Fruits and frugivory in neotropical primates and in Amazonian flooded and unflooded forests

Joseph E. Hawes

Thesis submitted for the degree of Doctor of Philosophy
School of Environmental Sciences
University of East Anglia, UK

September 2012

Contents

Title page photo: Várzea *forest of the Médio Juruá during the terrestrial phase*

Abstract

The richness and resilience of tropical forest ecosystems are best described by the myriad of ecological interactions linking co-occurring species together. The many functions previously served by ecological links are often only detected once these links are lost. Of particular interest in this regard are the mutualistic networks between fruiting plants and vertebrate frugivores, whose interdependent relationship is fundamental to the functioning of tropical forests. This thesis examined these fruit-frugivore interactions at two contrasting scales, and using two different approaches. On a landscape scale in western Brazilian Amazonia, the focus was on a community-wide assessment, with particular attention paid to the differences between two highly divergent but adjacent species-rich forest types, seasonally-flooded *várzea* forests and unflooded *terra firme* forests. As part of this comparison, the powerful role of the annual flood pulse was shown to determine both spatial patterns of forest structure and temporal patterns of fruit production. The strong influence of this seasonal cycle was apparent in the adaptive traits observed in plants and animals, with corresponding effects upon their networks of interactions. The role of frugivore body size as an important trait in relation to the degree of frugivory within consumers was emphasised via one of the most extensive compilations on the feeding ecology of any frugivorous vertebrate taxon. By amassing the observations of feeding records accumulated over several decades of neotropical primate field research, and accounting for the highly variable levels of sampling effort among primate species, the prevalence of frugivory at the mid-high spectrum of body mass was confirmed. This continental-scale meta-analysis also revealed that, despite representing arguably the most observable and well-studied group of vertebrate frugivores in tropical forests worldwide, most primate species were heavily undersampled in terms of the richness of fruits known to occur in their diets. These astounding gaps in our cumulative knowledge highlight the challenges faced in assembling comprehensive fruit-frugivore networks for entire communities, where the diets of most consumers are even more poorly understood than for primates. This is particularly pertinent in the face of ever-increasing threats to ecosystems comprised of, and sustained by, these complex webs of interactions.

Acknowledgements

Firstly I thank my supervisor Carlos Peres for the opportunity to undertake this project within the framework provided by the wider Projeto Médio Juruá. His knowledge and enthusiasm for all aspects of this combined research programme was inspirational, from the detailed observation to the bigger picture. I am grateful too for his support and for continuing to trust in me to reach the finish line.

It was a pleasure during the course of fieldwork in the Juruá to be part of the team effort of PMJ. The academic stimulation and logistical support from Pete, Liz, and Óleo was exceeded only in value by their friendships, which were sources of encouragement throughout. Welcome company was also provided by Leejiah, and I am particularly grateful to Louise for her tremendous efforts initiating the treeplot work.

My field campaigns, however, would not have been possible without the assistance from a large number of residents in various Médio Juruá communities, who helped make up the full PMJ team. Maria Francisca and Luisa spent many hours conscientiously drying and weighing the contents of litterfall traps. And I was grateful to spend time in the forest learning from the experiences of Fino, Marco Aurelio, José, Sabão, Zé, Chom, Itamar, Bé and Raimundo, amongst others. Away from the forest there are too many names to mention but I am especially touched to recall the welcome I received in homes up and down the Juruá river, whenever I turned up with my hammock. The community of Bauana and the family of Seu Antônio both deserve a special mention but I am truly grateful for the kind hospitality and honest friendship I encountered throughout the reserves, and in Carauari.

I am extremely thankful for the work by Agenor Bemtes Azevedo and Paulo Apostolo Assunção from the Instituto Nacional de Pesquisas da Amazônia (INPA) in identifying trees and fruit/seed specimens, and to Valdely Ferreira Kinupp for curating the specimens at the Herbário EAFM, of the Instituto Federal de Educação, Ciência e Tecnologia do Amazonas (IFAM). My identification skills were also aided by staff on the Royal Botanical Gardens Edinburgh field course, Maarten Christenhusz (Natural History Museum), and Wolfgang Stuppy (Royal Botanic Gardens, Kew). Thank-you too to Lidia Medina Araujo from the Universidade Federal do Amazonas (UFAM), and to Romulo Batista and Mike Hopkins for logistical support and hospitality in Manaus.

After such intense fieldwork experiences it was often challenging to cope with the alternative existence back in Norwich. I benefited greatly from the support of Carlos' Amazonian research group and fellow Strangles members at UEA, including Pete, Sue, Maira, Davi, Vanessa, Ricardo, Chris, Kabelo, Christina, Hugh, Miranda, Scott and Kelly. I would also like to thank previous members of these groups for inspiring me to take up this project, including Jos, Toby, Tor, Luke, Alex, Kirsten, Emily, Sharon, Ali and Maria. Thank-you to Ben Holt, Iain Lake, Richard Davies and Mauricio Schneider for advice on various chapters, and to Sarah Yeates for wise words when needed.

Laura Hess (UC Santa Barbara) provided valuable input for Chapter 2 with the remote sensing estimates of flood depth in *várzea* forests, and Marco Mello (UFMG) gave useful insights into the details of network analyses. Armando Calouro (UFAC) initiated the review of neotropical primate dietary studies , which was subsequently expanded upon and analysed by myself in Chapters 5 and 6. I wish to extend my acknowledgment to the multitude of primatologists whose dedicated field observations contributed towards the compilation.

On a personal note, it was often beneficial to escape from the desk to clear the head and stretch the legs – thanks to Norwich Parkrun and Norfolk Gazelles, and to Chris and my regular opponents in the squash league. Other opportunities to briefly forget about work during the last couple of years were provided by several special celebratory occasions courtesy of some of my closest friends. And after mentioning these school friends, I would like to recognise the value I place on the inspirational teachers, including those in biology and geography, that I was fortunate to have at that age.

Finally, thank-you to Jenny and to my sisters Martha and Anisa, for fun times and their interest in my studies. Sorry for not always being there during the last few years.

Special thanks to my parents Sarah and Dinny, for always supporting and encouraging my interests and travels.

This study was funded by a studentship from the Natural Environment Research Council (NERC) and was part of a DEFRA Darwin Initiative project (Ref. 16-001). I am also grateful to the Secretaria do Estado do Meio Ambiente e Desenvolvimento Sustentável of Amazonas (SDS) and the Instituto Brasileiro do Meio Ambiente e Recursos Naturais Renováveis (IBAMA) for authorising this research and providing inkind support.

Photo: *Rio Juruá at dawn.*

Chapter 1

Introduction

Photo: *Rio Juruá.*

1.1. Threats to tropical forest ecosystems

Tropical primary forests are essential for the maintenance of global biodiversity (Barlow et al. 2007, Gibson et al. 2011) but the profound existing threats to these ecosystems are now well documented (Laurance & Peres 2006, Gardner et al. 2009). Beyond the most conspicuous disturbances posed by deforestation, forest fragmentation, selective logging, understorey wildfires, hydroelectric dams, and other forms of land-use change, are a variety of more insidious threats such as overhunting. While overhunting frequently co-occurs with structural patterns of habitat disturbance (Peres 2001), defaunation of large forest vertebrates can also pass virtually undetected in vast tracts of intact canopy cover (Peres et al. 2006).

The disturbances outlined above, including overhunting, threaten not only individual species but also the complex networks of mutualistic and antagonistic interactions between species that define the very fabric of the ecosystem (Morris 2010). Antagonistic interactions include natural predation, resulting in effective top-down control of otherwise hyper-abundant herbivores that can degrade the structure of many terrestrial, freshwater and marine ecosystems (Estes et al. 2011). Mutualistic interactions include ecosystem services such as plant pollination and seed dispersal, and the loss of these links may therefore have potentially catastrophic cascading effects

(Wright 2003, Wright et al. 2007). In particular, the large-bodied vertebrates targeted most heavily by hunters, are typically important seed dispersers (Peres 2000). Their local depletion and extirpation is today turning the once envisioned ‘empty forest’ scenario into reality (Redford 1992, Wilkie et al. 2011).

1.2. Frugivory and seed dispersal

Seed dispersal is a crucial component of a functioning ecosystem (Nathan & Muller-Landau 2000, Levin et al. 2003) and there is now considerable attention focused on the resilience of tropical forests to cope with the loss of large-bodied frugivores (Peres 2000, Terborgh et al. 2008). Frugivores are particularly ubiquitous in tropical forests, where fruits provide an important resource for a wide range of vertebrate taxa (Smythe 1986, Fleming & Kress 2011). Fruit-frugivore interactions thus represent a mutually beneficial relationship between vertebrates and plants, which has developed through a long coevolutionary process over 90 Ma (Fleming & Kress 2011). However, it is thought unlikely that a local frugivore guild will contain sufficient redundancy in additional species that can adequately replace the function originally provided, particularly to large-seeded plants, by large frugivores targeted by hunters (e.g. Poulsen et al. 2002, Peres & van Roosmalen 2002).

1.3. Fruit-frugivore networks and trait matching

Such low levels of redundancy are expected following exploration of the networks from interactions across communities. Through this approach it is becoming apparent that fruit-frugivore interactions are typically weak and non-obligate, and therefore best defined as diffuse and generalised networks (Bascompte & Jordano 2007, Vázquez et al. 2009). Variation in the physical and behavioural characteristics of veterbrate consumers can dispose or restrict them to certain traits of plants and fruits, and *vice versa*. The concept of ‘dispersal syndromes’ proposes that a suite of plant traits, including fruit morphology, mode of presentation, colour and nutritional content, can be collectively matched to a functional group of fruit consumers (Janson 1983, Schupp 1993, Jordano 1995, van der Pijl 1969), yet this remains a contentious hypothesis (Howe 1993, Fischer & Chapman 1993, Lomáscolo & Schaefer 2010) and the evolution of fruit traits may relate more to a loose network of generalist interactions (Bascompte & Jordano 2007).

Few comprehensive assessments of such trait matching have been conducted across a broad guild of tropical forest frugivores (e.g. Gautier-Hion et al. 1985). Indeed, there are only a limited number of studies to have examined the degree of dietary overlap or partitioning of available fruit resources among all members of a large coterie of phylogenetically independent co-occurring frugivores (e.g. Kitamura et al. 2002, Donatti et al. 2011, Schleuning et al. 2011). One reason why efforts to construct networks across an entire frugivore assemblage at single tropical forest sites have proved difficult, is perhaps due to their high diversity of both fruiting plants and fruit consumers. This is exemplified by the dearth of such studies in lowland Amazonia (but see Link & Stevenson 2004), which holds both the highest diversity of terrestrial and aquatic frugivorous vertebrates (Fleming et al. 1987) and the widest spectrum of morphological fruit types (van Roosmalen 1985, Gentry 1996) anywhere in the world.

1.4. Regional meta-analyses

A more common approach has typically been to focus on the interactions of a single consumer or resource taxon. Frugivorous birds have received a large amount of attention worldwide (Kissling et al. 2009), but tropical frugivore/granivores also include primates (Fleagle 1998), bats (Muscarella & Fleming 2007), ungulates (Bodmer 1990), rodents (Dubost & Henry 2006), reptiles (Valido & Olesen 2007), carnivores (Ray & Sunquist 2001), and fish (Horn et al. 2011). As the number of individual dietary studies has grown, certain taxa have reached sufficient critical mass for regional scale compilations. These can serve as comparative analyses of different study sites or to construct cumulative interactions across multiple sites, and are particularly relevant when considering higher-order plant taxa (e.g. genera) as a frugivore’s geographic range may expose it to more congeners and many functionally equivalent fruit species. A major resource-based pan-tropical review focused on the known consumers of figs (*Ficus* spp.) (Shanahan et al. 2001), and recent consumer-focused examples include dietary reviews for hornbills (Kitamura 2011), tapirs (Hibert et al. 2011), and spider monkeys (González-Zamora et al. 2009). Again, limited attempts have been made to integrate such compilations across multiple taxa (e.g. Mello et al. 2011), with a conspicuous absence in the case of primates, which are arguably the most observable diurnal vertebrate frugivores in tropical forests worldwide.

1.5. Primate diets

As one of the best studied mammalian orders in tropical forests (Kappeler & Watts 2012), there is a wealth of information on the feeding ecology of primates. As a group they also represent key seed dispersal agents in tropical forests (Peres & van Roosmalen 2002) and are amongst the most susceptible to the pressures of deforestation (Harcourt & Doherty 2005) and overhunting (Peres & Palacios 2007). Primates though, represent a diverse array of life-history traits (Strier 1994), including diet, and their roles in seed dispersal are known to differ widely between functional groups (*sensu* Peres & Janson 1999). Yet this has been difficult to quantify to date as a result of varying field methods employed by primatologists and severe inequalities and systematic biases in the distribution of sampling effort. A compilation of fruit-frugivore networks for primates thus requires a systematic quantitative assessment of the biases in sampling effort which would represent a substantial contribution to our understanding of how diet, and levels of frugivory in particular, vary across functional groups.

1.6. Study objectives

This thesis examines the concept of fruit-frugivore interactions through two approaches at contrasting spatial extents — from a landscape to a continental scale — in order to address some of the gaps in the literature outlined above. Firstly, this study tackles the shortages in community-wide assessments of fruit-frugivore interactions, particularly in sites with complex species-rich resource and consumer assemblages. Secondly, this study accepts the challenges in compiling and comparing existing data on fruit-frugivore interactions for a large and important frugivorous taxon across multiple sites.

In both approaches, this thesis uses the forests of the Neotropics as a setting. In the former, the focus is on Amazonian forests, particularly in comparing the contrasting plant communities and frugivorous vertebrate assemblages of seasonally-flooded and adjacent unflooded forests in western Brazilian Amazonia. In the latter, the taxonomic focus narrows to concentrate on just one group of frugivores from that local assemblage: primates. The geographic focus in contrast, widens to investigate the dietary composition of 17 neotropical primate genera from across 17 countries in Central and South America, including sites in each of three major forest regions: Amazonia, the Atlantic Forest region, and Mesoamerica (Figure 1.1).

