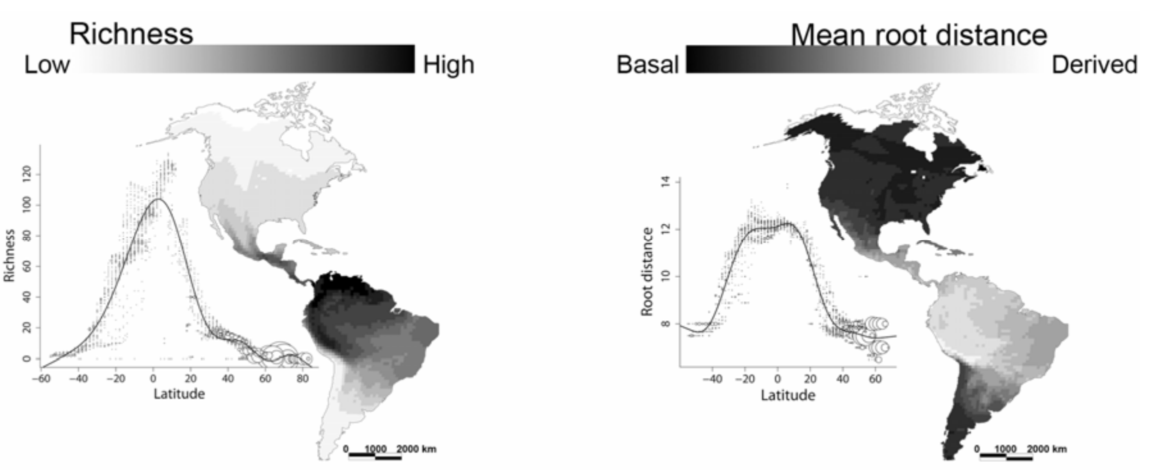

Figure 6.1 Geographical pattern of species richness (left) and mean root distance (right) in the Chiroptera resolved at a 1º grain size. The plots show the relationships between latitude and species richness and between latitude and root distance. The size of the circles is proportional to the number of grids with the same bat richness at the corresponding latitude. The line shows the adjustment of the GAM model. White areas on the map indicate the absence of bats.

Species richness is higher in tropical regions and more evolutionary basal species are found in higher latitudes. The percentage of deviance explained by the GAM was of 91.0% for species richness and 89.8% for MRD. Both models were significant at $p < 0.001$. With the exception of the Vespertilionidae (Figure 6.2) all the different families showed a richness latitudinal pattern similar to the general pattern of the Chiroptera, with an increase of the number of species towards tropical regions. However, the number of species in most bat families is too limited to generate robust spatial patterns in species richness and MRD, so we only present separate analyses for the three most specious families (Figure 6.2).

The Phyllostomidae are absent from high latitudes and their species richness tends to increase towards the Equator, reaching a clear peak just north of it (Figure 6.2). The percentage of deviance explained by the GAM was 90.6%. Within the range of the family more basal species tend to occur at higher latitudes, towards the temperate zones, but there is no discernable latitudinal trend within the tropical zones. The variation in root distance explained by the GAM was 43.9%.

The latitudinal patterns observed in the Molossidae are very similar to those of the Phyllostomidae. Their species richness also peaks just north of the Equator and declines with latitude, but they penetrate further into the temperate zones. MRD is greater in the tropics: more basal species are found at the highest latitudes within the distributional range of the family, but the MRD remains relatively stable across tropical latitudes. The percentage of deviance explained by latitude was 94.3% and 79.2% in the richness and MRD models, respectively.

The Vespertilionidae is the family with the broadest latitudinal range, and is present at almost all latitudes. The species richness pattern contrasts with those of the other families, as the peak of species richness is not located in the tropics but in temperate North America (Figure 6.2).

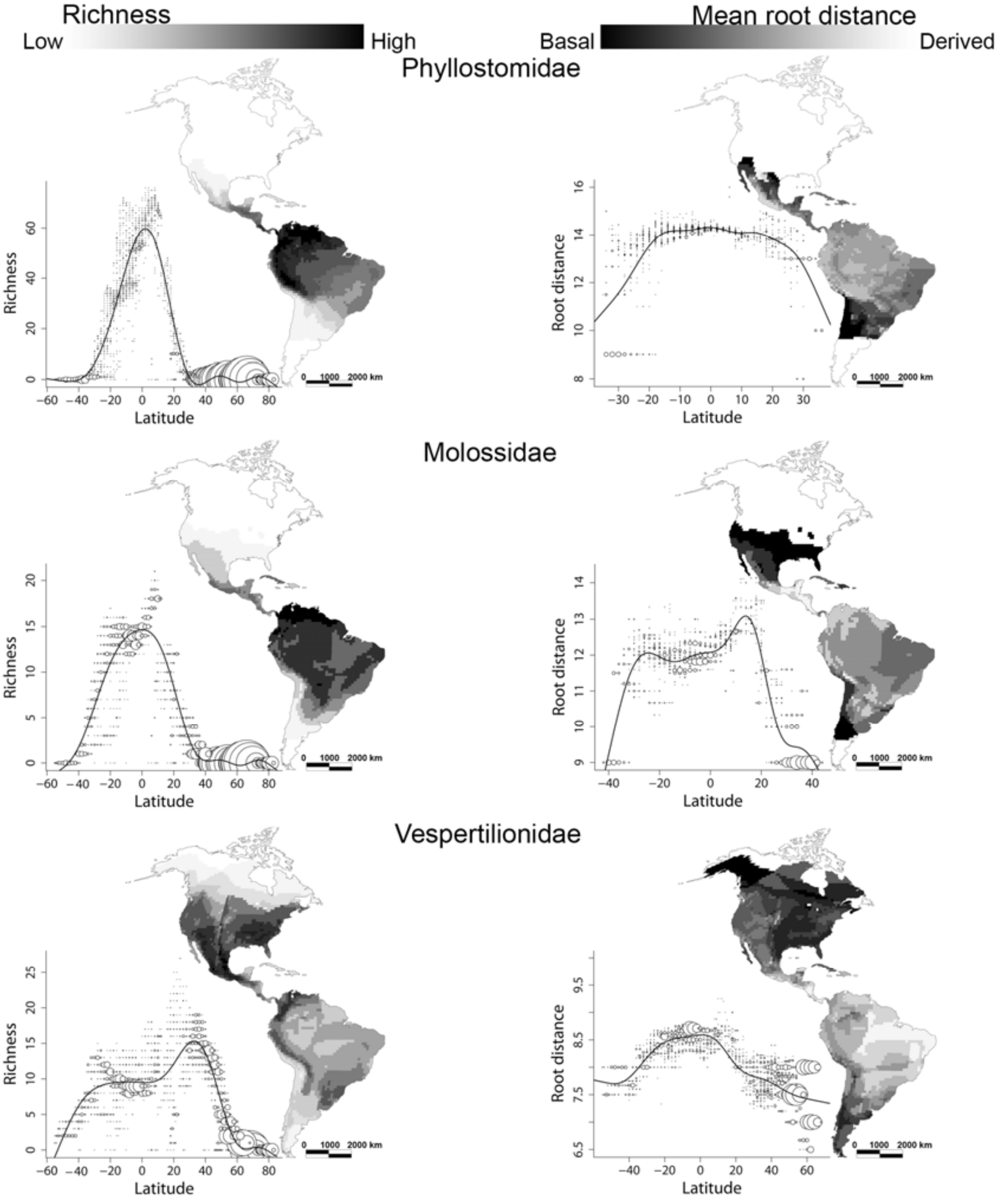

Figure 6.2 Geographical pattern of species richness (left) and mean root distance (right) in the Phyllostomidae, Molossidae, and Vespertilionidae resolved at a 1º grain size, and relationships between latitude and species richness and between latitude and root distance using GAMs. The size of the circles is proportional to the number of grids with the same bat richness at the corresponding latitude. The line shows the adjustment of the GAM model. White areas on the map indicate the absence of bats. All models were significant at $p < 0.001$.