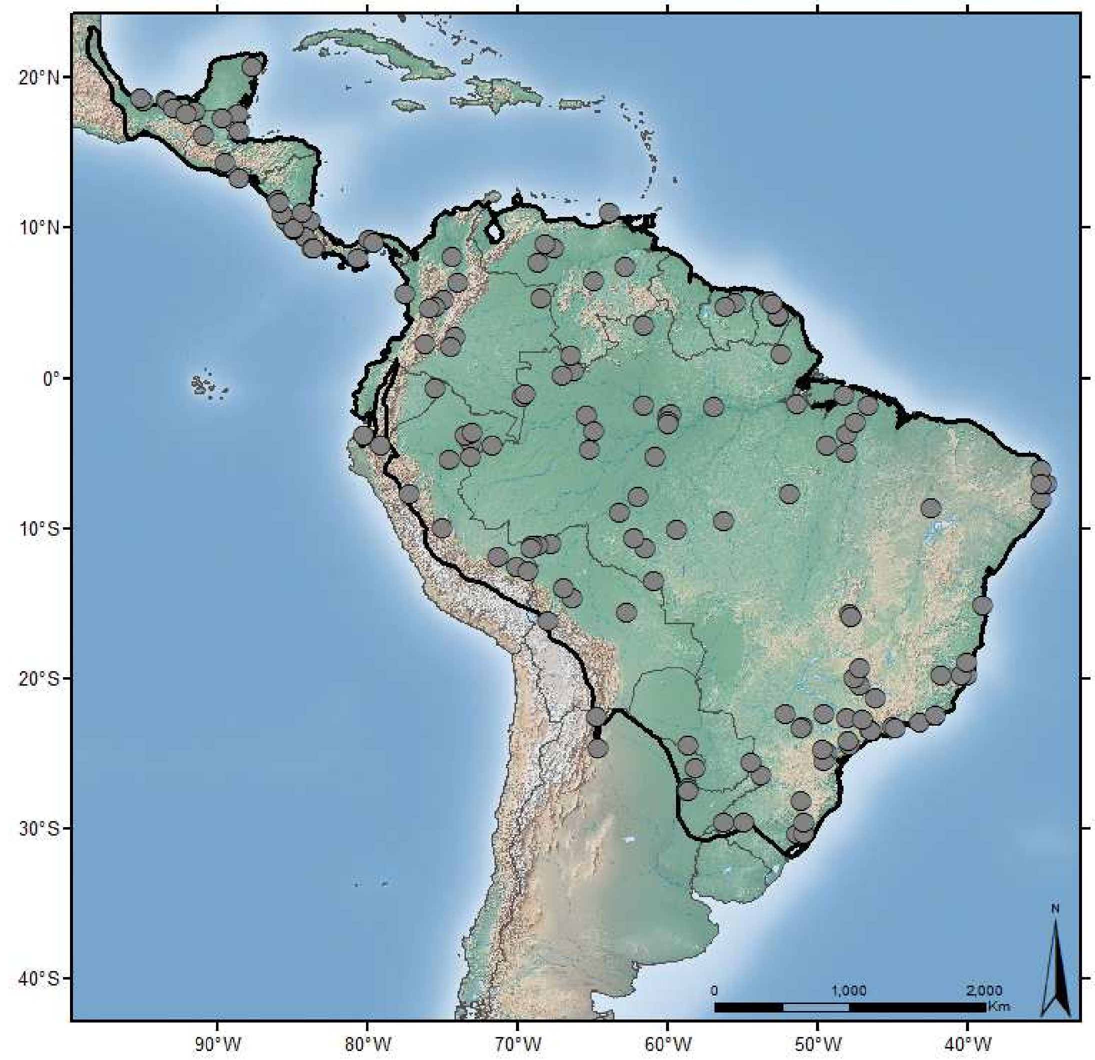

Figure 1.1. Aggregate geographic extent of neotropical primates (bold lines) and distribution of primate dietary studies (circles)

1.7. Study area: Médio Juruá

The fieldwork for the community-wide Amazonian case-study in this thesis was conducted within two contiguous sustainable-use forest reserves in the State of Amazonas, Brazil, namely the Médio Juruá Extractive Reserve (*ResEx Médio Juruá*, 253,227 ha) and the Uacari Sustainable Development Reserve (*RDS Uacari*, 632,949 ha). The Juruá region has a wet, tropical climate with a mean annual temperature of 27.1°C and annual rainfall, calculated from daily records over three consecutive years (2008 - 2010) at the Bauana Ecological Field Station (S 5°26'19", W 67°17'12"), averaging 3,679 mm. The elevation range is 65 – 170 m above sea level within the reserves which border the Juruá river, a major white-water tributary of the Solimões

(=Amazon) river. Both reserves contain large expanses of upland unflooded *terra firme* forest and, closer to the main river channel, seasonally-flooded *várzea* forest (Figure 1.2).

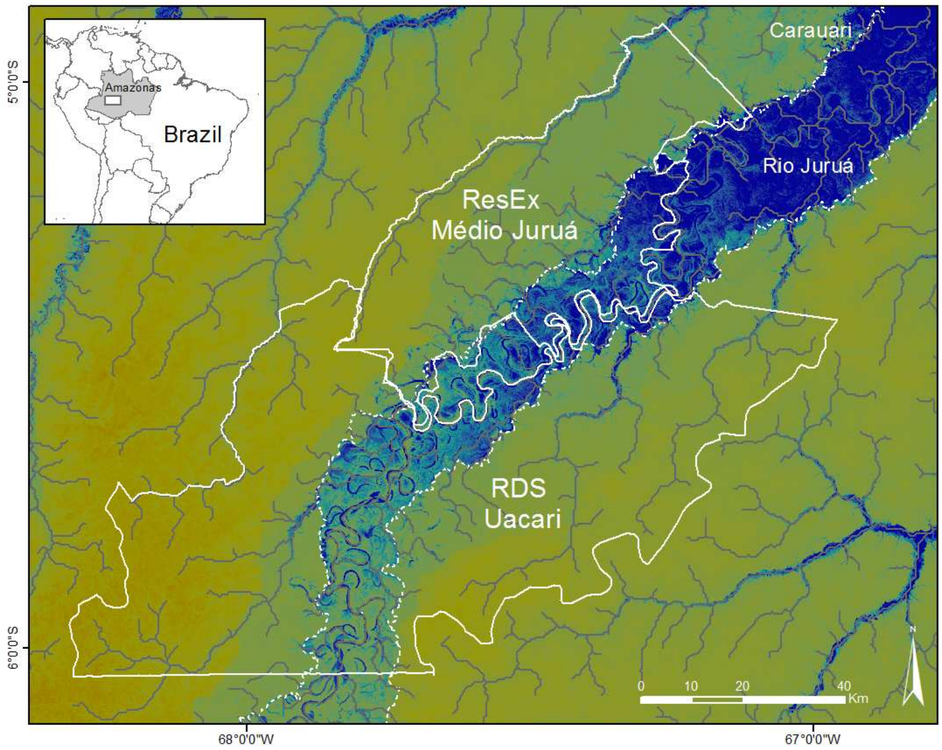

Figure 1.2. *Map of the Médio Juruá region of western Brazilian Amazonia, showing the distribution of forest types within the two study reserves. Colours indicate terrain elevation, which corresponds approximately with the boundary between* terra firme *and* várzea *forests more clearly shown by the dashed lines*

1.8. Seasonal-floods and *várzea* forests

Várzea forests are the most extensive of seven major wetland types identified across Amazonia (Pires & Prance 1985), accounting for >200,000 km^2 within Brazilian Amazonia alone (Junk 1997). They are defined as the white-water floodplains of the Amazon (=Solimões) river and its tributaries (Prance 1979) and can be inundated for up to 210 days per year, at depths rising to 10-15m (Parolin et al. 2004a). The ‘white-water’ of these rivers is derived from their high load of Andean alluvial sediments (Irion et al. 1997), of which 300-1000 mm of erosional nutrient-rich deposits can be contributed to *várzea* soils every year (Parolin 2009). This results in high fertility (Soili 1951) and primary/secondary productivity levels two to three times higher than in adjacent heavily leached and nutrient poor *terra firme* forests (Worbes 1997).

In addition to the high fertility of *várzea* forests, the regular annual ‘flood pulse’ (Junk et al. 1989) has many additional severe impacts. The extended period of submersion and waterlogging alternates with contrasting drought conditions when the floods retreat (Parolin et al. 2010), resulting in clearly demarcated terrestrial and aquatic phases (see Chapter 3: Figure 3.3). This cycle plays a fundamental role as a selective pressure on a range of phenological, physiological, and structural adaptations within the plant community (Parolin et al. 2004b) and can help explain many life-history traits of *várzea* tree species, including wood density, growth rates, crown architecture, phenological strategies, and fruit/seed morphology. Despite such extreme conditions, the regularity of the flood pulse over recent geological history has contributed to making *várzea* forests the most species-rich floodplain forests worldwide (Wittmann et al. 2006).

The impact of the seasonal flood cycle is also apparent within the animal community, including the resident frugivore assemblage (Ayres 1986, Haugaasen & Peres, 2005, 2008). For terrestrial vertebrates, such as caviomorph rodents, ungulates, and ground-dwelling birds and reptiles, the barrier imposed by the floodwaters is absolute during the aquatic phase. These frugivores are understood to migrate to and from adjacent *terra firme* forests over the course of the year, returning as fruits and seeds fallen during the aquatic phase are exposed or deposited on the forest floor by the receding floodwaters (Haugaasen & Peres 2007). The opposite scenario is the case for frugivorous fish, including characids and catfish, which abandon the river channel and oxbow lakes with the rising floodwaters to take advantage of canopy resources in *várzea* forests, including seeds, fruit pulp and arthropods (Goulding 1980). In contrast to terrestrial and aquatic species, most arboreal and scansorial vertebrates, including primates, squirrels, and canopy birds retain physical access to *várzea* forests all year-round, although their relative abundances and diet may vary throughout the year between the two forest types.

The relationship between the temporal variation in fruit production and the annual cycles in the frugivore assemblage is therefore likely to be key in determining the structure of fruit-frugivore networks in *várzea* forests. In addition, the unique environmental pressures within *várzea* forests are reflected in very low levels (10 - 30%) of floristic similarity with even adjacent *terra firme* forests (Wittmann et al. 2010). This extreme turnover in plant communities is also likely to be an important factor to consider when comparing interaction networks from flooded and unflooded forests. As a compilation of fruit-frugivore interactions in a species rich tropical forest site, this study therefore provides additional value in examining the differences between two such contrasting forest types in such close proximity (Figure 1.3).

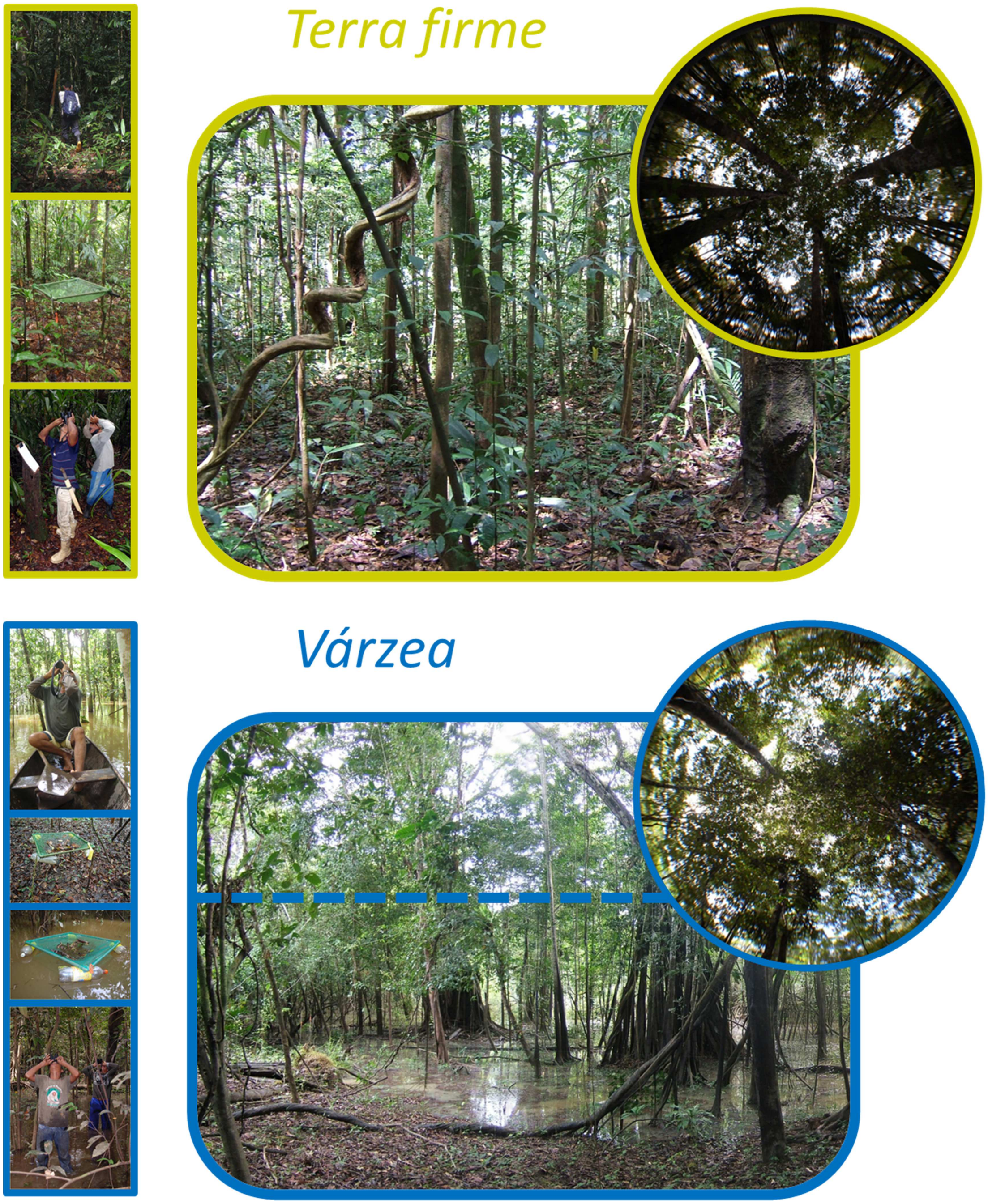

Figure 1.3. *Comparative views of* terra firme *and* várzea *forests, and corresponding field methods in each forest type.*

1.9. Thesis structure

The five data chapters are written in manuscript format with the intention of publishing each separately as peer-reviewed papers. Subsequently some sections, particularly within the methods, may be found to repeat material from previous chapters. Separate reference lists are also provided for each chapter. This approach hopefully allows readers to more easily access individual chapters, addressing varied aspects of my research project. I then hope to draw together the underlying themes running through all chapters in the final concluding chapter. By the time of submission, one chapter had already been published (Chapter 2: Hawes et al. 2012) and the remaining chapters will all be submitted to appropriate journals in due course.

The individual chapters of this thesis are presented in a conceptual sequence, as opposed to any chronological order. The first half of the thesis is essentially focused on my field study area of the Médio Juruá region of western Brazilian Amazonia, while the second half develops the principal objective of my project from a local case study to a continental-scale meta-analysis.

Chapter 2 describes the influence of the inundation regime on the spatial variation in forest structure and aboveground biomass in seasonally-flooded *várzea* forests, and makes the comparison with neighbouring unflooded *terra firme* forests. This comparison provides the structure for the following two chapters, which continue these two themes: (1) the role of the flood pulse on ecological processes in *várzea* forests, and (2) the comparison between flooded and unflooded forest (Figure 1.3). Chapter 3 compares the patterns of plant phenology in *várzea* and *terra firme* forests and the temporal variation in availability of reproductive plant parts, in particular fruit production which has a decisive bearing on fruit consumers in these environments. Chapter 4 then relates fruit production in *várzea* and *terra firme* forests to the contrasting frugivore communities of these forest types, on the basis of empirically constructed networks of fruit-frugivore interactions.

Fruit-frugivore interactions form the basis for the second half of the thesis as well, which focuses on a subset of the frugivore community from the Médio Juruá, namely primates. With the best studied diets of all neotropical frugivores, platyrrhine primates represent an ideal taxonomic group from which to compile one of the most complete datasets to date on fruit-frugivore interactions. Chapter 5 provides a necessary summary of the variability in sampling effort between primate studies, which allows Chapter 6 to subsequently present a thorough assessment of diet and frugivory in neotropical primates. Finally, Chapter 7 draws together the conclusions from across the preceding chapters, and suggests possible future research directions. In particular, this includes analysis of the resultant plant-primate networks revealed from the meta-analysis of neotropical primate dietary studies.

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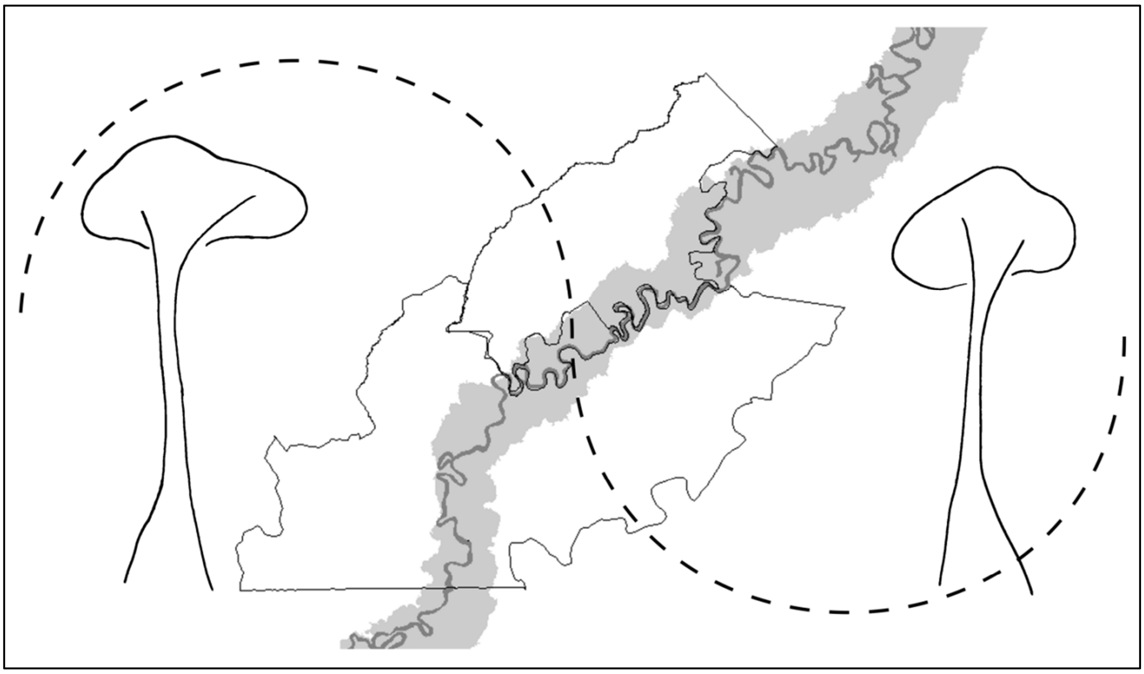
Photo: *Aerial views of* terra firme *and* várzea *forests in the Médio Juruá.*

Chapter 2

Landscape-scale variation in structure and biomass of Amazonian seasonally flooded and unflooded forests



Published as:

Hawes, J.E., Peres, C.A., Riley, L.B. & Hess, L.L. 2012. Landscape-scale variation in structure and biomass of Amazonian seasonally flooded and unflooded forests. *Forest Ecology and Management* 281: 163-176.

Abstract

Accurate estimates of current forest carbon stocks are required for efforts to reduce emissions from tropical deforestation and forest degradation. The relative contributions of different vegetation types to carbon stocks and potential emissions are poorly understood in highly heterogeneous forest mosaics, and further field-based measurements are necessary from severely undersampled regions and forest types to improve regional scale extrapolations based on remote sensing. We assessed the aboveground biomass (AGB) of two contiguous western Brazilian Amazonian protected areas totalling 886,176 ha, which contain vast expanses of seasonally flooded *várzea* (VZ) forest along the floodplain of the Juruá river and adjacent *terra firme* (TF) forest farther inland. Estimates were based on equations incorporating wood specific gravity (WSG) and tree height in addition to DBH, and derived from a network of 200 forest plots of 0.1 ha (= 20 ha) sampled across adjacent areas of flooded and unflooded forest. A large number of small plots stratified by forest type allowed a more representative sample, encompassing the considerable variation in forest structure and composition both within and between forest types. Mean basal area per plot was higher in *várzea* forest plots than in *terra firme* plots (VZ: 37.6 ± 1.2 m^2 ha^{-1}; TF: 32.4 ± 0.9 m^2 ha^{-1}) but AGB was lower in *várzea* (VZ: 281.9 ± 12.0 Mg ha^{-1}; TF: 358.4 ± 14.4 Mg ha^{-1}) due to lower WSG and tree height. Linear mixed effects models showed the overriding effect of forest type on AGB, and the roles of water stress and a historical signature of selective logging pressure, particularly within *várzea* forests. ALOS ScanSAR generated categories of flood duration provided a more relevant description of water stress than SRTM elevation data; AGB within *várzea* forest was higher in plots subjected to longer flood duration. *Várzea* forests store significant levels of forest carbon despite their lighter-wooded trees and lower canopy stature, and yet are heavily settled by rural Amazonians, and are increasingly vulnerable to deforestation and logging. This study helps understand how baseline environmental gradients and human disturbances in these unique forests affect their carbon storage value, and highlights their importance both within and outside existing protected areas.

2.1. Introduction

Amazonian forests are of utmost importance in the global carbon balance representing both a substantial source of emissions following deforestation and forest degradation, and a potential carbon sink if they can be adequately protected (Gibbs et al. 2007, Malhi et al. 2008). The historically high deforestation rates in Brazilian Amazonia are continuing to fall (INPE 2011) but estimates of carbon emissions still average 153 TgC yr^{-1} (Numata et al. 2011). Despite uncertainty over future international agreements (Venter & Koh 2012), much hope is still placed in the expansion of bilateral or multilateral Reducing Emissions from Deforestation and Forest Degradation (REDD+) schemes to shift the balance in global markets away from conditions favouring deforestation to those favouring forest protection and biodiversity conservation (Gardner et al., in press).

The effectiveness of such REDD+ policies, implemented by regional and national governments, through mechanisms such as the Amazonian Fund (BNDES 2010), will require accurate estimation of current carbon stocks within management areas (Salimon et al. 2011), as a pre-requisite to the continuing process of ‘Monitoring, Reporting and Verification’ (MRV). Protected areas are therefore encouraged to assess their carbon stocks to demonstrate their ‘readiness for REDD’ (Cerbu et al. 2011, FCPF 2012). This task is complicated since carbon stocks are far from spatially homogenous, especially within structurally complex tropical forest mosaics (Gibbs et al. 2007), including marked variation across landscapes and forest types (Asner et al. 2010). As a consequence, the large uncertainties in emission estimates (Olander et al. 2008) arise not just from difficulties in tracking the true extent of deforestation and forest degradation, but also from knowledge of the spatial distribution of forest types, including wetland forests (Melack & Hess 2010), and their respective biomass levels (Achard et al. 2004, Melack & Hess 2010).

Levels of aboveground biomass (hereafter, AGB) are usually assessed using a combination of remote and field-based measurements (Stickler et al. 2009), the latter of which remain essential to high-resolution verification of the assumptions behind remotely sensed indicators over large spatial scales (e.g. Keith et al. 2009) despite recent advances in high resolution LiDAR technology (Asner et al. 2010). Field-based measurements have the advantages of being low-tech, easily understood, and relatively inexpensive with the principal cost comprising field labour (Gibbs et al. 2007). They have, however, several potential sources of error, including variation in plot sizes and the allometric equations used (Chave et al. 2004). In addition, current estimates of AGB and carbon stocks in tropical forests (Malhi et al. 2006, Saatchi et al. 2007) are still based on extrapolations from a limited number of field sites (Houghton 2005, Houghton et al. 2009), leaving many regions and forest types underrepresented.

Floodplain forests are one of the most undersampled forest types and their contribution to regional and global scale carbon stocks remains highly uncertain (Anderson et al. 2009), even though wetlands comprise 17% of central Amazonia (Hess et al. 2003). The most extensive of seven wetland types identified across Amazonia (Pires & Prance 1985) are *várzea* forests, defined as the white-water floodplains of the Amazon (=Solimões) river and its tributaries (Prance 1979), and accounting for >200,000 km^2 within Brazilian Amazonia alone (Junk 1997). The ‘white-water’ of these rivers is derived from their high load (100 mg l^{-1}) of Andean alluvial sediments (Irion et al. 1997); 300-1000 mm of nutrient-rich deposits (Parolin et al. 2009) can be added to the soil during the annual invasion of floodwaters into the adjacent *várzea* (Sioli 1984). This cyclic land renewal results in high fertility (Sioli 1951, Irion et al. 1983) and productivity levels two to three times higher than in adjacent *terra firme* forests (Worbes 1997).

The flooding of the *várzea* lasts for up to 210 days per year, rising to a depth of 10-15m (Parolin et al. 2004a). This extended period of submersion and waterlogging has severe impacts, notably in oxygen deficiency (Parolin 2009), reduced photosynthesis from low light penetration through water and mud deposited on leaves, and low water conductance which can paradoxically result in water deficits in the tree crown (Parolin et al. 2004a). Flooding is typically a more frequent source of mortality in trees than desiccation, but the environmental harshness of the *várzea* is compounded by the contrasting drought conditions also experienced when the floods retreat (Parolin et al. 2010). Despite the marked seasonality of *várzea* forests, the annual regularity of the ’flood pulse’ (Junk et al. 1989), which drives the timing of many ecological processes within the *várzea*, has operated as a stable selective agent for the evolution of a variety of mechanisms in both adult trees and seedlings to cope with the dramatic annual transition between severe inundation and severe drought (Parolin et al. 2004b, Ferreira et al. 2010, Junk et al. 1989, Worbes et al. 1992, Wittmann et al. 2002).

Such extreme conditions within *várzea* forests may partly explain our poor current understanding of their forest structure (Table 2.1) but also raise questions over extrapolations in AGB estimates from other forest types, even when in close proximity. Indeed, trees in *várzea* forests display a range of phenological, physiological, and structural adaptations to the annual flood pulse (Parolin et al. 2004b), and many life-history traits are strongly influential on AGB estimates. For example, the hyper-abundant nutrient conditions in the disturbance-prone *várzea* environment favours fast life-histories of short-lived individuals with rapid growth rates, frequently resulting in low wood densities (Fearnside 1997, Baker et al. 2004b). In addition, unstable soils coupled with the persistent flood pulse promote high rates of tree-falls and canopy fracture, reducing competition for light, and substantially lowering the canopy stature in comparison to *terra firme* forests (Souza & Martins 2005). Such differences in wood density and tree height suggest that AGB estimates from *terra firme* forests may not be reliably extrapolated across *várzea* plots.

Of the few *várzea* forest inventories available, most are centred around the large urban centres of Tefé, Manaus, and Belém, in the western, central and eastern Brazilian Amazon, respectively. More generally, the small areas of *várzea* sampled to date throughout Amazonia are unlikely to be representative, with vast regions remaining entirely unknown (Parolin et al. 2004a). We are aware of only two *várzea* studies within the vast tracts of forest between existing plot-scale inventories in central Brazilian Amazonia and those in the upper Ecuadorian, Bolivian and Peruvian Amazon (see Saatchi et al. 2007), both along the upper Juruá river: Rodrigues Alves, Acre (Campbell et al. 1992) and Eirunepé, Amazonas (C.A. Peres & J.R. Malcolm, unpublished data). This study in the remote central Juruá region begins to redress this regional imbalance using a highly dispersed arrangement of small 0.1-ha plots to assess variation in forest structure over a large landscape mosaic, in contrast to the traditional approach of sampling a single or few larger plots.

The study landscape also provides the ideal opportunity to examine differences between *terra firme* and *várzea* forests, which diverge markedly in environmental gradients and life-history traits, and yet typically occur side-by-side. The marked flood regime is expected to drive differences in forest structure and biomass between flooded and unflooded forests but water stress is also likely to have an effect within each forest type, particularly within *várzea* forests. However, environmental stressors may affect plant physiology in different ways across these two forest types.

Table 2.1. *Summary of* várzea *forest structure studies from white-water flooded forests across Amazonia.*

Region	Country	Source	Location	*Várzea* forest category	No. plots	Area (ha)	TF [a] (ha)	Criteria [b] (cm DBH)	Age (yrs)	Mean flood depth (m)	Stem density (ha^{-1})	BA (m^2ha^{-1})	Mean WSG ($g\ cm^{-3}$)	AGB ($Mg\ ha^{-1}$)	AGB/BA ($Mg\ m^{-2}$)
Guiana Shield															
	Venezuela	Colonello (1990) [c]	Rio Orinoco		4	0.16		2m height			1308				
Upper Amazon															
	Bolivia	RAINFOR [d]	Las Londras 1		1	1						18.0		177.2	
		RAINFOR [d]	Las Londras 2		1	1						23.0		205.7	
		Arroyo & Killeen (unpub.) [d]	Noel Kempff		1	1	12					34.5		359.2	
		Arroyo & Killeen (unpub.) [d]	Noel Kempff		1	1	12					27.9		291.1	
		Comiskey et al. (2000) [d]	Beni		1	1	6					30.9		315.5	
	Ecuador	Balslev et al. (1987) [c]	Añagu		1	1	yes	≥ 10			420	35.5			
		Korning & Balslev (1994) [d]	Anangu		1	1.1	2					33.5		327.3	
		RAINFOR [d]	Tiputini		1	1	0.8					24.2		260.5	
	Peru	Gentry (1988) [c]	Yanamono	tahuampa	10	0.1	0.2	≥ 2.5							
		Gentry (1988) [c]	Mishana	tahuampa	10	0.1	0.1	≥ 2.5							
		Gentry (1988) [c]	Mishana	floodplain	10	0.1	0.1	≥ 2.5							
		Foster (1990) [c]	Cocha Cashu		5	5		≥ 30			66-86				
		Freitas (1996) [c]	Braga-Supay	bosque ribereno	8	8		≥ 10			510	24.1			
		Freitas (1996) [c]	Itahuaya	restinga de tahuampa	3	3		≥ 10			522	22.0			
		Freitas (1996) [c]	Itahuaya	bajeal de tahuampa	3	3		≥ 10			517	24.5			
		Freitas (1996) [c]	Itahuaya	palmeral de tahuampa	4	4		≥ 10			490	32.7			
		Nebel et al. (2001)	Braga-Supay	high restinga	3	3		≥ 10			456	24.7		251.3 [d]	
		Nebel et al. (2001)	Braga-Supay	low restinga	3	3		≥ 10			566	22.6		233.5 [d]	
		Nebel et al. (2001)	Lobillo	tahuampa	3	3		≥ 10			520	27.7		278.0 [d]	
		RAINFOR [d]	Sucusari C		1	1	4					26.4		315.9	

cont.

Table 2.1. cont.

Region	Country	Source	Location	*Várzea* forest category	No. plots	Area (ha)	TF [a] (ha)	Criteria [b] (cm DBH)	Age (yrs)	Mean flood depth (m)	Stem density (ha^{-1})	BA (m^{2}ha^{-1})	Mean WSG (g cm^{-3})	AGB (Mg ha^{-1})	AGB/BA (Mg m^{-2})
Lowland Amazon															
	E. Brazil	Black et al. (1950) [c]	Rio Guamá	estuarine [e]	1	1	1	≥ 10			564				
		Pires & Koury (1959) [c]	Rio Guamá	estuarine	1	3.8		≥ 10			484				
		Pires & Koury (1959) [c]	Rio Guamá	estuarine	1	1		≥ ~8			539				
		Pires & Prance (1977) [c]	Catú		?	?									
		Pires & Prance (1977) [c]	Aurá		?	?									
		Campbell et al. (1986)	Rio Xingu	igapo [f]	1	0.5	3	≥ 10			440	31.4			
		Almeida et al. (2004) [g]	Chaves, Marajó	estuarine	1	1		≥ 10			809	24.0		195.1	8.1
		Almeida et al. (2004) [g]	Ilha do Cajuúna, Afuá	estuarine	1	1		≥ 10			691	30.4		215.0	7.1
		Almeida et al. (2004) [g]	Ilha Trambioca, Rio Pará		1	1		≥ 10			735	26.5		171.0	6.4
		Almeida et al. (2004) [g]	Baixo Rio Xingu	igapo?	1	1		≥ 10			676	38.7		323.0	8.4
		Anderson et al. (1985)	Ilha das Oncas	estuarine	?	0.25		≥ 5							
	C. Brazil	Worbes (1983, 1986) [c]	Ilha de Marchantaria		?	0.21		≥ 5			795	60.0			
		Klinge et al. (1989, unpub.) [c]	Ilha de Marchantaria		?	?		≥ 10			737				
		Revilla (1989) [c]	Manaus		15	15		≥ 5			2160				
		Worbes (1997)	Manaus	pioneer	?	?		≥ 5?	2					3	
		Worbes (1997)	Manaus	pioneer	?	?		≥ 5?	4					14	
		Worbes (1997)	Manaus	pioneer	?	?		≥ 5?	12					98	
		Worbes (1997)	Manaus	early secondary	?	?		≥ 5?	44					258	
		Worbes (1997)	Manaus	late secondary	?	?		≥ 5?	80					279	
		Ayres (1986)	Mamirauá	high restinga	16	1		≥ 10		1 - 2.5	580	49.8			
		Ayres (1986)	Mamirauá	low restinga	16	1		≥ 10		up to 5	416	32.6			

cont.