In South America there are regions of greater diversity but located in temperate or montane areas. The percentage of deviance explained by the GAM was 80.7%. Like in other bat families MRD increases towards the tropics, with more basal species present at the highest latitudes. Although the density of basal species is higher in the Northern Hemisphere, they also occur in temperate areas of South America. The deviance explained by latitude on the root distance GAM was 32.7%.

Moran's *I* values did not show significant spatial autocorrelation even at the finest scale of analysis, for both the richness and root distance GAM (Figure 6.3). Indeed, even in the models with lowest percentage of deviance explained by latitude, Moran's *I* values rarely exceeded 0.1. For this reason, there was no need to subsample cells to generate spatially independent data sets to adjust the final GAM.

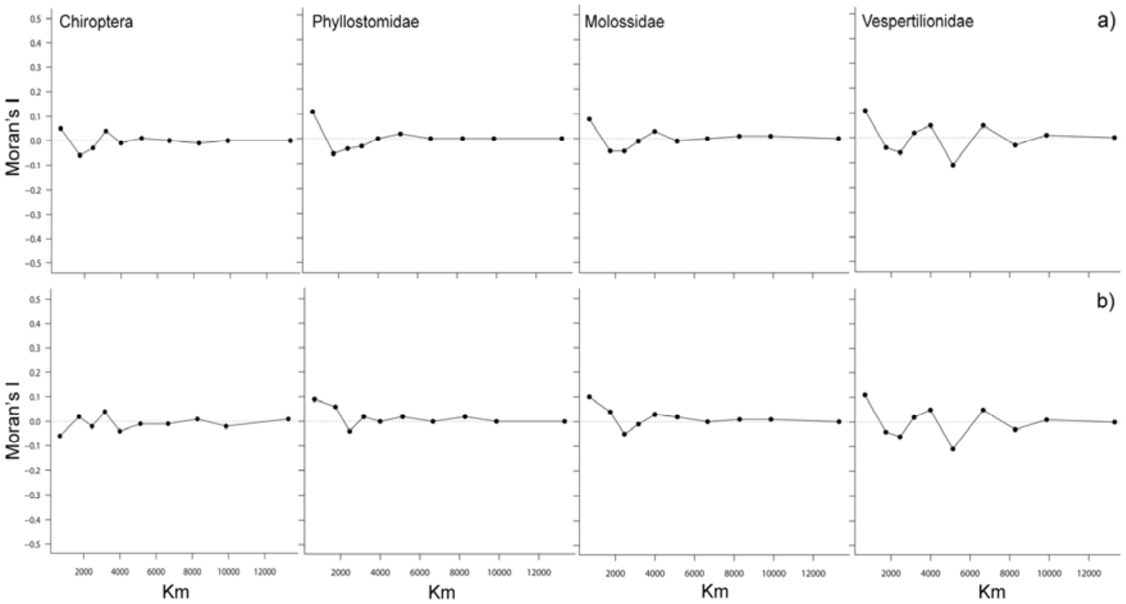

Figure 6.3 Moran's *I* correlograms of residuals after fitting the models for species richness (top) and mean root distance (bottom). None of the values is significant at α = 0.05.

Relationship between total, basal, and derived species richness

In the whole of the Chiroptera and in the Phyllostomidae, Molossidae and Vespertilionidae, both the basal and the derived species richness are strongly correlated with the overall species richness (Figure 6.4).

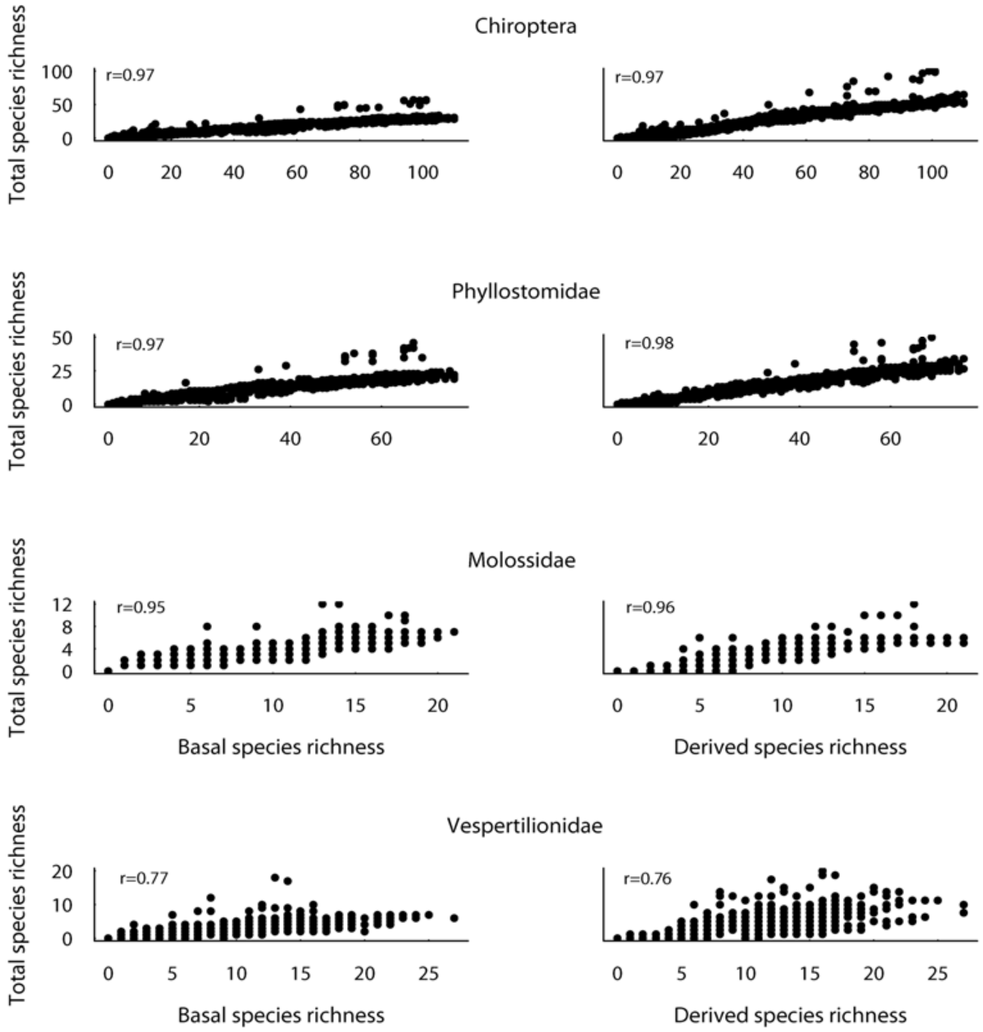

Figure 6.4 Relationships between total species richness and the richness of basal and derived bats for the Chiroptera and the families Phyllostomidae, Molossidae and Vespertilionidae. Pearson correlation coefficient (r) between total richness and basal and derived richness is shown above each figure.