Table 2.1. cont.

Region	Country	Source	Location	*Várzea* forest category	No. plots	Area (ha)	TF [a] (ha)	Criteria [b] (cm DBH)	Age (yrs)	Mean flood depth (m)	Stem density (ha^{-1})	BA (m^2ha^{-1})	Mean WSG ($g\ cm^{-3}$)	AGB ($Mg\ ha^{-1}$)	AGB/BA ($Mg\ m^{-2}$)
Lowland Amazon cont.															
	C. Brazil	Schöngart et al. (2010)	Mamirauá	young pioneer	1	0.05		≥ 10	7	3.36	1220	13.8	0.32	18	1.3
		Schöngart et al. (2010)	Mamirauá	early secondary	1	1		≥ 10	20	3.47	838	30.5	0.35	117	3.8
		Schöngart et al. (2010)	Mamirauá	late secondary	1	1		≥ 10	50	4.65	487	50.5	0.42	261	5.2
		Schöngart et al. (2010)	Mamirauá	intermediate	1	1		≥ 10	125	4.14	504	26.9	0.6	230	8.5
		Schöngart et al. (2010)	Mamirauá	late succession	1	1		≥ 10	240	3.36	462	27.3	0.7	239	8.8
		Haugaasen & Peres (2006) [h]	Lago Uauaçú, Rio Purús		3	3	3	≥ 10			515.3	29.6		417.1	14.1
	W. Brazil	Campbell et al. (1992)	Rio Juruá, Acre	late secondary	1	1		≥ 10	50	0	523	25.5			
		Campbell et al. (1992)	Rio Juruá, Acre	early secondary	1	1		≥ 10	14-50	1.16	420	27.0			
		Campbell et al. (1992)	Rio Juruá, Acre	young pioneer	1	1		≥ 10	14	4	777	25.7			
		Peres & Malcom (unpub.)	Rio Juruá, Amazonas		2	2	2	≥ 10							
		Hawes et al. (this study)	Rio Juruá, Amazonas	various	100	10	10	≥ 10	var.	1.84	633.2	37.6	0.58	281.9	7.3
		Hawes et al. (this study)	Rio Juruá, Amazonas	terra firme	100	10	n/a	≥ 10	n/a	n/a	638.9	32.5	0.67	358.4	10.8

[a] *terra firme* plots included in study as a comparison (structural details only presented for this study)

[b] stem size criterion for inclusion in survey

[c] cited by Nebel et al. (2001)

[d] cited by Malhi et al. (2006)

[e] incorrectly described by authors as *igapó* forest

[f] described by authors as *várzea* forest because of high sediment load despite clear waters

[g] cited by Schöngart et al. (2010)

[h] study includes comparison with *igapo*, in addition to *terra firme*

Higher elevation corresponds to increased water shortages in *terra firme* forest but to less severe hydrological stress in *várzea* forests. Conversely, lower elevation may reduce root depth to the water-table and seasonal hydrological deficit in *terra firme* forests but extends the periods of anoxia resulting from water-logging and inundation in *várzea*. We therefore tested the *a priori* hypotheses that AGB is (1) lower in *várzea* than in *terra firme* forest; and (2) negatively related to water stress (i.e. water scarcity in *terra firme*, but water surplus in *várzea*) and to a greater degree in *várzea* than in *terra firme* forest. To fully understand the distribution of AGB in forests with a long history of human occupation it is necessary to examine not only environmental variables related to water stress but also accessibility variables potentially related to logging, which was historically more common in *várzea* than in *terra firme* forests (Scelza 2008). We therefore examine the additional hypothesis that (3) AGB is negatively related to accessibility (e.g. greater distances from the nearest local community), and to a greater degree in *várzea* than in *terra firme* forest. Finally, we use our findings to provide AGB estimates for two large Amazonian protected areas consisting of both *terra firme* and *várzea* forest, with existing or proposed REDD+ schemes involving payments for forest ecosystem services (Newton et al. 2012a).

2.2. Methods

2.2.1. Study area

This study was conducted in the state of Amazonas, Brazil, within two contiguous sustainable use reserves, namely the Médio Juruá Extractive Reserve (*ResEx Médio Juruá*, 253,227 ha) and the Uacari Sustainable Development Reserve (*RDS Uacari*, 632,949 ha) (Figure 1). The two reserves border the Juruá river, a major white-water tributary of the Solimões (=Amazon) river, and contain large expanses of upland unflooded *terra firme* forest (80.6% of combined reserve area) and, closer to the river channel, seasonally flooded *várzea* forest (17.9%).

The Juruá region has a wet, tropical climate with a mean annual temperature of 27.1°C and annual rainfall, calculated from daily records over three consecutive years (2008-2010) at the Bauana Ecological Field Station (S 5°26’19”, W 67°17’12”), averaging 3,679 mm. The elevation range within the reserves is 65 – 170 m above sea level (TF plots: 93-123 m; VZ plots: 76 –110 m). *Terra firme* soils are typically heavily leached and nutrient poor in comparison to the eutrophic alluvial soils of *várzea* forests. All forest surveyed represent primary forest, although commercially valuable timber species along the Juruá river have experienced some selective logging from 1970-1995, especially in *várzea* forest (Scelza 2008).

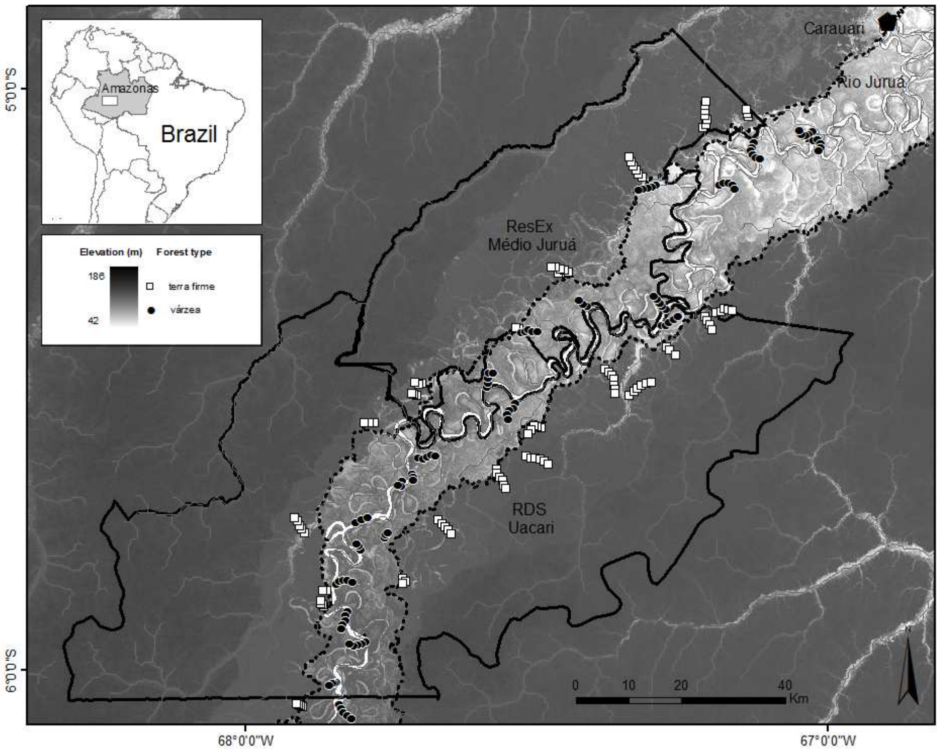


Figure 2.1. *Map of the Médio Juruá region of western Brazilian Amazonia showing SRTM elevation and locations of 200 0.1-ha forest plots in* terra firme *forest (open squares) and* várzea *forest (solid circles). Solid lines represent reserve boundaries; dashed lines represent the extent of the* várzea *floodplain: ALOS ScanSAR image © JAXA/METI 2009.*

2.2.2. Forest plot surveys

We sampled 20 ha of forest across 200 ‘Gentry-style’ 0.1-ha tree plots (100 m x 10 m), with two sets of 100 plots divided equally across *terra firme* and *várzea* forests (Figure 1). These provide an efficient method for assessing forest structure and composition across large tropical forest landscapes (Laumonier et al. 2010), and have been used to compare physical structure among different forest types (Phillips et al. 2003). Plots were distributed across the two reserves in proportion to their overall area, and survey effort was divided equally between the left and right banks of the Juruá river. Vegetation sampling was conducted during three periods: July-September 2008, November 2009-March 2010, and August 2011. Plots were located along 46 existing linear transects (2-7 plots per transect; mean 4.35) of up to 5,500 m in length, with all plots at least 800 m apart. At the ends of each plot, we recorded the x,y coordinates using a GPS (Garmin 60 CSx) and, in a subset of 73 *várzea* plots, the approximate maximum flood depth. This was accomplished by recording the previous year's high-water level from the band of alluvial sediment frequently visible on tree trunks, with a mean value extracted from three neighbouring trees in each case.

Although plots were the same dimensions as those sampled by Gentry (1982), we did not record the smaller stem sizes, which are generally included in 0.1-ha plots. Within each of our plots, all live stems (including palms but excluding woody lianas and non-free-standing hemi-epiphytes) ≥ 10 cm in diameter at breast height (DBH) were measured, above buttress roots where required, and identified by a knowledgeable local field assistant. This process was strengthened and verified by *in situ* identifications provided on a subset of 17 plots by a trained technician from the Botany Department of the Instituto Nacional de Pesquisas da Amazônia (INPA, Manaus), which maintains the largest herbarium of the central-western Amazonian flora. Vernacular names were attributed to the highest possible level of taxonomic resolution (species 18.4% of individuals, genus 59.8%, family 19.5%). Only 2.4% of all trees (N = 12,721) within the 200 plots remained unidentified (mean ± SE = 2.5% ± 0.25, range = 0 – 19.7%). Synonyms in plant taxonomy were condensed (The Plant List 2010, IPNI 2008) and family nomenclature was updated on the basis of the APG III system (APG 2009).

2.2.3. Wood density

We compiled wood density data based on the Global Wood Density Database (GWDD: Chave et al. 2009, Zanne et al. 2009), which represents the best available source of wood specific gravity (WSG) values (Flores & Coomes 2011). Although the full global dataset generally out-performs regional subsets, this is predominantly due to greater sample size. Conversely, large regional sets (e.g. tropical South America) perform better (Flores & Coomes 2011) because of differences between tropical and temperate regions (Coomes & Bellingham 2010). We therefore used the tropical South America regional subset of the GWDD, supplemented with two additional sources, notably values for *várzea* tree species from measurements carried out primarily in the Mamirauá Sustainable Development Reserve, Amazonas (Wittmann et al. 2010a), and for *terra firme* trees from the Jari region of northeastern Brazilian Amazonia (Jari Celulose 2002).

We used a hierarchical system to assign WSG values to each live stem in our plots, depending on the taxonomic resolution of the field identification and the available WSG data. We used, in decreasing order of preference: (1) species-specific WSG values for all stems identified to species-level with corresponding WSG values available, (2) genus-level mean WSG values, or (3) family-level mean WSG values. As a last resort (4), unidentified stems were assigned to the mean WSG value from all other stems in their plot. In all cases, priority was given over values from the GWDD to values from Jari Celulose (2002) and Wittmann et al. (2010a) for stems in *terra firme* and *várzea* forest plots, respectively.

2.2.4. Forest structure and biomass

Both LiDAR data (Palminteri et al., 2012) and field measurements (Campbell et al., 1986) indicate that canopy tree heights are substantially lower in Amazonian floodplain forests than in upland forests. However crown heights, in addition to WSG, are frequently overlooked in AGB estimates (Chave et al. 2005). We derived height estimates for each *terra firme* stem from measured DBH values, using the nonlinear relationship between tree DBH and crown height measured from 996 randomly selected trees (DBH ≥10 cm) occurring in the same interfluvial region (Urucu forest: $R^2 = 0.65$; Appendix 2.1; Peres 1994). This general relationship was also used to infer height values for *várzea* stems, assuming an average upper canopy height of 30 m on the basis of observations in multiple *várzea* plots and the 30-35 m estimates of the upper canopy height in high-*várzea* by Wittmann et al. (2010b).

Total basal area was calculated for each plot following $BA = \sum\pi(DBH_i/2)^2$, where DBH_i is the diameter at breast height (cm) for each tree, and subsequently converted to basal area per hectare ($m^2\ ha^{-1}$). No allometric models to predict AGB have yet been developed specifically for *várzea* forests but a recent assessment of seven models for this forest type showed the importance of including wood density and tree height as predictors (Schöngart et al. 2010), in addition to DBH measurements. Schöngart et al.

(2010) recommend using the mean from three empirically tested models which showed good congruence across *várzea* stands of differing ages (Table 2.2). The resulting stem-specific AGB values (kg) were aggregated within a plot and converted to biomass per hectare (Mg ha^{-1}). We also calculated the AGB per tree basal area, defined as the structural conversion factor (SCF; Mg m^{-2} basal area) (Malhi et al. 2006).

Table 2.2. *Allometric models for predicting aboveground biomass (Mg ha^{-1}) from forest inventory data incorporating DBH (d, in cm), wood specific gravity (ρ, in g cm^{-3}), and total tree height (h, in m).*

	Allometric model [a]	Variables included	Source
1	$42.69 - 12.8d + 1.242d^2$	DBH only	Brown (1997)
2	$\rho/0.67 \times \exp(0.33(\ln(d)) + 0.933(\ln(d^2)) - 0.122(\ln(d))^3) - 0.37$	DBH and WSG only	Baker et al. (2004a)
3	$0.6 \times \rho \times h \times \pi \times (d/2)^2$	DBH, WSG and height	Cannell (1984)
4	$0.112 \times (\rho \times h \times d^2)^{0.916}$	DBH, WSG and height	Chave et al. (2005)
5	$0.0509 \times \rho \times h \times d^2$	DBH, WSG and height	Chave et al. (2005)

[a] Schöngart et al. (2010) recommend using the mean value of equations 3-5 for *várzea* forests.

2.2.5. Landscape predictors of AGB

2.2.5.1. Water stress

We extracted Shuttle Radar Topography Mission (SRTM) (Jarvis et al. 2008) digital elevation data for the midpoint of each plot. There is a considerable drop in elevation along the river course within the study region (15m height along 135 km straight line or 305 km including meanders). SRTM elevation provides a clear delineation between floodplain and *terra firme* for most high-order rivers, and can be combined with other remotely sensed data as an aid in mapping floodplain habitats (Hamilton et al. 2007). However, direct use of SRTM elevation (or SRTM elevation relative to nearest channel elevation) to map flooding zones within *várzea* forest is limited by three main factors: (1) for forested areas, SRTM elevation represents the height of the C-band scattering phase centre within the upper forest canopy, rather than the ground surface; the difference between surface and phase centre elevation varies with forest structure but, based on estimates for structurally similar stands (Hofton et al. 2006), SRTM elevations for Juruá forest stands are 5 to 15 m greater than ground elevations; (2) inundation of large river floodplains is a complex process affected by many variables in addition to floodplain surface topography (Alsdorf et al. 2007, Bonnet et al. 2008); and (3) phase noise and other error sources typically degrade the accuracy of single-pixel SRTM elevation estimates by several meters for 30 m forest stands (Walker et al. 2007); block averaging of pixels, which reduces such errors, was not feasible for this study owing to the small forest plot sizes.

L-band synthetic aperture radar (SAR) sensors such as ALOS PALSAR (Rosenqvist et al. 2007) provide optimal satellite data sets for mapping flooded forests, owing to their ability to penetrate forest canopies and yield an enhanced signal from reflections between tree trunks and underlying water surfaces (Hess et al. 2003). As part of a JAXA initiative targeting global wetlands (Lowry et al. 2009), extensive multi-temporal imagery of the Amazon basin was acquired between 2006 and 2011 using the ALOS ScanSAR configuration, a regional mapping mode with 100 m spatial resolution. We used a time series of 12 ScanSAR scenes (Appendix 2.2) to assess the local conditions in *várzea* forests relative to the river channel. The ScanSAR image stack was first classified into broad land cover types (upland *terra firme* forest, *várzea* forest, non-forest) using an object-oriented approach implemented in the eCognition Developer 8 software package. Flooding state of *várzea* forest areas was then mapped for each date.

Daily river stage readings at the downriver Porto Gavião gauge near Carauari was used as an index to link flooding states on the ALOS ScanSAR imaging dates to long-term inundation periods (Appendix 2.2). Inundation periods were based on a 38-year record (1973-2010) obtained from Brazil's Agência Nacional de Águas (ANA; http://hidroweb.ana.gov.br). The range of river stage and flooding extent captured by the ScanSAR record included relatively low-flood years (low water recurrence interval of 3-4 years) as well as high-flood years (high-water recurrence interval of 7-8 years). We grouped the *várzea* forest sites into areas flooded 9-12 months/yr, 6-8 months/yr, 3-5 months/yr, 1-2 months/yr, and < 1 month/yr. We then extracted the value for each forest plot, using the mean flood duration whenever a plot spanned more than one flood duration category (21 of the 100 *várzea* plots). In addition to flood duration and SRTM terrain elevation per plot we used distance to the nearest perennial stream as a potential proxy of water stress. This was calculated from the HydroSHEDS data (Lehner et al. 2006) using the network analyst extension in ArcGIS 9.2.

2.2.5.2. Logging accessibilty

Using the same GIS procedure we calculated the distance of each plot to the nearest point along the Juruá river channel and the nearest semi-permanent human settlement (defined as a >25 yr old cluster of more than one stable household), using a digital map of all households within the two focal reserves (Newton et al. 2012b). These values were employed as proxies for accessibility to selective logging.

2.2.6. Data analyses

We used multi-level generalised linear mixed models (GLMMs) to relate variation in landscape variables (water stress and historical logging access) to AGB. This approach was the most appropriate to account for potential spatial autocorrelation (Bolker et al. 2008), with our global model incorporating a random term nesting ‘plot’ within ‘transect’ (a total of 200 plots nested within 46 transects). Models were built using the package ‘lme4’ in R (R Development Core Team 2010), and we used the ‘MuMIn’ package (Bartón 2010) to test models of every possible first-order combination of variables and rank them based on the Akaike Information Criterion (AIC) (Burnham & Anderson 2002). This package also determined the relative importance of explanatory variables given their frequency in those models and their cumulative Akaike weight.

2.3. Results

2.3.1. Stem identification and wood density

We sampled a total of 12,721 stems ≥ 10cm DBH (*terra firme* - TF: 6,389; *várzea* - VZ: 6,332) across the 200 plots (= 20 ha), from 191 genera in 55 families (TF: 152 genera, 50 families; VZ 126 genera, 44 families). Despite low levels (18.4%) of identification to species (TF: 9.9%; VZ: 26.9%), over three quarters (78.1%) of all stems were successfully identified to at least the level of genus (TF: 79.9%; VZ: 76.3%) and we unambiguously identified 97.6% of all stems to at least the family level (TF: 96.9%; VZ: 98.4%). The WSG values assigned to each stem showed that the variation in wood density was significantly lower within genera than between genera (ANOVAs: GWDD $F_{573,1430} = 8.85$, $p < 0.001$, Jari $F_{186,210} = 1.92$, $p < 0.001$, Mamirauá $F_{107,18} = 4.35$, $p < 0.001$).

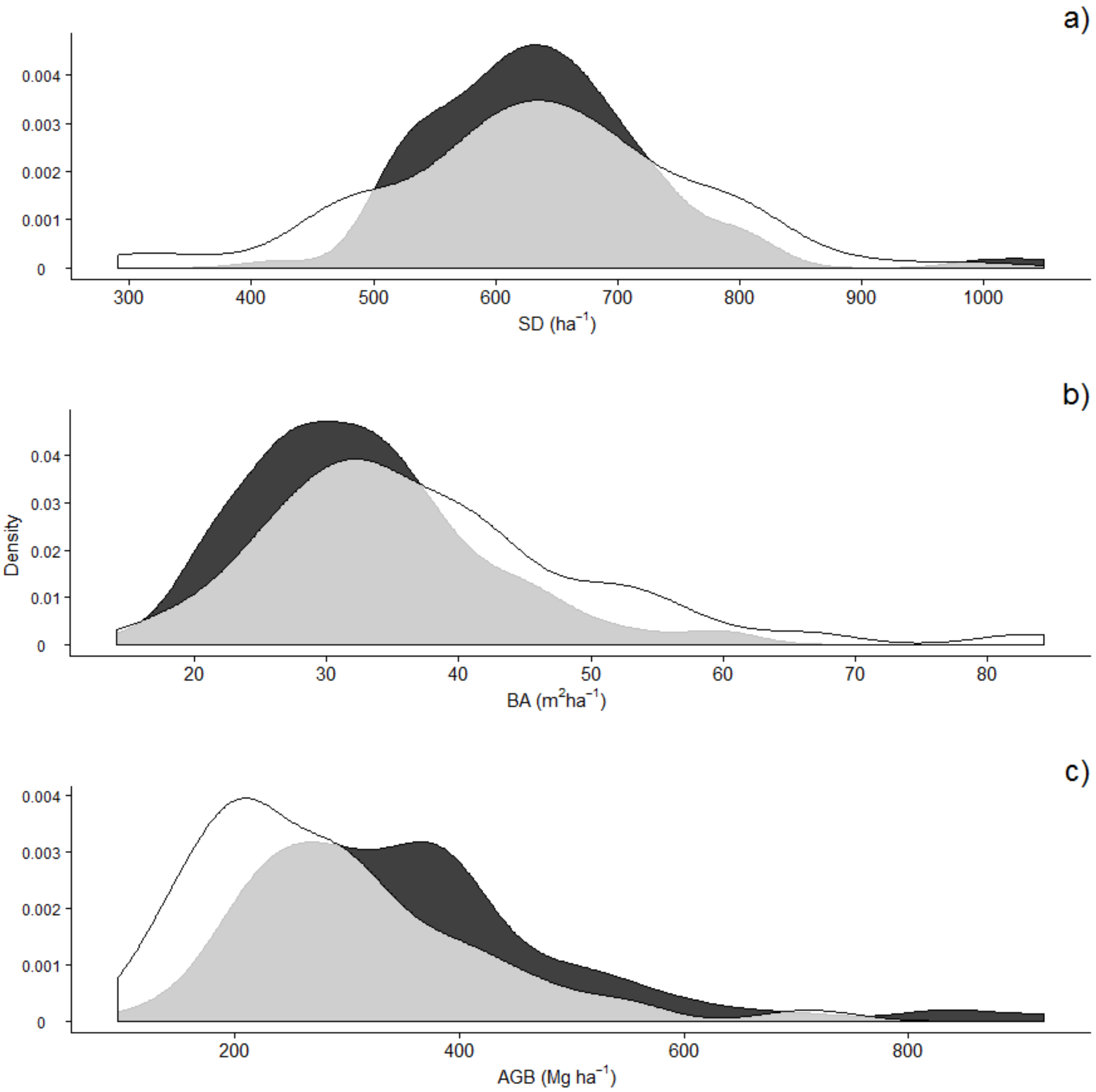


Figure 2.2. *Density distribution of (a) stem density (stems ha^{-1}), (b) forest basal area (m^2 ha^{-1}) and (c) aboveground forest biomass (Mg ha^{-1}) for* terra firme *(white curve) and* várzea *(black curve) forests.*

2.3.2. Forest structure and biomass

Stem density was similar in *terra firme* and *várzea* forests with both forest types dominated by smaller stems (Appendix 2.3) although large emergent trees (> 100cm DBH) had a disproportionately large influence on plot basal area, particularly in *várzea* forests (Figure 2.2). As a result, mean plot basal area was greater and more variable in *várzea* than in *terra firme* forest (Figure 2.3; TF mean ± SE: 32.4 ± 0.9 m^2 ha^{-1}; VZ:

37.6 ± 1.2 m^2 ha^{-1}; t-test: $t = -3.411$, $p < 0.001$). AGB estimated using the simplest allometric equation, based on DBH only, was similar across forest types. However, mean WSG per plot was significantly lower in *várzea* forest (TF: 0.67 ± 0.003 g cm^{-3}; VZ: 0.58 ± 0.003 g cm^{-3}; $t = 20.085$, $p < 0.001$), where canopy height rarely exceeded 30 m. Employing more complex allometric equations incorporating both WSG and tree height significantly lowered AGB estimates for *várzea* forest plots compared to those in *terra firme* (TF: 358.4 ± 14.4 Mg ha^{-1}; VZ: 281.9 ± 12.0 Mg ha^{-1}, $t = 4.077$, $p < 0.001$). The relative difference between forest types was even more apparent when considering the structural conversion factor (TF: 10.7 ± 0.2 Mg m^{-2} basal area; VZ: 7.3 ± 0.1 Mg m^{-2} basal area; $t = 18.154$, $p < 0.001$), reinforcing the notion that *várzea* sites were predominantly comprised of light-wooded tree species.

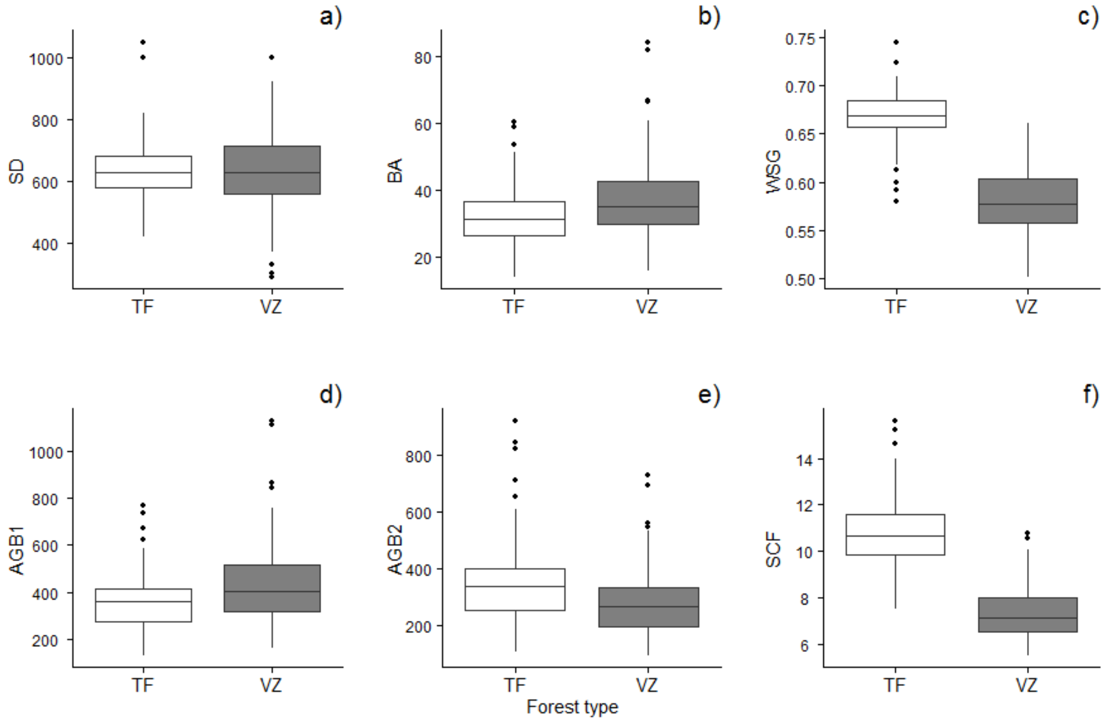


Figure 2.3. *Mean values per forest plot of (a) stem density (stems* ha^{-1}*), (b) forest basal area (*m^2 ha^{-1}*), (c) wood specific gravity (g* cm^{-3}*), (d) aboveground biomass (Mg* ha^{-1}*) from DBH-only equation, (e) aboveground biomass (Mg* ha^{-1}*) from equations also including wood specific gravity and tree height, and (f) the structural conversion factor (Mg* m^{-2} *basal area) for* terra firme *(open boxes) and* várzea *forests (solid boxes). Horizontal bars indicate medians; boxes indicate interquartile ranges; whiskers indicate minimum and maximum values; and circles indicate outliers (observations 1.5 times higher or lower than 1st and 3rd quartile, respectively).*

The AGB values for plots in both *terra firme* and *várzea* forest were significantly positively related to basal area (TF: $R^2 = 0.92$, $p < 0.001$; VZ: $R^2 = 0.88$, $p < 0.001$) and, to a lesser degree, to plot-scale WSG (TF: $R^2 = 0.06$, $p = 0.009$; VZ: $R^2 = 0.09$, $p = 0.002$) (Figure 2.4). There was also a significant positive relationship between AGB and stem density in *terra firme* forests but not in *várzea* forests (TF: $R^2 = 0.05$, $p = 0.013$; VZ: $R^2 = 0.01$, $p = 0.170$), and between basal area and stem density in both forest types (TF: $R^2 = 0.17$, $p < 0.001$; VZ: $R^2 = 0.04$, $p = 0.026$) (Figure 2.4). WSG, however, was unrelated to both stem density (TF: $R^2 = 0.0006$, $p = 0.31$; VZ: $R^2 = 0.003$, $p = 0.26$) and basal area (TF: $R^2 = 0.011$, $p = 0.15$; VZ: $R^2 = 0.015$, $p = 0.12$) (Figure 2.4.)