The spatial correlogram for total species richness shows a strong positive autocorrelation at distances <2000 km in the order and in all families (Figure 6.5). The patterns for basal and derived species are very similar to the general pattern in the Phyllostomidae and Molossidae. Type II major-axis regression of the Moran's *I* values of the total richness against the *I*s of basal and derived richness resulted in slopes approximately equal to 1 in the Phyllostomidae (total *vs* basal: b = 1.01 ± 0.02, R^2 = 0.99; total *vs* derived: b = 1.04 ± 0.01, R^2 = 0.99) and Molossidae (total *vs* basal: b = 1.00 ± 0.03, R^2 = 0.99; total *vs* derived: b = 1.09 ± 0.01, R^2 = 0.99). Only in the Vespertilionidae there was a slight deviance of the Moran *I*s of the total richness against the *I*s of basal richness (total *vs* basal: b = 1.33 ± 0.36, R^2 = 0.67; total *vs* derived: b = 1.07 +- 0.19, R^2 = 0.83).

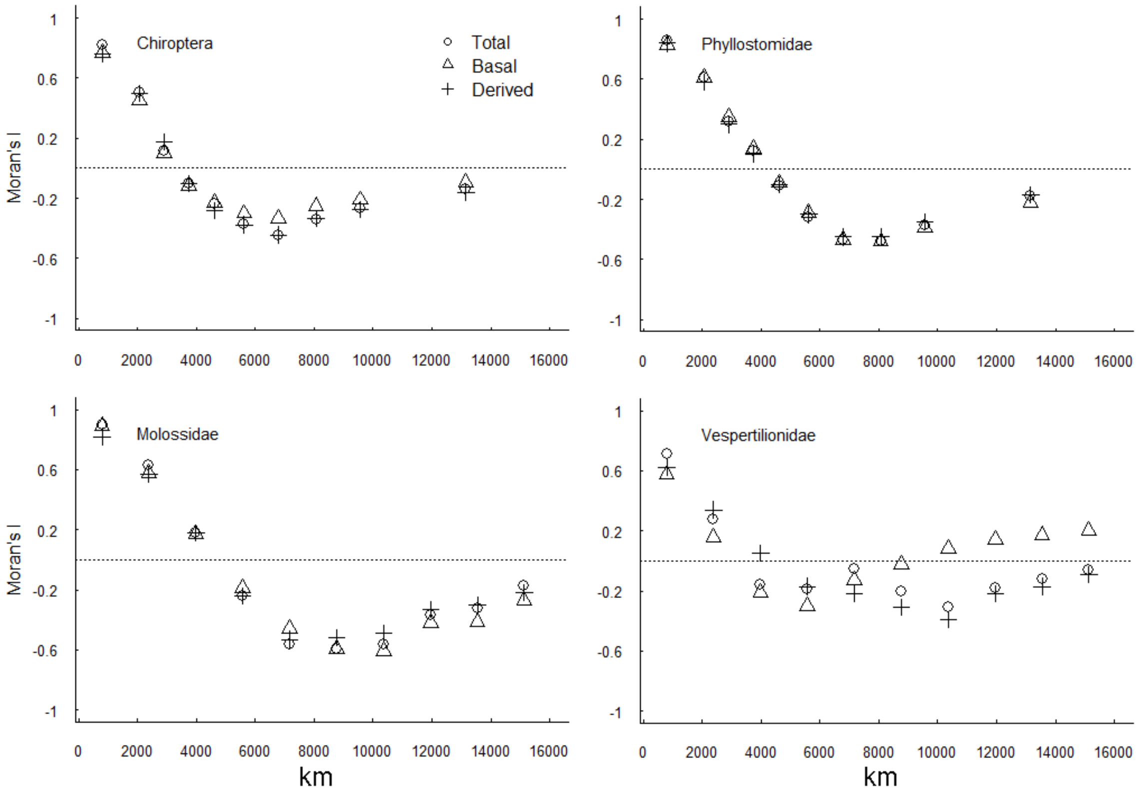

Figure 6.5 Spatial correlograms for total species and for basal and derived species in the Chiroptera and in the families Phyllostomidae, Molossidae and Vespertilionidae.

6.5 Discussion

General patterns of richness and mean root distance

All bat super-families appear to have originated within a narrow time frame between 52 to 50 Mya, following the Paleocene-Eocene Thermal Maximum (Teeling *et al.* 2005), when most of the world climate was tropical. Niche conservatism would then predict the existence of greater bat richness in the tropics because most clades originated and had more time to speciate under a tropical environment, and this was indeed observed in our analysis with all bat families pooled (Figure 6.1). The increase of bat richness towards the New World tropics has been described before by several authors, and is generally interpreted as a consequence of contemporary ecological factors correlated with latitude (Willig & Selcer 1989; Kaufman 1995; Patten 2004).

The second prediction of niche conservatism, assuming a tropical origin for most bat families, is that more basal clades should be found in the tropical region, while derived taxa that have gained adaptations to survive colder temperatures should be more prevalent in temperate regions. However, this prediction was not upheld in our analysis, as the highest latitudes in average harbour more basal bat clades than the tropics (Figures 6.1 and 6.2). This result contrasts with that reported for New World birds (Hawkins *et al.* 2006), which are represented by more derived clades at higher latitudes, thus in line with the predictions of niche conservatism. The difference may be due to the fact that some ancient and highly specious bird families, such as the Tinamidae, Cracidae, and Psittacidae, are restricted or nearly restricted to the tropics, whereas in bats most of the families of Neotropical origin are quite derived. This is the case of the phyllostomids, a comparatively derived clade that is very influential in the analysis because it includes many species.

Contrarily to the predictions of the niche conservatism hypothesis, the spatial correlation between the Chiroptera total species richness and the species richness of basal taxa was not higher than that between species richness of the group and the species richness of derived taxa. It follows from these results that the overall increase of bat diversity towards the equator should not be interpreted as a simple consequence of niche conservatism, which would have resulted in a greater preponderance of basal clades in the tropics, where they evolved, than at higher latitudes.

However, even if all the super-families of bats presumably originated in a tropical environment, the various families may have radiated under different climatic origins. In particular, the Vespertilionidae, may have not diversified in the tropics, as suggested by the molecular phylogeny of some of its genera (*e.g. Myotis*, Stadelmann *et al.* 2007). Because the predictions made under the niche conservatism hypothesis are relative to the origin of the clades, if all families do not have the same origin then their individual trends may cancel out and hide patterns.

To avoid this potential confounding effect of pooling species from families with different climatic origins we also analysed the predictions of niche conservatism separately for the three families with more species in the New World. In the Phyllostomidae and Molossidae species richness increases towards the equator, and more basal clades are found at the highest latitudes. However, the Vespertilionidae show a different pattern exhibiting more species and in average more basal in temperate areas. Though belonging to the same super-family, the current geographical distributions of molossids and vespertilionids suggest different initial radiation points and/or times. Indeed, the Molossidae is mostly a tropical and sub-tropical family worldwide, whereas the Vespertilionidae are the dominant bats of temperate areas (Fenton 2002).