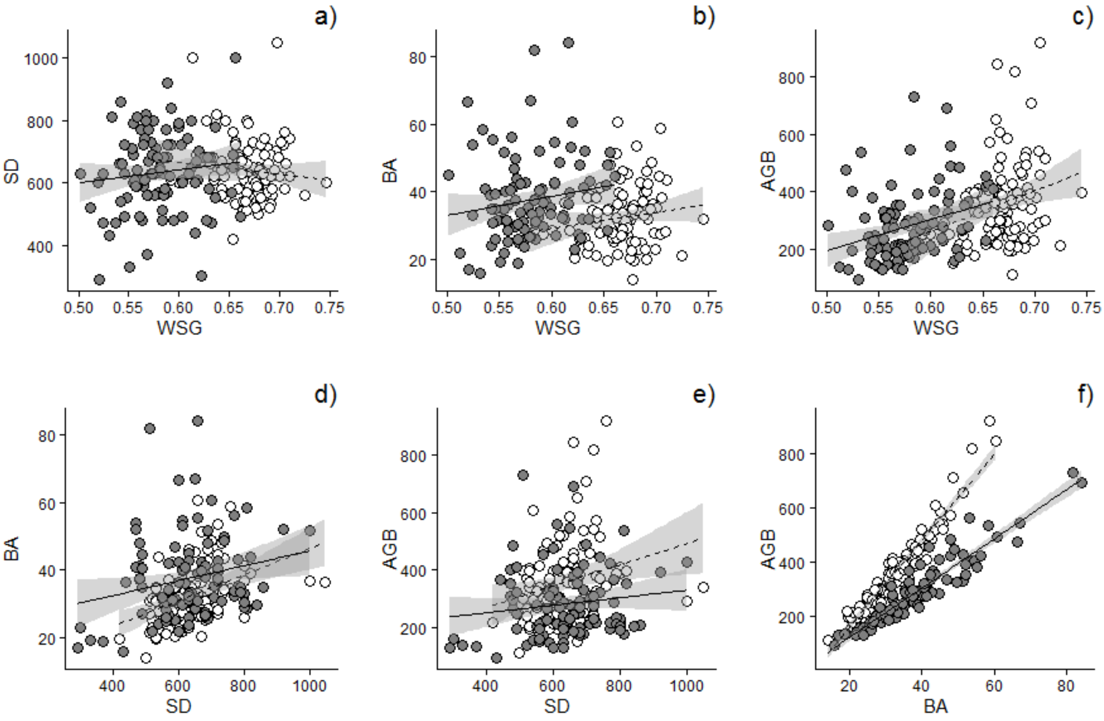


Figure 2.4. *Pairwise relationships between plot-scale mean wood specific gravity (WSG, g cm^{-3}), stem density (SD, stems ha^{-1}), basal area (BA, m^2 ha^{-1}), and aboveground biomass (AGB, Mg ha^{-1}) for 200 forest plots in* terra firme *(open circles, dashed line) and* várzea *forests (solid circles, solid line). Lines represent linear models; grey shading represents 95% confidence intervals.*

2.3.3. Landscape predictors of AGB

2.3.3.1. Water stress

The top-ranking model predicting AGB across both forest types on the basis of landscape variables had a low Akaike weight of 0.24 (Table 2.3) suggesting uncertainty in identifying a single best model and supporting the adoption of a multi-model approach. Twelve alternative models comprised the 95% set of models (cumulative $\omega_i \geq 0.95$). The single best model contained only the variable forest type, which appeared in 10 of the 12 models with a cumulative Akaike weight of 0.86, confirming the lower aboveground biomass values across *várzea* forest compared to *terra firme* forest. The next most important variable was terrain elevation, with a positive influence on AGB across all plots, although this is mostly explained by elevation differences between forest types (Table 2.3, Figure 2.5). We therefore examined the potential effects of elevation and other landscape variables further within forest types by constructing models in the same fashion for *terra firme* and *várzea* forest separately.

Indicators of water stress had contrasting influences in each forest type, and greater importance in *várzea* forest. Elevation had a weak positive effect on AGB in *terra firme*, in contrast to a strong positive effect of greater flood duration in *várzea* forest (Table 2.3, Figure 2.5). The positive effect of distance to the nearest stream on AGB in *terra firme* is at odds with the negative effect in *várzea* forest, but low cumulative Akaike weights in each case show the low relative importance of this variable in the models (Table 2.3, Appendix 2.4). Most strikingly, flood duration (on the basis of ALOS ScanSAR flood mapping) had a positive effect on AGB in *várzea* forest.

2.3.3.2. Logging accessibility

In addition to water stress, many of the 95% set of models for each forest type contained the variables describing the historical accessibility of forest to selective timber extractors. Distance to the nearest community was particularly prominent across models and notably was positively related to AGB in *várzea* forest, in contrast to a negative relationship in *terra firme* forest (Table 2.3, Appendix 2.4).

Table 2.3. *Summary of multi-level mixed effects models of mean aboveground forest biomass within 200 biomass plots in both* terra firme *(TF) and* várzea *(VZ) forests, and for each forest type separately. All top-ranking models within 95% of the cumulative Akaike weight (ωi) are shown. Variables included in each model are shaded grey. Model averaged Akaike weights for each variable are shown in the first line.*

	No. models in 95% set	Model no.	Intercept	Forest type	Water stress		Logging accessibility		IC	ΔIC	ω_i
					Elevation (m) (TF)/ Flood (months) (VZ)	Distance to stream (km)	Distance to river (km)	Distance to community (km)			
All plots	12	1	▨ 1.00	▨ 0.86	0.36	0.26	0.21	0.17	2527	0.00	0.24
		2	▨	▨		▨			2528	1.37	0.12
		3	▨	▨	▨				2528	1.38	0.12
		4	▨	▨				▨	2529	2.10	0.08
		5	▨	▨			▨		2529	2.15	0.08
		6	▨		▨				2530	2.76	0.06
		7	▨	▨	▨	▨			2530	2.95	0.05
		8	▨	▨		▨		▨	2530	3.39	0.04
		9	▨		▨		▨		2530	3.43	0.04
		10	▨	▨		▨	▨		2530	3.47	0.04
		11	▨	▨	▨			▨	2530	3.52	0.04
		12	▨	▨	▨		▨		2530	3.56	0.04
		β	262.01	-70.14	1.94	9.86	0.45	-1.04			
Terra firme	10	1	▨ 1.00		0.20	0.22	0.30	▨ 0.67	1282	0.00	0.22
		2	▨				▨	▨	1283	0.97	0.14
		3	▨						1283	0.98	0.14
		4	▨			▨		▨	1284	1.50	0.11
		5	▨		▨			▨	1284	1.90	0.09
		6	▨			▨			1285	2.71	0.06
		7	▨		▨		▨	▨	1285	2.72	0.06
		8	▨			▨	▨	▨	1285	2.84	0.05
		9	▨		▨				1285	2.89	0.05
		10	▨				▨		1285	2.91	0.05
		β	352.50		1.30	11.51	5.09	-11.74			
Várzea	6	1	▨ 1.00		▨ 0.70	0.20	0.22	▨ 1.00	1233	0.00	0.41
		2	▨					▨	1235	1.78	0.17
		3	▨		▨	▨		▨	1235	2.07	0.15
		4	▨		▨		▨	▨	1235	2.15	0.14
		5	▨				▨	▨	1236	3.29	0.08
		6	▨			▨		▨	1237	3.93	0.06
		β	193.24		8.05	-7.62	4.77	24.03			

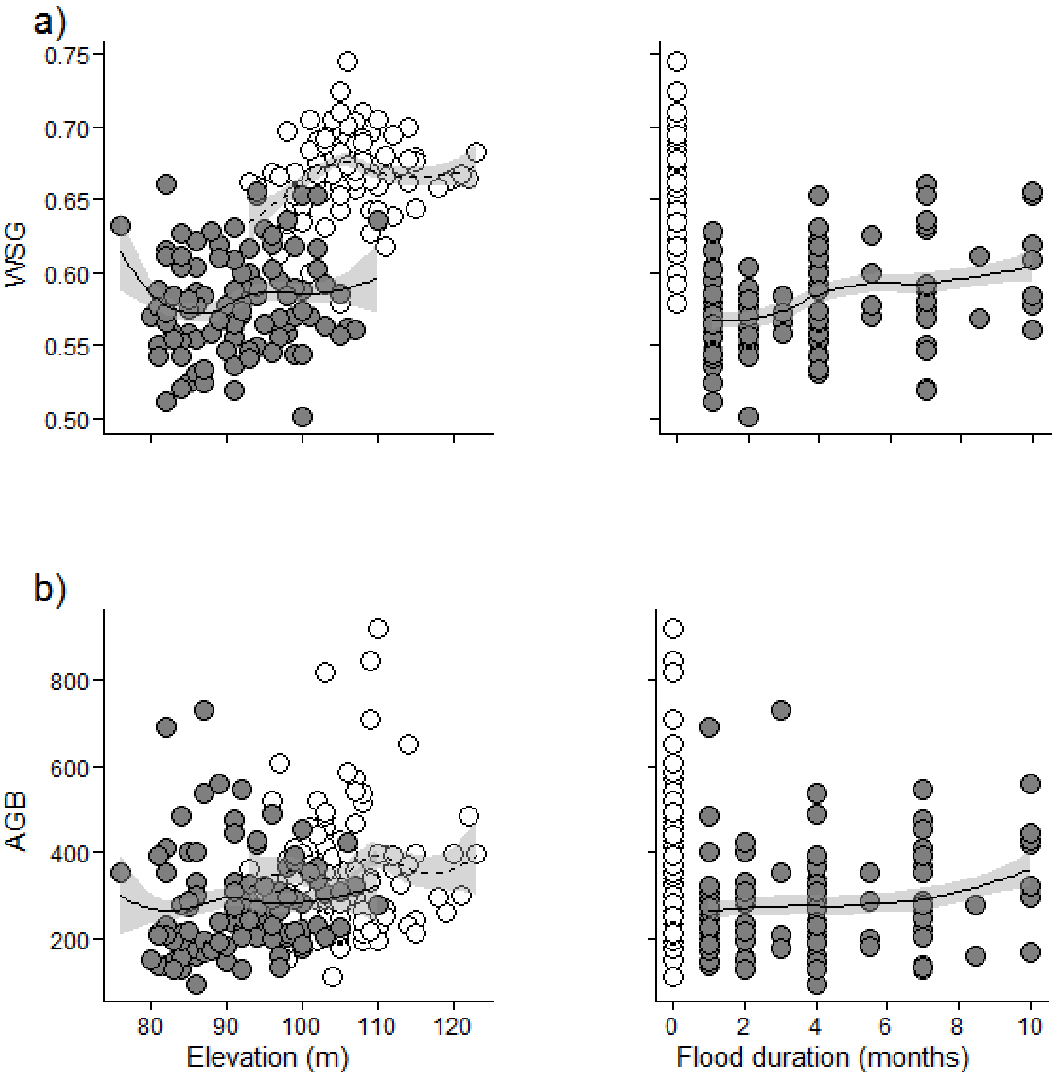


Figure 2.5. *Relationships between SRTM-measured elevation (m) and ScanSAR-measured flood duration (months) with (a) wood specific gravity (WSG, g cm*$^{-3}$*) and (b) aboveground biomass (AGB, Mg ha*$^{-1}$*) for 200 forest plots in* terra firme *(open circles, dashed lines) and* várzea *forests (solid circles, solid lines). Curves represent smoothed means; grey shading represents 95% confidence intervals.*

2.3.4. Reserve-wide carbon stocks

ALOS ScanSAR analysis quantified the spatial extent of *várzea* forest in each reserve (RDS Uacari: 18.1%; ResEx Médio Juruá: 17.4%) and the extent of each flood pulse duration category (Appendix 2.5). We extrapolated estimates of mean plot-scale AGB per hectare for each forest type to the aggregate area of the two reserves, while incorporating ScanSAR flood duration categories for *várzea* forest across the entire study area, and excluding areas identified as non-forested. This resulted in an AGB estimate of 297.8 Tg (RDS Uacari: 212.2 Tg; ResEx Médio Juruá: 85.6 Tg; TF: 252.3 Tg, VZ: 45.5 Tg), which corresponds to a total carbon stock of 106.1 Tg C within the RDS Uacari (TF: 84.4%, VZ: 15.6%) and 42.8 Tg C within the ResEx Médio Juruá (TF: 85.5%, VZ: 14.5%).

2.4. Discussion

This study provides a robust examination of the variation in AGB both within and between seasonally flooded and unflooded forest along the Rio Juruá, a poorly known major white-water tributary of the Amazon. Our network of 200 forest plots in the Médio Juruá region of western Brazilian Amazonia, stratified by forest type, includes a far more extensive effort in *várzea* forests than previously accomplished at a single site, and represents a substantial contribution to understanding variation in forest structure within this forest type. Our study reports three important patterns: (1) AGB is generally lower in low-lying *várzea* forest than in upland *terra firme* forest as a result of lower wood density and lower canopy height; (2) landscape-scale variation in AGB across the two reserves is principally explained by forest type, namely whether or not the forest experiences a prolonged annual flood pulse; and (3) water stress appears to play a greater role in determining AGB in *várzea* forests than in *terra firme* forests but, in contrast to our hypothesis, AGB in *várzea* forest was greatest where the local inundation period associated with persistent water stress was longer.

2.4.1. Low wood density and AGB in *várzea* forest

The overriding importance of forest type in our models shows the critical influence of the dramatic annual flood pulse. Even low-lying *terra firme* forests just above the supra-annual average of maximum water-level (including *paleo-várzeas*) have been completely free from the marked flood pulse of *várzea* forests for thousands of years. The annual submergence cut-off point marks a change in many environmental variables including soil fertility, soil texture, and stability of aboveground vegetation, in addition to physiological stress associated with the prolonged inundation period. It is unsurprising, therefore, to confirm significant differences in AGB between these forest types.

However, these differences were not determined by stem density or forest basal area. Stem densities recorded in this study were generally higher than in previous studies from Western and Central Amazonia, with the exception of the youngest *várzea* stands (Table 1), but did not differ significantly between forest types. Indeed, it is revealing that AGB estimates for *várzea* forest plots calculated from DBH or basal area alone were actually similar or higher than those of adjacent *terra firme* forest; only by including stem-specific wood density and tree height, which account for a considerable proportion of the variation in AGB estimates (Fearnside 1997, Nogueira et al. 2008), could AGB values for *várzea* forest be shown to be lower than those for adjacent *terra firme* forests.

Wood density has been recognised to vary on a regional basis across the Amazon basin, but independently of basal area (Malhi et al. 2006) and, while there is no consistent regional scale relationship between wood density and AGB (Stegen et al. 2009), wood density may be more important in driving differences between different forest types. The inverse correlation between mean wood density and growth rates (Malhi et al. 2006) seems relevant both locally and regionally, with lower values expected in highly dynamic floodplain environments. Yet wood density has not been considered in previous *várzea* forest studies apart from those at Mamirauá (Schöngart et al. 2010). The use of different allometric equations, particularly those excluding wood density or tree height, in *várzea* studies elsewhere renders comparisons of aboveground biomass estimates problematic. For example, our AGB values for *várzea* forest were generally lower than those reported previously for other *várzea* sites in the Upper Amazon but since these estimates failed to consider wood density they are likely to represent overestimates. In contrast, our plot-scale AGB estimates for *várzea* forest were higher than those elsewhere in Amazonia including Mamirauá, despite similar mean wood density values. Our AGB estimates are also generally consistent with the predicted pattern across the Amazon including all forest types (Saatchi et al. 2009).

Our results show significantly lower wood density in *várzea* forest than *terra firme*, as a result of a markedly different tree community composition, and highlight the importance of including wood density estimates in AGB estimates, even where field measurements of wood density are unavailable. Wood density exhibits strong phylogenetic conservatism, with more similar WSG values in closely related than distantly related species (Chave et al. 2006, Swenson & Enquist 2007), and differences between genera accounting for the largest proportion of variation (Baker et al. 2004b). This was confirmed for each of the WSG datasets we used, clearly supporting the validity of our approach where most stems (78.1%) were unambiguously identified to at least the resolution of genus.

Ideally tree height would also be measured for each stem, rather than predicted from DBH data, but practical difficulties often prevent this in the field (Brown 2002). Since this study is focused on the comparison between *várzea* and adjacent *terra firme* forests, we also note our deliberate use of the allometric equations proposed by Schöngart et al. (2010) for *várzea* forests to calculate AGB in both forest types, although alternative estimates for *terra firme* may be possible using equations specifically developed for this forest type. A study of four 1.0 ha plots in *terra firme* forest near Carauari, just downriver from our study area (Silva et al. 1992), reported slightly higher density values for stems ≥10cm DBH (range 668 – 862 stems ha^{-1}) but basal areas (range 27.0 – 33.9 m^{2} ha^{-1}) were consistent with our findings. A basin-wide forest biomass interpolation produced AGB values of 286 – 360 Mg ha^{-1} for this site (Malhi et al. 2006), placing the mean value derived from our plots at the top end of this range.

2.4.2. Advantages and disadvantages of small forest plots

Forest inventories using small plots, such as the 0.1-ha plots sampled in this study, potentially overestimate AGB due to the disproportionately large influence of very large (i.e. > 100 cm dbh) emergent trees (Clark et al. 2001). This tendency is apparent in our results (Figure 2), regardless of the care with which large-girthed trees are recorded as either in or out of the plot boundaries, especially in *várzea* forests where single emergents contributed disproportionately to the plot basal area value compared to *terra firme* forests despite similar stem densities in the two forest types.

The disproportionate influence of large trees in small plots may in part explain the higher values of basal area per hectare in this study compared to most *várzea* studies elsewhere in Amazonia, although our results were within the range of values reported from Mamirauá (Ayres 1986, Schöngart et al. 2010). The mean AGB value from our *terra firme* plots is also relatively high compared to regional interpolations based on a set of old-growth forests plots scattered across Amazonia (Malhi et al. 2006, Saatchi et al. 2007). However, these values are not excessively high compared to other plots, some of which stand out as local ‘bulls-eyes’ on regional interpolated surfaces.

Several additional considerations can be made regarding plot size, with further pros and cons in terms of sampling efficiency (Phillips et al. 2003). An assessment in Sumatran forests strongly supports small plots as a successful protocol for stratified sampling on a landscape scale, concluding that an area of 10 ha would allow AGB to be estimated to within 5.5% (Laumonier et al. 2010). Our sampling protocol covered this total area in each forest type and, as such, we believe our approach enabled the best possible comparison, despite the challenges in accurately estimating AGB in two contrasting forest types.

2.4.3. Landscape predictors of AGB

In addition to differences between *várzea* and *terra firme*, we recorded considerable plot-scale variation in AGB within each forest type. The most important factors proposed to influence forest structure on a regional scale, include climate and soil fertility (Malhi et al. 2002, Clark & Clark 2000). Climate was identified as the most important variable in Bolivian lowland forests but the impact of soils was less clear (Toledo et al. 2011a) and the low variation in soil nutrients can probably be safely ignored within *várzea* forests (Wittmann et al. 2006). Other potential drivers on a local scale include human disturbance (Alves et al. 2010), topography and water availability (Malhi et al. 2002, Murphy & Lugo 1986, Toledo et al. 2011b).

2.4.3.1. Water stress: elevation and flood duration

Topography is closely related to water availability, and elevation in unflooded forests has a strong positive relationship with water stress during droughts. Flooding, however, reverses the direction of water stress so that elevation becomes inversely related with stress through excessive waterlogging in *várzea* forests. *Várzea* forest landscapes, despite their generally low elevation, comprise a mosaic system of depressions, levées, plateaus and oxbow lakes. Thus, while elevation was identified by our models as an important determinant of AGB across all plots, classes of flood duration (measured using ScanSAR) was a more relevant indicator of water stress in *várzea* forests

(Appendix 2.6). The marked importance of flood duration within *várzea* forests compared to the minor influence of elevation in *terra firme* forests highlights the greater role of forest hydrology in driving forest structure in seasonally flooded forests. This was expected since small differences in the micro-topography of *várzea* forests may drastically alter exposure to anoxia during the flood pulse, whereas similar differences in elevation in *terra firme* forests may only slightly affect dry season access of deep roots to the water table.

The direction of the relationship with water stress, however, was contrary to our expectations. AGB in *várzea* forest was lowest in plots flooded for the shortest annual periods and actually increased with greater flood stress, although never reaching the mean AGB of unflooded forest. This presents an apparent paradox whereby flooded forests exhibited lower AGB than unflooded forests but higher levels of AGB with increased flood duration. This phenomenon is thought to be induced by inundation stress restricting the growth period of trees to the terrestrial phase of the year, thereby resulting in the formation of distinctive annual growth rings (Worbes 1997, Worbes & Fichtler 2010). Deep, prolonged inundation thus encourages accelerated growth over a reduced growing season, resulting in the accumulation of densely packed tree rings and associated with higher WSG (Wittmann et al. 2006).

This relationship between flooding and tree growth is further complicated by the constant state of flux, both spatially and temporally, as a result of the ever-changing course of fluvial meanders. The constant disturbance results in a permanent process of succession and the formation of vegetation zones. These zones were first described by Ayres (1986), with particular emphasis on low-lying '*chavascal'* swamps, and the gradually higher (low) '*restinga baixa*' and (high) '*restinga alta*'. These distinctions have been maintained and elaborated upon by further studies at Mamirauá (e.g. Wittman et al. 2002), including the recognition of successional stages of different stands. Our results coupling elevation with seasonal water-level and the irregular nature of *várzea* drainage systems suggest that flood duration is more important than elevation alone. The distinctions between floodplain vegetation zones may therefore be more complex locally than previously recognised and may also vary substantially along the length of rivers across the Amazon, especially considering our over-reliance on a handful of *várzea* study sites (Table 2.1).

2.4.3.2. Logging accessibility: management implications

In addition to the effects of baseline landscape variables related to water stress, we found clear indication of the possible role of the historical accessibility by small-scale timber extractors on forest biomass. We hypothesised that AGB was negatively related to accessibility, particularly in *várzea* forests which are both more accessible to loggers and involve easier removal of roundlogs. Inundation actually facilitates extraction; felled trees can be floated out to the main river channel during high-water floods, and even timber species denser than water can be attached to rafts of light-wooded species felled solely for this purpose. In support of this hypothesis, AGB was positively related to the distance to the nearest community within *várzea* forests but not in *terra firme*, although the reliability of this relationship is reduced by the strong influence of two outlier plots and the inevitable lack of *várzea* plots at greater distances from communities; only 8 of the 100 *várzea* plots are located more than 5km from a community (Appendix 2.4). This poses obvious questions over the repeated history of selective logging which was once extensive throughout the mature floodplain forests along the major white-water tributaries of the Amazon, particularly since the collapse of the rubber-boom (Scelza 2008). The impact of this historical logging pressure on the patterns of forest structure and biomass observed today remains poorly understood.

The legacy of historical logging can still serve as a warning for the future. V*árzeas* are the source for 60-90% of timber harvests from central and western Amazonia (Klenke & Ohly 1993, Higuchi et al. 1994) and the nutrient-rich productive soils also make the land an attractive proposition for agricultural expansion (Fageria & Baligar 1996). Finally, *várzeas* are located along the principal Amazonian transport routes, placing them at close proximity to the most densely settled and rapidly expanding human populations in the Amazon (Parolin et al. 2004a). This highlights the severe threats faced by the most species-rich floodplain forest on Earth (Wittmann et al. 2002), which hosts a plant community composition almost completely distinct from adjacent *terra firme* forests.

2.4.4. Reserve-wide carbon stocks

Assessing carbon stocks in Amazonian forest reserves is a critical first step to judge the effectiveness of protected areas in reducing emissions from deforestation and degradation (Ricketts et al. 2010, Soares-Filho et al. 2010) but few such assessments of reserve stocks have been conducted to date. This study provides a useful benchmark for the RDS Uacari and the ResEx Médio Juruá to use for future Monitoring, Reporting and Verification of carbon loss in these protected areas. A potential weakness in this study is the lack of sampling at the high *terra firme* plateaus coinciding with the least accessible extremes of the two reserves (Figure 2.1). It is possible that these areas would respond differently to the variables included in our models than those from the lower *terra firme* forests we were able to sample.

Despite the typically lower aboveground biomass compared to *terra firme*, *várzea* forests still account for substantial carbon stocks. In our study landscape, *várzea* forests accounted for 17.9% of the total area and 15.3% of the total carbon stock. Yet our results highlight the vulnerability of *várzea* carbon stocks, due to close proximity to human populations and the potentially severe impact of selective logging on single emergent trees. Within the study reserves, there is strong protection from existing management plans but *várzea* forests face increasing threats outside existing protected areas.

2.5. Conclusions

To meet one of the requirements for a successful REDD scheme, namely the provision of accurate current carbon stocks estimates, we highlight the value of an extensive sampling program using a large number of small plots scattered across different forest types, in a poorly sampled region of Brazilian Amazonia. In addition, we recommend the use of allometric equations including both tree height and wood density, accompanied by expansion of the Global Wood Density Database, to improve AGB estimates across forest types. Adopting this approach, we confirmed the dominant influence of the flood pulse in Amazonian seasonally flooded forests, not only in determining differences between *várzea* and *terra firme*, but also within *várzea* forest. This water stress was best described not by elevation but by flood duration, as measured by ALOS ScanSAR, and AGB was notably highest in areas experiencing longer periods of inundation. Incorporating our robust data on variation in AGB, both between and within forest types, allowed an accurate assessment of carbon stocks in two contiguous reserves, and highlighted the valuable contribution made by vulnerable *várzea* forests.

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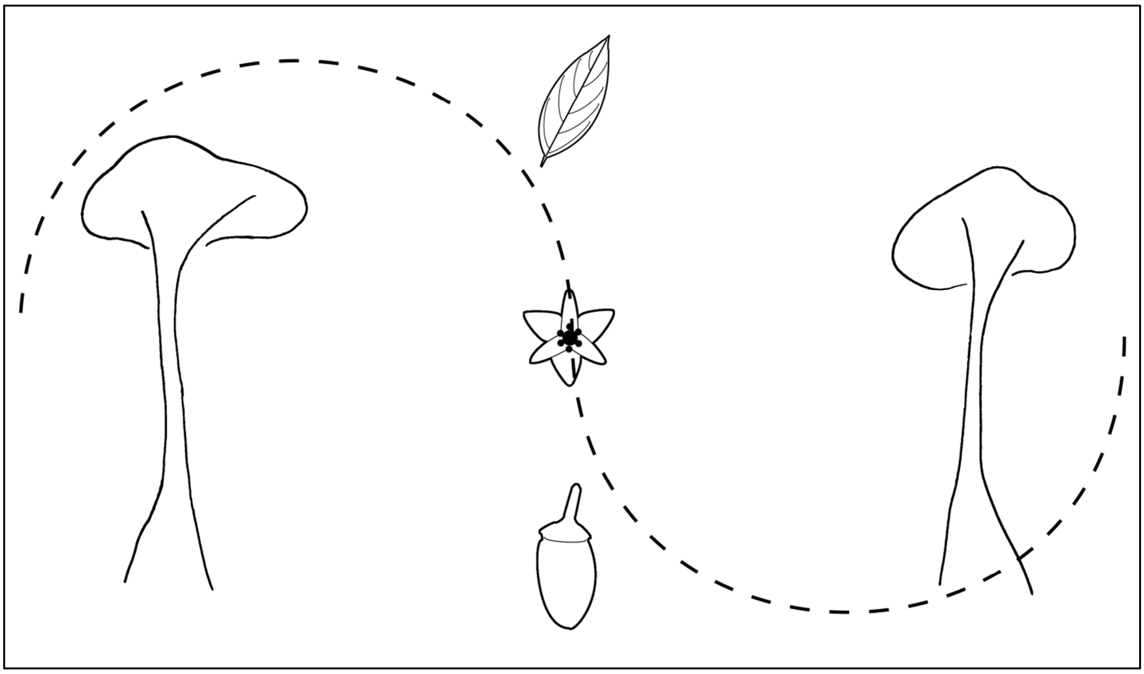
Chapter 3

Patterns of plant phenology
in Amazonian seasonally flooded and unflooded forests



To be submitted to *Biotropica* as:

Hawes, J.E., & Peres, C.A. Patterns of plant phenology in Amazonian seasonally flooded and unflooded forests.

Abstract

Understanding plant phenology is crucial for predicting the temporal availability of fruit resources for frugivorous animals in tropical forests. Few studies have successfully monitored community-wide phenological patterns in the seasonally flooded *várzea* forests of Amazonia, where an annual flood pulse creates arguably the most extreme seasonal conditions found in low-latitude forests anywhere in the world. We monitored vegetative and reproductive plant phenology within two contiguous protected areas bisected by the Juruá river, consisting of both *várzea* (VZ) floodplain and adjacent upland tracts of unflooded *terra firme* (TF) forest. We employed three complementary methods: monthly canopy observations of 1,056 individual plants (TF: 556, VZ: 500; 120 genera, 45 families; April 2009 – March 2010), bimonthly collections from 0.5-m^2 litter traps arranged in a grid across two 100-ha plots (1 TF, 1 VZ; 96 traps per plot; May 2009 – April 2010), and monthly ground surveys (April 2008 – July 2010; TF: total 18 months; VZ: total 26 months) for residual fruit-fall along transect grids within each 100-ha plot (12 km per plot). All surveys in *várzea* forest encompassed the entire flood cycle, employing a novel floating trap design to cope with fluctuating water-levels. Leaf fall peaked during the aquatic phase in *várzea* forest, and in the dry season in *terra firme*. Flowering typically followed leaf fall and leaf flush, extending into the start of the terrestrial phase and rainy season in *várzea* and *terra firme*, respectively. The main peak in fruit availability within *várzea* occurred at maximum flood levels (comprising plants with mainly abiotic seed dispersal modes), in addition to a secondary peak at the start of the rainy season (dominated by vertebrate-dispersed plants) as in *terra firme* forest. These results suggest a primary role of the flood pulse as a proximate trigger determining phenological patterns in *várzea* forest, compared to rainfall in *terra firme*.

3.1. Introduction

Plant phenology, the timing of plant reproductive and vegetative cycles, typically displays strong periodicity in both tropical and temperate zones (Newstrom et al. 1994, van Schaik et al. 1993), and is increasingly relevant to a wide range of applied issues (Morisette et al. 2009). For example, the ephemeral nature of plant productivity, combined with the patchy distribution of fruits and flowers in tropical forests (Levey 1988), drives the temporal and spatial availability of food sources for animal consumers. Since most large vertebrates in tropical forests are at least partially frugivorous (Fleming & Kress 2011), quantifying the availability of fruit resources in particular, is critical for understanding the behavioural ecology of faunal communities in tropical forests. While the recognition of patterns in plant phenology is improving, there remains much uncertainty over the processes involved, including the potential triggers responsible for the timing of such events.

At first glance tropical forests appear to lack the seasonal extremes of temperate forests, although they typically experience a distinct seasonality in climatic variables, particularly precipitation. Rainfall is thus frequently proposed as a potential trigger for the phenological patterns observed in tropical forests (Bradley et al. 2011), particularly in upland forests where dry season water stress is regarded as key. Extensive lowland floodplain forests (e.g. those of the Amazon, Congo, and Mekong rivers), however, are subjected to an additional annual force, in the form of a predictable ‘flood pulse’ (Junk et al. 1989), which can result in dramatic seasonal differences. For example, the white-water floodplain forests of the Amazon (=Solimões) river and its tributaries, which are known as v*árzea* forest (Prance 1979), can flood to a depth of 10-15 m for up to 210 days per year (Parolin et al. 2004a). This extended period of submersion and waterlogging has severe consequences for plant physiology, notably oxygen deficiency (Parolin 2009), reduced photosynthesis due to low light penetration through water and silt deposited on leaves, and low water conductance which can paradoxically result in water deficits in the tree crown (Parolin et al. 2004a).

The regularity of this powerful flood pulse is expected to drive the timing of many ecological processes within *várzea* forests, and phenological strategies are amongst the mechanisms proposed as adaptations to cope with the drastic annual transition between aquatic and terrestrial phases (Parolin et al. 2004b, Ferreira et al. 2010, Junk 1989, Worbes et al. 1992, Wittmann et al. 2002). However, despite accounting for >200,000 km^2 within Brazilian Amazonia alone (Junk 1997), *várzea* forests are one of the most poorly studied Amazonian forest types, and the relative importance of potential phenological triggers is even less clear than those in unflooded forests (Parolin et al. 2010). In particular, there remains a shortage of quantitative assessments on a community-wide scale, with most studies focusing on the phenology of a select few tree species (Table 3.1). With the exception of one study (Haugaasen & Peres 2005), which also compares *várzea* to *igapó* (black water flooded forests), there is also a distinct lack of direct comparisons between *várzea* (VZ) and *terra firme* (TF) forests.