There are then two families – Phyllostomidae and Molossidae – with tropical distribution and eventual origin, and a third – Vespertilionidae – mainly with a temperate distribution, potentially due to an initial point for dispersal located in a cooler, temperate region. So, besides the general idea of 'tropical' niche conservatism, the pattern shown by vespertilionids could suggest some kind of ‘temperate’ niche conservatism. These two ideas will be discussed separately.

Does ‘tropical’ niche conservatism explain the latitudinal diversity patterns in the Phyllostomidae and Molossidae?

The Phyllostomidae apparently radiated in the warm and wet Middle Eocene South America (Teeling *et al.* 2005), and nowadays they reach their peak of richness just north of the Equator (Figure 6.2). There is virtually no latitudinal trend in MRD within the tropics but, contrarily to the predictions of niche conservatism, the few species present in the temperate zones tend to be in average more basal than the ones in the tropics (Figure 6.2). Using data from bat assemblages of 30 New World sites, Stevens (2006) reported a slight decline in root distance towards higher latitudes. To investigate if this apparent conflict with our results was due to the use of distinct phylogenetic trees or different distributional data, we applied MRD measured on the tree used by Stevens (2006) (Baker *et al.* 2003) to our dataset of distributional ranges. The results were very similar to those we had obtained with the Bininda-Emonds *et al.* (2007) supertree. This suggests that the disagreement is due to the differences in the distributional data, presumably mostly because his sites range from 21.1ºN to 24.1ºS, whereas our distribution maps reach the northern and southern limits of the family (37ºN and 35ºS, respectively), according to the range maps obtained from NatureServe (Patterson *et al.* 2005).

The results that we obtained for the molossids, which also have their peak of richness just north of the Equator, parallel those obtained for the phyllostomids; there is no clear trend in MRD within the tropics, but the few species present at the northern and southern limits of the range of the family are very basal (Figure 6.2). The great similarity in the patterns observed in the two families suggest that the factors determining the latitudinal trends in richness and in MRD are very similar for both families. The analyses of the spatial correlation between total, basal, and derived richness did not yield results consistent with the predictions of the niche conservatism hypothesis. In fact, both in molossids and phyllostomids basal richness was not more correlated to total richness than derived richness. It seems clear that, with the exception of an increase in diversity towards their tropical origin, none of the analysed predictions niche conservatism was upheld for the two largest New World tropical bat families. So can we rule out a role of tropical niche conservatism to explain the latitudinal richness trend in these families?

As Wiens & Donoghue (2004) point out, strong evidence for a role of niche conservatism can come from finding the eco-physiological traits that underlie the limits of the ranges of the clades, and for both families that trait is quite evident: the lack of adaptations to cold winters, especially the capacity to hibernate. Without the ability to hibernate, which is useless in the warm tropics, these bats cannot survive the cold and food scarcity that prevails in temperate zone winters (Speakman & Thomas 2003). Therefore, it can be said that the northern and southern limits of the two families are indeed a consequence of niche conservatism.

The near absence of phyllostomids and molossids from the mid and high latitudes of the New World may be a consequence of their current lack of adaptive capacity to colonize these colder regions. However, it seems quite likely that these families once occupied a broader latitudinal band, and that their present distribution is relictual, reflecting a contraction of the range into regions where warmer climates persist, as suggested by Hawkins *et al.* (2006) for the ‘tropical’ clades of New World birds. In fact, during the warm early Eocene, tropical and other thermophilic vegetation extended into higher latitudes (Utescher & Mosbrugger 2007), and this may have allowed the expansion and diversification of tropical bat families up to the mid-latitudes of North America. The climate cooling towards the Late Eocene and the consequent turn-over of the vegetation and plant diversity (Wilf 2000), presumably caused the latitudinal retreat of clades specialised in thermophilic environments, such as the phyllostomids and molossids, because they lacked the plasticity to adapt to the new ecological and climatic conditions.

However, the scarcity of bats of these families in the temperate zones may have been accentuated by competition with vespertilionids. In fact, at least one Old World molossid, *Tadarida teniotis*, has the capacity to enter lethargy during the winter (Arlettaz *et al.* 2000), and thanks to that it ranges well into the temperate zone. This shows a potential of molossids to adapt to cold winters, but their radiation in the temperate zones is probably constrained by the competition with the very diverse insectivorous vespertilionids, which have much more developed hibernation capacities.

It is worth noting in our results that there is a clear decline in richness of phyllostomids and molossids with latitude within the tropical region, which is not accompanied by a corresponding decline in MRD. This suggests that niche conservatism is not a major determinant of this intra tropical richness trend, which may instead be caused by ecological factors. There are other important macrogeographic trends, such as the east-west richness decline in South America, presumably due to factors like topography and rainfall, which are known to influence bat species richness (Patten 2004).

Does 'temperate' niche conservatism explain the latitudinal diversity patterns in the Vespertilionidae?

The precise geographical origin of vespertilionids is still equivocal, but their radiation is presumably temperate, in the sequence of the conquest of hibernation. The niche conservatism hypothesis would then predict higher species richness and more basal clades in temperate areas than in the tropics, and indeed both predictions are consistent with the observed trends (Figure 6.2). This result, interpreted in the light of niche conservatism, would suggest that having radiated under a temperate climate the basal vespertilionids would have reduced ability to colonize tropical environmental conditions, because some element of the fundamental niche had limited their expansion towards the equator. Only the most derived clades had evolve to brake the barriers of this fundamental niche and expanded to the tropics.

However, we find that this simple scenario is not very likely for several reasons. The number of vespertilionid species in the neotropics is lower than in the temperate zones, but the contrast between the two regions is much less marked than that observed for the molossids and phyllostomids, which are virtually absent from regions with conditions different from those under which they originally evolved. The penetration of several genera of vespertilionids in the neotropics is thus very substantial, weakening the argument that there is an element in the fundamental niche of this group of bats that prevents them from adapting to tropical conditions. The argument is further weakened by the even greater success of vespertilionids in the Old World tropics, under climatic conditions very similar to those existing in the neotropics. Finally, New World vespertilionid clades are actually very diverse in Northern Central America and parts of Mexico that have tropical and subtropical climates.

All this evidence argues against any intrinsic inability of the vespertilionids to adapt to the Neotropical climatic conditions, and thus argues against a dominant role of niche conservatism to explain the decrease of richness of this family towards the tropics. Then how can this departure from the trend that is so typical of bats be explained? The Neotropics harbour by far the richest existing bat fauna, and this includes many insectivorous species of the tropical families Emballonuridae, Furipteridae, Mormoopidae, Thyropteridae and Phyllostomidae. The vespertilionids presumably had a laurasian origin (Teeling *et al.* 2005) and, when they started to disperse into South America, they met a well established and diversified fauna of insectivorous bats, which had evolved over a long period to fill the available niches. Competition from these pre-existing bat families may have kept vespertilionids from diversifying. This scenario of “late arrival” is compatible with the known molecular phylogenies of New World vespertilionids, such as that of the genus *Myotis* (Stadelmann *et al.* 2007), the vespertilionid genus with most species in South America. Indeed *Myotis* presumably arrived to South America only 7-10 Mya (Stadelmann *et al.* 2007) thus well after the appearance of the above referred Neotropical families (Jones *et al.* 2005; Teeling *et al.* 2005), and of the arrival of the Emballonuridae to South America (Lim 2007).

This "competition hypothesis" has been suggested before to explain the decrease in richness towards the Equator of the vespertilionid genus *Myotis* (LaVal 1973; Stadelmann *et al.* 2007). It is supported by the fact that the areas with greater richness of vespertilionids in intertropical South America are located in montane regions, where the colder climate may give them an adaptive advantage over the tropical bat clades (Figure 6.2). In addition, the richness of vespertilionids is almost the "negative" of that of the other New World insectivorous bats taken together (Figure 6.6).

Figure 6.6 Geographical pattern of species richness in insectivorous bats belonging to the families Emballonuridae, Furipteridae, Molossidae, Mormoopidae, Phyllostomidae, and Thyropteridae resolved at a 1° grain size. White areas indicate the absence of bats of those families.

In summary, if temperate niche conservatism was the explanation for the decrease of richness towards the Equator observed in the Vespertilionidae, then the tropical richness of this family in the Neotropics would be constrained by some element of its fundamental niche, related to abiotic conditions. Although we can not entirely dismiss this possibility, the available evidence supports instead that the constraint to vespertilionid radiation in the neotropics results from competition with other pre-established insectivorous clades.

How to explain the increasing proportion of derived bat species towards the equator, regardless of their climatic origin?

The overall latitudinal trend in MRD in bats, regardless of their origin, was an increase from the temperate to the tropical region, which suggests that niche conservatism is not the major determinant for the relative representation of basal and derived bat clades at different latitudes. It has been suggested that the greater prevalence of derived taxa of certain groups of organisms in the tropical regions may be a consequence of a tendency for faster rates of evolution in the tropics (Cardillo 1999; Bromham & Cardillo 2003). Still, latitudinal differences in rates of evolution need further evaluation as the recent findings of Weir & Schluter (2007), according to which the time to divergence for sister species is shorter at high latitudes and longer in the tropics, conflict to prevailing views.

In the case of bats faster tropical speciation rates have not been demonstrated, but they can be considered plausible. Higher tropical temperatures may lead to faster individual growth rates and to shorter generation times which could speed the rate of molecular evolution (Rhode 1992). Indeed at least in the temperate zones the development of the embryos and the growth of young bats can be slowed by low environmental temperatures (Racey 1969;1973; Racey & Swift 1981) and, whereas holarctic bats are monoestrous, many tropical species are polyestrous (Racey & Entwistle 2000). Continual asynchronous breeding is common in Neotropical Phyllostomidae and Molossidae and is usually related to food availability. This strategy is also found in some Neotropical vespertilionids such as *Myotis nigricans* (Wilson & Findley 1970), where the reproductive cycle seems to be related to insect supply. These differences in the life cycle of temperate and tropical bats lead to shorter generation times in the latter; this decrease in generation times could eventually lead to an increase in the rates of evolution and diversification, but the existence of such relation is still unclear (Barraclough & Nee 2001).

An alternative explanation for the greater prevalence of derived bats in the tropics could be related to the environmental complexity hypothesis (Pianka 1966), according to which this complexity increases towards the tropics. So, as older species occupied the comparatively few niches available in temperate regions it became more difficult for new species to succeed because they would need to compete for niches with the older, well adapted clades. In the ecologically more diverse tropics, more niches could allow a greater success in speciation.

The increase in the proportion of basal species at higher latitudes in families of bats with a tropical origin, such as the Molossidae and Phylostomatidae, could also be a consequence of a greater difficulty of successfully speciating in these regions with cold winters. Over time a few basal species of phyllostomids and molossids, such as *Macrotus californicus*, *Leptonycteris curasoae*, and *Tadarida brasiliensis* developed strategies to cope with the conditions of the southern part of the temperate zones. However, without capacities to hibernate, additional successful adaptations are quite unlikely to occur, so speciation may actually be less frequent than in the tropical zones. This would justify the more basal character of the bats living on the temperate edges of the distribution ranges of the two families.

Conclusions

In general, the predictions of niche conservatism related to the latitudinal distribution of derived and basal clades were not supported by our results, but this does not entirely rule out a role of niche conservatism to explain the marked latitudinal richness trends in New World bats. Our analysis revealed that the situation is quite different for bats with a temperate origin (vespertilionids) and tropical origin (phyllostomids, mollossids, and others).

Bat families with a tropical origin are virtually absent from the temperate zones because their evolution in a tropical environment did not prepare them for coping with cold winters, which requires the capacity for hibernation, so tropical niche conservatism does play a role in the decrease of bat richness with latitude. However, competition with the vespertilionids, which are well adapted to winter conditions, may also contribute to the near absence of tropical families in the temperate zones.

The only bat family with a presumed temperate origin, the vespertilionids, declines in diversity towards the equator, which contrasts with the general trend in the order. However, there is no evidence of any element of the fundamental (abiotic) niche of the family that would constrain its diversification under tropical conditions, so niche conservatism may not play an important role in the observed latitudinal richness trend. Instead, the available evidence suggests that competition from the very diverse bat fauna that already existed in South America before the arrival of the vespertilionids may limit its richness in the region.

So, our results suggest that the latitudinal patterns in species richness of New World bats, and the likely mechanisms explaining them, are not the same for all bat families. In particular they are different for families with temperate and tropical origins. This suggests that in analyses done at the level of the order there is a risk that the patterns are confounded by different, and even opposing, tendencies. Although we tried to use the best possible information available, our conclusions may suffer from incomplete data on phylogenies and distributions data, and from several uncertainties regarding the time and place of dispersal of bat clades. However, the results suggest that even if the predictions of niche conservatism about the latitudinal distribution of basal and derived clades are theoretically sound, they are not suitable to test for a role of niche conservatism in the development of latitudinal richness patterns in bats. This limitation may apply to other groups of organisms, so the testing of the theoretical predictions of niche conservatism must be address with caution.

Chapter 7

General discussion

7 General discussion

Understanding the patterns and processes in the distribution, diversity and abundance of species is the main question of community ecology and paramount to the conservation of biological diversity. In this dissertation some of the factors that influence community structure and biogeographical patterns in New World bats were analysed. Bats were chosen because they are species-rich, widespread, and responsive to environmental changes; Neotropical bats in particular are locally abundant, ecologically diverse, and most species are relatively easy to sample.

Specific questions on the factors that affect bat diversity and abundance at local scales, and large scale geographical patterns in bat species distribution and richness were addressed in the previous chapters. Here we intend to integrate some of our major findings under the light of the current knowledge on the community ecology and macroecology of bats, to set them in an evolutionary framework, to outline some of the major conservation implications, and finally to make some suggestions for future research.

7.1 Factors affecting the distribution, diversity and abundance of Amazonian bats at local scales

Bats are highly mobile and able to fly large distances (Bonaccorso 1979; Fleming & Eby 2003) so one could assume that in undisturbed environments they would not be substantially affected by local limitations in feeding and roosting resources, because they have the ability to shift habitats. So, in Neotropical rainforests, seasonal flooding would eventually not represent an important determinant of the structuring of bat species assemblages as happens with non-volant mammals (Haugaasen & Peres 2005a) and the more sedentary understorey bird species (Beja *et al.* 2010).

However, in Central Amazonian lowland forests, the flooding pattern and the geochemistry of floodwaters proved to be key abiotic factors influencing the structure of bat assemblages. These factors determine spatial variations in soil fertility, habitat structure, and floristic composition, which in turn affect bat species diversity, composition and abundance.

Inundation seems to shape bat assemblages through its influence on spatial heterogeneity and vegetation structure. Vegetation structure has been recognized as a chief determinant of mammal diversity and composition, including bats (*e.g.* Ochoa 2000; Aguirre 2002; Mancina *et al.* 2007). Bat species richness and assemblage composition in Amazonian rainforests seem to be determined, to some degree, by differences in the structural heterogeneity of distinct forests types. In fact, the structuring of bat assemblages in terra firme, igapó and várzea forests revealed sharp differences. The highly structured terra firme is more diverse than any of the seasonally flooded forests. This seems to be related to the degree of specialization that some species have reached in niche dimensions such as diet and roost (Medellin *et al.* 2000). Indeed, terra firme presents a higher diversity of foraging opportunities and roosting sites, allowing the coexistence of a larger number of highly specialized species. So, terra firme complexity seems to have provided a greater diversity of potentially suitable niches for the wide array of species present.

It is interesting to note that though várzea and igapó show lesser vegetation complexity and overall lower tree canopy height than terra firme, due to the stress caused by seasonal floods, they also revealed a strong pattern of vertical stratification of bat assemblages. So, bats seem to have taken advantage of one more physical niche dimension accounting for additional spatial and resource partitioning in complex tropical forest communities (McNab 1971; Fleming *et al.* 1972; Lim & Engstrom 2001a). Differences in the vertical distribution of bats are explained by diet, foraging behaviour, roost-site selection, and wing morphology (Bernard 2001; Kalko & Handley 2001).

The nutrient load of the water and the correlated soil fertility result on different productivity levels in the three studied habitats. Terra firme and igapó are poorer and produce less fruits than the nutrient-rich várzea, at least during the prime time of fruit production, the high-water season. At fine spatial scales productivity seems to promote an increase in the number of bat species present, as indicated by the differences between várzea and igapó, which remain flooded during the same period of the year and that, in our study area, reveal similar vegetation complexity. The higher productivity of várzea also seems to promote higher densities and bat biomass because it allows the presence of larger populations and of large bodied bat species. In the absence of other abiotic and biotic factors, the results seem to indicate a linear relationship between species richness and productivity, but only more detailed measures of productivity in a wide range of similar habitats would allow testing this assumption.

There were no significant differences in the composition of bat assemblages between seasons within each forest type, presumably because the effects of inundation are reflected all year round in terms of vegetation structuring. However, the seasonality of food resources did have eco-physiological impacts on bats. Changes in abundance, body condition and reproductive activity of frugivorous bats seem to be correlated to the availability of fruits. Habitat shifts in response to changes in fruit availability were not particularly evident, perhaps because the partial synchrony in the periods of fruit abundance and scarcity in terra firme, várzea and igapó brings little advantage in seasonally shifting one’s foraging habitat.

In conclusion, vegetation complexity and spatial and temporal heterogeneity are central in determining spatial and temporal patterns of bat diversity and abundance in Amazonia. By increasing the availability of niches, these factors probably contribute to the high diversity of Neotropical forest bats, both in terms of species richness and ecological strategies.

7.2 Factors affecting the distribution and diversity of New World bats at regional and continental scales

As found for smaller scales, productivity also seems to influence the patterns of bat richness at regional scales. In fact, the productivity hypothesis seems to explain well the patterns of bat richness in the rainforests of the Amazon basin. Annual maximum NDVI showed a strong and positive relation with the richness of frugivore bats, and was chosen as the best predictor of richness among several climatic and productivity variables. Within Amazonian rainforests, the sites with highest NDVI and, consequently with predicted higher richness, are found in the Guyana shield region, followed by areas in Central Amazonia. Some areas, especially in Southern Amazonia, are expected to show lower richness, probably because deforestation and agricultural conversion are reflected by lower NDVI values.

In temperate and subtropical areas a good predictor of bat richness is temperature (Patten 2004; Ulrich *et al.* 2007) – high species richness is found in regions with higher winter temperature because in cooler areas bats must present the ability to hibernate, or at least migrate, to deal with the low winter temperature. In an area where the climatic stability is relatively high, other factors seem to account for the geographic variation in bat richness. In fact, in the Amazonian region it seems to be the conversion of energy into food available (sensu Wright 1983) that best explains the patterns of bat richness. Our results apply only to frugivores, but because the species-energy hypothesis predicts that high energy levels promote species richness by increasing the number of trophic levels of the assemblages, it is reasonable to expect a similar pattern in other guilds. However, other guilds may show different strength of the relationship as occurs with different bird guilds (Bailey *et al.* 2004; Evans *et al.* 2005).

The analysis of the distribution ranges of 305 New World bat species presented in chapter 6 confirm the results of previous studies (Patten 2004; Stevens 2004), indicating that New World bats follow the typical latitudinal increase in species richness towards the tropics. However, the patterns of the three most specious families are distinct, with the Phyllostomidae and Molossidae following the general trend, but the Vespertilionidae presenting the peak of species richness in temperate North America.

While niche conservatism could explain the general and family patterns in species richness, according to the probable places of radiation (Teeling *et al.* 2005), the same does not occur with the patterns found for the age of the taxa. Indeed, for the whole of New World bats and in the Phyllostomidae and Molossidae, more derived clades are found in the extremes of the distribution ranges. However, in vespertilionids, regions with older taxa coincide with diversity hotspots.

Niche conservatism does seem to have limited the expansion and radiation of phyllostomids and molossids at high latitudes. There is a relatively low number of species in high latitudes, but these are in general more basal to the family than derived. Most of those species cope with adverse environments, either in terms of climate or food resources, by seasonally migrating to regions with better conditions. While the pattern in the age of the taxa found in vespertilionids respects the prediction of the niche conservatism hypothesis (assuming that the family has radiated from temperate areas) it is more parsimoniously explained by factors acting outside the fundamental niche, in particular competition.

In conclusion, niche conservatism seems to only partly explain the latitudinal diversity gradients in New World bats. Complementary explanations, such as factors acting outside the fundamental niche of the clades and spatial differences in both the rates of evolution and in the existence of ecological opportunities are necessary to fully understand the latitudinal trends in species diversity.

7.3 Conservation implications

Neotropical bats provide essential ecosystem services: they are the main pollinator and dispersal vectors of many tropical plants (Fleming 1988; Galindo-Gonzalez *et al.* 2000), actively promoting the regeneration of disturbed areas (Kelm *et al.* 2008). As such, changes in diversity, species composition, abundance and eco-physiological patterns as response to natural or anthropogenic disturbance, seasonality, and habitat physiognomy are of special conservation concern because those changes may lead to the loss or disruption of essential, and often irreplaceable, ecosystem goods and services.

The results of chapters 2, 3 and 4 add to the growing evidence that seasonally flooded forests play an important role in promoting the maintenance of high levels of bat diversity in Amazonian lowlands. Although terra firme forest holds the richest bat assemblage, and flooded forests may not hold exclusive species, they harbour higher densities of species that are rare elsewhere. The maintenance of the integrity of the vertical stratification of the forests also revealed to be essential to the preservation of diverse bat assemblages.

As referred in chapter 2, regional gamma diversity depends largely on the species richness of the historically and geographically dominant assemblage, but has a mutual correlation with both local diversity and species turnover (Whittaker 1972). In addition, source-sink dynamics (Pulliam 1988; Dias 1996) possibly integrates the mosaic of terra firme, várzea and igapó, with each forest type acting more decisively to the long-term survival of different species. For instance, várzea forests seem to be able to sustain large populations of a few species (as indicated by the pattern of captures and relative biomass), possibly promoting high levels of genetic diversity – with positive consequences for the fitness of those species – and acting as a source patch.

Several studies indicate that habitat loss and fragmentation are serious threats to bat diversity in tropical forests (*e.g.* Klingbeil & Willig 2009; Presley *et al.* 2009) and that the loss of genetic variation in response to habitat fragmentation is more likely in less mobile species (Meyer *et al.* 2009). So, in order to conserve species richness and genetic diversity, it is essential to maintain not only relatively large bat population sizes but also the connectivity among populations of the different forest patches throughout the species' ranges.

Food production, at least in terms of fruits, is a highly seasonal, and synchronous, event in the three forest types. This may indicate that fruits are scarce for bats during part of the year. More specialized and less versatile species may eventually become more susceptible to disturbance during this period. In fact, the patterns in bat activity, reprodution, and body condition associated to the natural seasonal changes in food availability indicate that anthropogenic modifications in ecosystem structure and function may have drastic consequences in bat populations by disrupting those patterns.

Neotropical bats have several attributes that make them good bioindicators: they are abundant and taxonomically and ecologically diverse. They have an important role in the ecosystems and, according to the results of chapters 2, 3, 4 and abundant literature (*e.g.* Medellin *et al.* 2000; Kelm *et al.* 2008; Meyer *et al.* 2008), they respond to environmental changes in a reasonably predictable way. Though a single indicator group does not provide enough bases for decision making and management for conservation, the responses of bats to habitat heterogeneity emphasize the conservational value of maintaining the mosaic of different natural habitats that characterizes the lowland Amazon. If bats – which are highly mobile and do not move through the ground, as occurs with many other animals – are clearly influenced by the heterogeneity caused by seasonal floods, it is logical to assume that the assemblages of most of the remaining terrestrial vertebrates will be even more influenced by that heterogeneity. Indeed, this mosaic is already known to contribute significantly to the persistence of diverse communities of birds (Beja *et al.* 2010), fishes (Henderson & Crampton 1997), primates and small non-volant mammals (Peres 1997; Haugaasen & Peres 2005a;b).

The creation of more protected areas that include floodplain forests is of particular importance; they are still underrepresented in Amazonian reserve networks and, due to their greater accessibility, are particularly vulnerable to impacts resulting from human disturbance, logging, and land conversion (Fearnside & Ferraz 1995; Borges & Carvalhães 2000; Fearnside 2001; Vale *et al.* 2008). In fact, deforestation and fragmentation of tropical forests persist at alarming rates; in the Amazon over 20 x 10^3 km^2 are deforested annually (Fearnside 2005), and this rate will probably increase as more paved roads and large dams are constructed within the region.

It is thus necessary to designate sufficiently large and environmentally heterogeneous protected areas that include terra firme, seasonally flooded forests and other Amazonian biomes, such as cerrado and campinarana, to guarantee the long-term persistence of Amazonian biota (Peres 2005). According to the results of chapter 5, high-productivity areas should receive special conservation attention. These areas promote high levels of diversity, apparently because they have resources abundant enough for species to specialize on few food types, creating narrower niches and thus promoting the existence of more species (Vazquez & Stevens 2004). These high-productivity areas are mainly located in the Guayanian shield and Central Amazonian region, while some Southern Amazonian areas show lower levels of productivity perhaps partly due to deforestation and agricultural conversion (Nogueira *et al.* 2008).

Protected areas show gains in terms of legal and governance clarity, capacity and effectiveness when compared to other natural and managed ecosystems (Dudley *et al.* 2010). Creating a solid and well-connected network of such Neotropical forest protected areas seems to be essential for biodiversity conservation and to mitigate and adapt to climate change. Indeed, such network would provide complementary conditions for a wide range of species with different habitat requirements (Lees & Peres 2008). In addition, tropical forests are also the largest terrestrial carbon stores and supply essential ecosystem services like preventing or reducing the effects of natural disasters, providing secure and potable water supply, addressing climate related health issues and protecting food supplies including wild foods, fisheries and crop wild relatives; floodplain forests, in particular, also help to regulate water flow, and their protection can help to alleviate climate-induced water stress.

7.4 Future research

While this study has contributed to the understanding of some patterns and processes associated to bat distribution, diversity and abundance, several related questions remained unanswered.

We revealed differences between the assemblages of bats of terra firme, várzea and igapó, the main forest types in lowland Amazon. However, it would be interesting to broaden the range of this study towards other biomes occurring in the Amazonian region, such as mountain and cloud forests, igapó forests seasonally flooded by clear-water rivers, and non-forested areas like cerrado and campinarana. Would there still be sharp differences among all biomes? For instance, are the bat assemblages of black-water igapó forests significantly distinct from those of clear-water ones, considering that they are similar in terms of vegetation structure and water nutrient-load? If not, which other factors could be accounted for differences between the assemblages?

For completeness, bat inventories should include more than one detection method, for instance combining mist-net captures with ultra-sound detection and/or roost search. In fact, though not included in this dissertation, ultra-sound sampling was also conducted in the ten sampled locations, simultaneously with the mist-netting. Automatic stations, consisting of sound-triggered detectors and recorders were set at three distinct heights (canopy, subcanopy and understorey) within terra firme, várzea and igapó sampling areas. Preliminary data analysis indicates: (1) a whole new range of insectivorous species (mainly of the Emballonuridae and Molossidae) to add to the published inventory; (2) differences in the composition of those species among forest types; (3) within each forest type, differences in species composition among forest interior and edge; and (4) a pattern of vertical stratification of those bat species. Future work involves the analysis and publication of those data, part of which will be integrated in other PhD thesis.

In chapter 4, plant phenology was studied by counting fruits in 20 km of transects in both the high- and the low-water seasons. Despite this intensive effort, it was difficult to associate bat activity to the availability of fruits eaten by different bats. In fact, the global vegetation trends may have masked individual trends of plants known to be important food resources for different bat species. So, it would be interesting to choose a few model species and to conduct a food selection study, based on the relation between individual resources and intake by each bat species all year-round. Ideally, in each of the model species, several individuals of diverse age-guilds should be radio-tracked to clearly determine their activity patterns and the existence of habitat shifts due to changes in food availability.

Regionally, an investigation of the relative contributions of environmental and landscape characteristics to determine how local and regional processes structure the Amazonian bat metacommunity would also be of key relevance. For this, several Amazonian sites spanning environmental gradients should be subject to intense and equivalent bat sampling effort. This would allow determining if the Amazonian bat metacommunity follows the species-sorting model, *i.e.*, environmental variation accounts for the variation in bat species composition over that of spatial autocorrelation, or the mass-effects model, according to which species are responsive to environmental characteristics associated with sites, but dispersal allows species to persist in less suitable patches via source–sink dynamics. Of particular interest would also be to determine how much information in the genetic data of a few model species is attributable to historical and contemporary processes; indeed, by confronting genetic data with models of historical and contemporary landscapes, dispersal processes could also be identified.

The results of such study would have major conservation implications: due to the high rate of deforestation in the Amazon, a well-connected network of protected sites would be a promising conservation tool if the bat metacommunity is integrated by dispersal, and would contribute to enhance resilience to climate change. In any case, spatial integration would eventually need to be coupled with factors such as the level of environmental heterogeneity or the size of the protected areas.

The results of chapter 6 indicate that niche conservatism only partly explains the latitudinal gradient in the species richness of New World bats, and that competition may have had an important role in the richness and distributional patterns of some families. As such, it would be interesting to develop studies that would allow the testing of the influence of other factors in that latitudinal gradient, in particular biotic factors like competition.

7.5 Concluding remarks

The results obtained in this thesis contributed towards the understanding on how different factors act on the patterns of distribution, diversity and abundance of New World bats, in particular those of Amazonian communities.

Overall, the results provided evidence that spatial heterogeneity, promoted by distinct inundation patterns and nutrient supplies, is a key factor in the structuring of Amazonian communities. This heterogeneity is reflected in terms of vegetation complexity, and consequently of the diversity and abundance of food and roost resources for bats. Spatial and temporal changes in food supply were shown to influence patterns in bat activity, body condition and reproductive cycles. At a regional scale, the productivity hypothesis is the one best explaining the patterns of diversity, being strongly and positively correlated with frugivore bat richness. In Amazonia, high productive areas are found in areas that were not subject to significant levels of deforestation and land conversion. These results underline the conservational value of maintaining the mosaic of different natural habitats that characterizes the Amazonian region. Within a continental context, several factors, both contemporary and historical, seem to drive the latitudinal patterns of bat species richness, apparently acting not only on the fundamental niche, as predicted by niche conservatism, but also at the level of the realized niche.

Annex I. Species list and number of bats captured with ground and canopy mist-nets in the three habitats and in both seasons. The values correspond to a total of four sampling stations in terra firme and three in várzea and in igapó. FG - feeding-guilds following Kalko (1997) and Schnitzler & Kalko (1998).

Taxon	**FG**	**Terra firme**				**Várzea**			**Igapó**		
		High-water		**Low-Water**		**High-water**	**Low-water**		**High-water**	**Low-Water**	
		Under-storey	**Canopy**	**Under-storey**	**Canopy**	**Under-storey**	**Under-storey**	**Canopy**	**Under-storey**	**Under-storey**	**Canopy**
Emballonuridae											
Centronycteris sp.		0	1	0	0	0	0	0	0	0	0
Rhynchonycteris naso	I	0	0	0	0	4	1	0	5	0	0
Cormura brevirostris	II	2	0	0	0	0	1	0	0	0	0
Peropteryx leucoptera	II	0	1	0	0	0	1	0	0	0	0
Peropteryx macrotis	II	0	1	0	0	1	0	0	0	0	0
Saccopteryx bilineata	I	1	4	0	0	9	9	0	0	3	1
Saccopteryx canescens	II	0	1	0	0	0	1	0	1	2	0
Saccopteryx leptura	II	0	2	0	0	0	0	1	0	2	0
Phyllostomidae											
Phyllostominae											
Chrotopterus auritus	V	2	0	3	0	0	0	0	0	1	0
Glyphonycteris daviesi	IV	0	0	1	0	0	1	0	0	0	0
Glyphonicteris sylvestris	IV	1	0	0	0	0	0	0	0	0	1
Lampronycteris brachiotis	IV	0	2	0	1	0	0	0	0	0	0
Lophostoma brasiliense	IV	0	0	1	0	0	0	0	0	0	0
Lophostoma carrikeri	IV	0	0	1	0	0	0	1	0	0	0
Lophostoma silvicola	IV	9	0	2	0	1	8	0	3	1	0
Micronycteris megalotis	IV	1	0	0	0	0	0	0	0	1	0
Micronycteris microtis	IV	1	0	0	0	0	0	0	0	0	0
Micronycteris minuta	IV	0	0	1	0	0	1	1	0	0	0
Micronycteris schmidtorum	IV	0	1	1	0	0	1	0	0	0	0
Mimon crenulatum	IV	1	1	1	0	1	3	0	0	4	0
Phylloderma stenops	VIII	2	1	1	0	1	0	0	0	1	0
Phyllostomus discolor	X	1	0	0	0	0	0	1	0	0	0
Phyllostomus elongatus	X	21	0	11	0	38	39	0	6	20	0
Phyllostomus hastatus	X	2	2	0	1	6	2	3	0	0	0
Tonatia saurophila	IV	6	2	6	3	1	0	0	1	5	1
Trachops cirrhosus	V	9	0	3	0	1	18	0	5	3	0
Trinycteris nicefori	X	0	0	1	0	1	0	0	0	0	0
Vampyrum spectrum	V	3	0	0	0	0	2	0	0	0	0

Annex I *(cont.)*

Glossophaginae											
Glossophaga comissarisi	IX	0	0	0	0	0	0	0	1	1	0
Glossophaga longirostris	IX	0	0	0	0	0	0	0	1	0	0
Glossophaga soricina	IX	7	7	3	11	8	15	5	4	5	0
Carollinae											
Carollia brevicauda	VIII	3	1	5	0	0	0	0	0	0	0
Carollia castanea	VIII	8	2	7	0	1	0	0	1	0	0
Carollia perspicillata	VIII	28	11	30	1	81	23	5	21	37	16
Rhinophylla pumilio	VIII	14	12	17	1	0	0	0	1	0	1
Stenodermatinae											
Ametrida centurio	VIII	0	0	0	1	0	0	0	0	0	0
Artibeus cinereus	VIII	0	1	0	0	0	0	0	1	0	0
Artibeus (Koopmania) concolor	VIII	0	1	1	2	0	0	1	1	0	1
Artibeus glaucus	VIII	0	2	1	3	0	0	1	0	0	0
Artibeus gnomus	VIII	1	3	0	0	1	0	0	0	0	1
Artibeus phaeotis	VIII	0	0	0	1	0	0	0	0	0	0
Artibeus watsoni	VIII	1	3	1	2	1	0	0	0	0	2
Artibeus obscurus	VIII	19	6	10	3	2	0	0	18	9	3
Artibeus lituratus	VIII	1	4	1	0	3	0	2	7	1	0
Artibeus planirostris	VIII	5	2	5	5	40	74	37	7	8	10
Chiroderma trinitatum	VIII	0	0	0	2	1	0	0	0	0	0
Chiroderma villosum	VIII	0	0	0	1	2	1	0	0	0	0
Mesophyla macconnelli	VIII	21	5	7	2	2	0	0	3	0	2
Platyrrhinus helleri	VIII	0	0	1	0	17	6	13	0	2	2
Sturnira lilium	VIII	0	0	0	0	1	0	0	0	0	0
Sturnira tildae	VIII	1	3	7	0	0	0	0	12	2	1
Uroderma bilobatum	VIII	1	2	2	0	3	0	1	3	1	7
Vampyressa pusila	VIII	1	0	2	0	0	0	0	0	0	1
Vampyriscus bidens	VIII	0	0	0	0	0	0	0	1	0	0
Vampyriscus brocki	VIII	1	3	2	9	0	0	0	1	0	0
Desmodontinae											
Desmodus rotundus	VII	2	0	0	0	0	5	0	1	0	0
Thyropteridae											
Thyroptera discifera	II	0	0	1	0	0	0	0	0	0	0
Vespertilionidae											
Myotis albescens	II	1	1	2	0	2	3	0	1	0	1
Myotis nigricans	II	3	0	0	0	1	0	0	0	0	0
Myotis riparius	II	0	0	0	0	1	2	0	0	1	0

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