Comparisons within phenology studies must also pay attention to which plant parts are observed and to the sampling protocols employed to measure them. For example, because of their importance for frugivorous animals, many studies focus on fruits and flowers but frequently ignore leafing phenology (but see Schöngart et al. 2002). While leaves appear less scarce than fruits and flowers, mature leaves are high in unpalatable toxins and leaf flush can represent an important resource for herbivores. As an adaptation to the flood regime, the timings of leaf fall and flush (and the degree of deciduousness) may also be critical (Parolin et al. 2004b), thereby accruing additional value to phenology studies that include both reproductive and vegetative characters. However, observations on different plant parts are frequently obtained using a variety of sampling methods without a common standardised procedure (Morellato et al. 2010), each of which with their own advantages and disadvantages.

The two most common methods in plant phenology studies are direct observation of the tree (or liana) crown and fruit/seed/litter trapping, and their relative merits have been best examined in regard to fruit productivity (Chapman et al. 1994, Zhang & Wang, 1995, Stevenson et al. 1998). A more general recent assessment, however, considered flowering as an example (Morellato et al. 2010). Direct observation, whereby the phenology of leaves, flowers and fruit can be quantified using a scoring system (Fournier 1974), is perhaps the simplest method but is more problematic in high-statured, dense forests without the construction of purpose-built canopy platforms (Zhang & Wang 1995, Parrado-Roselli et al. 2006). Fruit (or seed-rain) traps have thus been particularly useful in tropical forests to systematically quantify fruit- or seed-fall independently of potentially high levels of observer bias and variability (Chapman et al. 1992). Leaf phenology has also often been best recorded using traps (Clark et al. 2001,

Table 3.1. *Summary of* várzea *phenology studies from seasonally flooded forests across Amazonia.*

Source	Study site	Method	Species	n	Trap area (m^2)	Frequency	Duration	Dates
Ayres (1986)	Lago de Teiú, Mamirauá, nr Tefé	Canopy obs	174	996 inds.	-	Monthly	18 months	07/1983-12/1984
Ziburski (1990) [a]	Ilha de Marchantaria, nr Manaus [c]	Canopy obs	18	?	-	?	16 months	01/1988-04/1989
Worbes (1996) [a]	Ilha de Marchantaria, nr Manaus	Canopy obs	7	?	-	?	12 months	1981-1982
Parolin (1997) [a]	Costa do Catalão/Ilha de Marchantaria, nr Manaus	Canopy obs	6	5 per sp.	-	?	15 months	04/1994-06/1995
Wittmann (1997) [a]	Ilha de Marchantaria, nr Manaus	Canopy obs	6	2 per sp	-	?	4 months	06/1996-09/1996
Gribel et al. (1999) [a]	Costa do Catalão, nr Manaus	Canopy obs	1: *Ceiba pentandra*	12 inds.	-	Monthly	6 years	1992-1997
Oliveira & Piedade (2002)	Ilha de Marchantaria/Rio Solimões, nr Manaus	Canopy obs	1: *Salix martiana*	75 inds.	-	Weekly	14 months	04/1993-05/1994
Schöngart et al. (2002) [a]	Ilha de Marchantaria, nr Manaus	Canopy obs	23	66 inds.	-	Monthly	26 months	06/1998-08/2000
Armbrüster et al. (2004)	Ilha de Marchantaria, nr Manaus	Canopy obs	2: *Laetia corymbulosa, Pouteria glomerata*	1 per sp.	-	?	11 months	08/1997-06/1998
Cattanio et al. (2004)	Ilha do Combú, nr Belém [d]	Canopy obs	15	5 per sp.	-	Bi-weekly	12 months	01/1989-12/1989
Haugaasen & Peres (2005) [a]	Lower Purús, central-western Brazilian Amazonia [ce]	Canopy obs	45 genera	400 inds.	-	Monthly	35 months	08/2000-11/2003

cont.

Table 3.1. cont.

Source	Study site	Method	Species	n	Trap area (m^2)	Frequency	Duration	Dates
Addis (unpubl.) [b]	?	Traps	-	?	?	?	?	?
Nebel et al. (2001a)	Braga-Supay and Lobillo, Peruvian Amazonia [f]	Traps	-	75 traps [g]	0.25	Weekly	12 months	12/1997-11/1998
Cattanio et al. (2004)	Ilha do Combú, nr Belém [d]	Traps	-	30 traps	1	Monthly	12 months	01/1989-12/1989
Schongart et al. (2010)	Mamirauá, nr Tefé	Traps	-	20 traps [h]	1	Bi-weekly	12 months	11/2002-10/2003
Hawes & Peres (this study)	Médio Juruá, western Brazilian Amazonia [e]	Canopy obs	88 genera	500 inds.	-	Monthly	12 months	04/2009-03/2010
		Traps	-	96 traps	0.5	Bi-weekly	12 months	05/2009-04/2010
		Residual fruit-fall	-	12 km	-	Monthly	26 months	04/2008-07/2010

[a] cited by Parolin et al. (2010)

[b] cited by Worbes (1997)

[c] Study includes comparison with *igapó* (black water flooded forest)

[d] Estuarine *várzea*

[e] Study includes comparison with *terra firme* (unflooded forest)

[f] Upper Amazon *várzea*

[g] 25 traps in each of three *várzea* forest types: high restinga, low restinga, tahuampa.

[h] 10 traps in each of two *várzea* forest types: high and low *várzea.*

Schöngart et al. 2010) during the course of fine litterfall collections, which represent an important component in estimates of net primary productivity (NPP). The effectiveness of various trap designs in investigating fruit production has been well examined (Stevenson & Vargas 2008), and issues of cross-study comparability (including the definition of litterfall) has also been assessed for leaves (Clark et al. 2001). In addition, traps are potentially costly in terms of materials and effort, and may severely underestimate fruit production at least due to the omission of any fruits/seeds consumed previously in the canopy by arboreal frugivores (Terborgh 1983). This issue is compounded in a third fruit sampling method, namely ground surveys of residual fruit-fall, which may be subsequently affected by fruit/seed removal by terrestrial frugivores/granivores (Zhang & Wang 1995).

The consensus appears to be that, in addition to a large sample size, adequate spatial replication, and frequent (at least monthly) records, it is useful to use a combination of monitoring methods (Morellato et al. 2010). Few studies to date have achieved this, especially in flooded forests, although traps have been successfully employed in monodominant tidal forests of the Amazonian estuary (Cattanio et al. 2004) and in the upper Amazon, where traps were strung from branches during high water levels (Nebel et al. 2001). In the central Amazon, flood depths are far greater and have severe impacts on the practicalities of alternative phenology monitoring techniques (e.g. Haugaasen & Peres 2005). We therefore developed a novel floating trap to cope with the variable water level, and conducted residual fruit-fall surveys in addition to canopy observations, to track tree phenology and fruit productivity.

This study presents the community-wide phenology patterns, recorded using three methods (canopy observations, trap collections, and residual fruit-fall surveys), from *terra firme* and *várzea* forests of the Juruá floodplain in a remote part of western Brazilian Amazonia. Due to the immense size of the Amazon basin, the flood regime can vary substantially throughout the catchment (Kubitzki 1989). For example, the water-level near Manaus reaches its maximum in June and falls to its minimum in November (Schöngart et al. 2002), representing a lag longer than a month compared to the Juruá. To investigate the role of the flood pulse as a trigger for phenology, it seems crucial to widen the distribution of studies across the full range of flood regimes available. Moreover, of the few phenology studies available for *várzea* forests, almost all were conducted in close proximity to Manaus (Table 3.1), with the farthest removed study site located in the lower Purús of central-western Brazilian Amazonia (Haugaasen & Peres 2005).

Our study begins to redress this regional imbalance and our landscape-scale approach provides an ideal opportunity to examine differences between *terra firme* and *várzea* forests, which typically occur side-by-side, yet diverge strikingly in environmental gradients and the corresponding life-history traits of their plant communities. The dramatic flood pulse is expected to drive phenological patterns in flooded (*várzea*) forests (Parolin et al. 2010), as prolonged waterlogging and submersion are known to have severe effects of plant physiology (Parolin 2001). This is in marked contrast to unflooded (*terra firme*) forests, where cycles of precipitation and water scarcity are likely to be more relevant. In addition to the timing of fruiting, further adaptations in *várzea* forests are expected to include many other plant traits (Parolin et al. 2004b), including seed dispersal modes that take advantage of the flood pulse. We therefore tested the *a priori* hypotheses that (1) seed dispersal modes dominated by abiotic processes, such as anemochory and hydrochory, are more prevalent in *várzea* forest, compared to vertebrate gut dispersal (endozoochory) in *terra firme* forest; and (2) flood water-level is the most important proximate phenological trigger in *várzea* forests, compared to rainfall in *terra firme* forest.

3.2. Methods

3.2.1. Study area

This study was conducted in the state of Amazonas, Brazil, within two contiguous sustainable use reserves encompassing nearly 0.9 Mha, namely the Médio Juruá Extractive Reserve (*ResEx Médio Juruá*, 253,227 ha) and the Uacari Sustainable Development Reserve (*RDS Uacari*, 632,949 ha) (Figure 3.1). These two reserves border the Juruá river, a major white-water tributary of the Solimões (=Amazon) river, and contain large expanses of upland unflooded *terra firme* forest (80.6% of combined reserve area) and seasonally flooded *várzea* forest (17.9%) closer to the main river channel (Chapter 2: Hawes et al. 2012).

The Juruá region has a wet, tropical climate with a mean annual temperature of 27.1°C and annual rainfall, calculated from daily records over three consecutive years (2008-2010) at the Bauana Ecological Field Station (S 5°26’19”, W 67°17’12”), averaging

3,679 mm^{-yr}. Additional rainfall data were obtained from Eirunepé meteorological station (315 km from the study area, 2000-2010, source: INMET), and water-level data from the Rio Juruá at Porto Gavião, Carauari (90 km from the study area, 1972-1994, source: Petrobrás S.A.). The elevation range within the reserves is 65 – 170 m above sea level. *Terra firme* soils are typically heavily leached and nutrient poor in comparison to the eutrophic alluvial soils of *várzea* forests. All forest sites surveyed represent primary forest, although commercially valuable timber species along the Juruá river have experienced some selective logging from 1970-1995, especially in *várzea* forest (Scelza 2008).

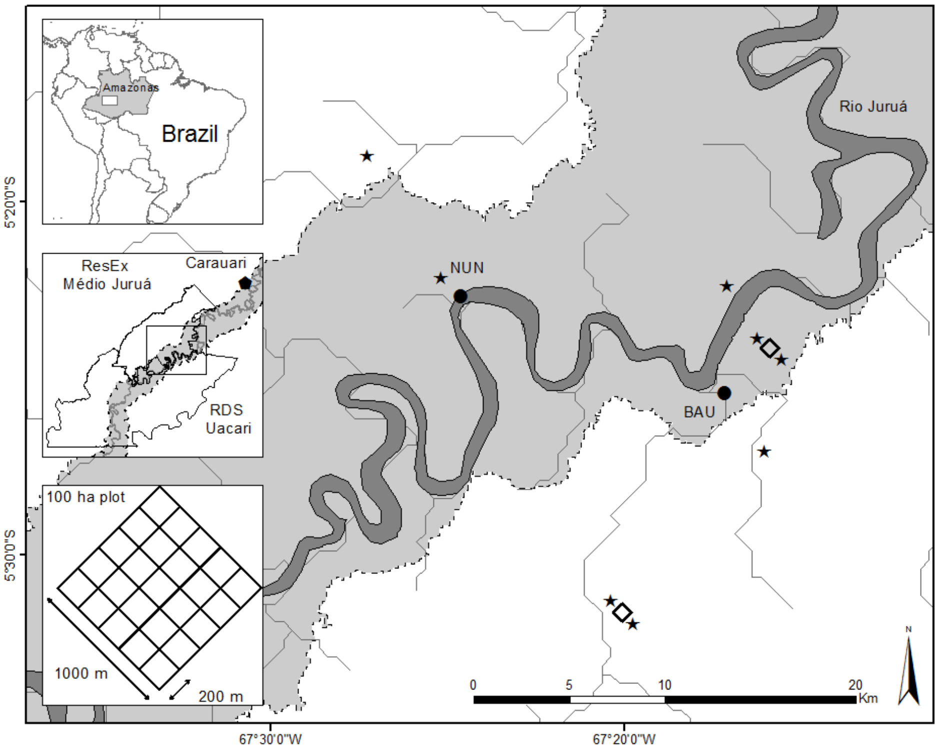


Figure 3.1. *Map of the Médio Juruá region of western Brazilian Amazonia showing locations of eight 1-km phenology transects (stars) and two 100-ha plots (squares) in* terra firme *forest (no shading) and* várzea *forest (grey shading). Black circles represent local communities (BAU=Bauana, NUN=Nova União); grey lines represent perennial streams; dashed lines represent the spatial extent of the* várzea *floodplain according to ALOS ScanSAR imagery (Hawes et al. 2012).*

3.2.2. Canopy observations

We conducted monthly crown inspections for twelve consecutive months (April 2009 – March 2010) along eight 1-km transects (April: 2 TF, 2 VZ; May-June: 3 TF, 3VZ; 4 TF, 4 VZ thereafter), divided equally across *terra firme* and *várzea* forests (Figure 3.1). All live trees (including arborescent palms) ≥30 cm in diameter at breast height (DBH), and all live woody lianas or hemi-epiphytes ≥10 cm, within 5 m either side of the transect line were measured (above buttress roots where required), aluminium tagged, and identified by a trained technician from the Botany Department of the Instituto Nacional de Pesquisas da Amazônia (INPA, Manaus), which maintains the largest herbarium of the central-western Amazonian flora. We examined a total of 1,056 live stems (TF: 556, VZ: 500) across the combined survey area of 8 ha.

The phenophase of each stem was recorded at monthly intervals using a pair of 10x40 binoculars, assigning an abundance score of 0-5 (Fournier 1974) for each plant part: leaves (new, mature, shedding), flowers, and fruit (immature, mature). Transects in *várzea* forest were surveyed using dugout canoes during the aquatic phase. Phenophase activity was estimated as the proportion of individual stems (and genera) bearing a given phenophase in each forest type. For fruit availability we calculated the Fruit Availability Index (FAI), multiplying the monthly fruit production score of each stem by its basal area (Develey & Peres 2000), which is a strong predictor of fruit crop size in trees (Chapman et al. 1992). This value was summed for all stems per transect to give FAI ha^{-1}. For lianas, canopy area is a much more reliable predictor of fruit crop size than basal area. We therefore estimated the elliptical canopy area for each tagged liana and derived tree-equivalent basal area estimates, using the nonlinear relationship between DBH and canopy area measured from 996 randomly selected trees (DBH ≥ 10cm) occurring in the same interfluvial region (Urucu forest: $R^2 = 0.53$; Appendix 3.1; Peres 1994).

3.2.3. Trap collections

We used square traps constructed of polyester mesh with PVC tubing support (Stevenson & Vargas 2008). Each trap had a collection area of $0.5m^2$ (0.71 x 0.71 m) and were supported 1 m above the ground. To cope with the seasonal fluctuation of floodwaters in *várzea* forest, we added buoyancy to this basic design using four empty, water-tight 2-litre plastic bottles at each corner of the trap, to keep the polyester mesh above water. Traps were also tied loosely with string to the upper branches of surrounding vegetation to stabilize the trap position within a vertical column, as it rose above its supports with the floodwater (Figure 3.2).

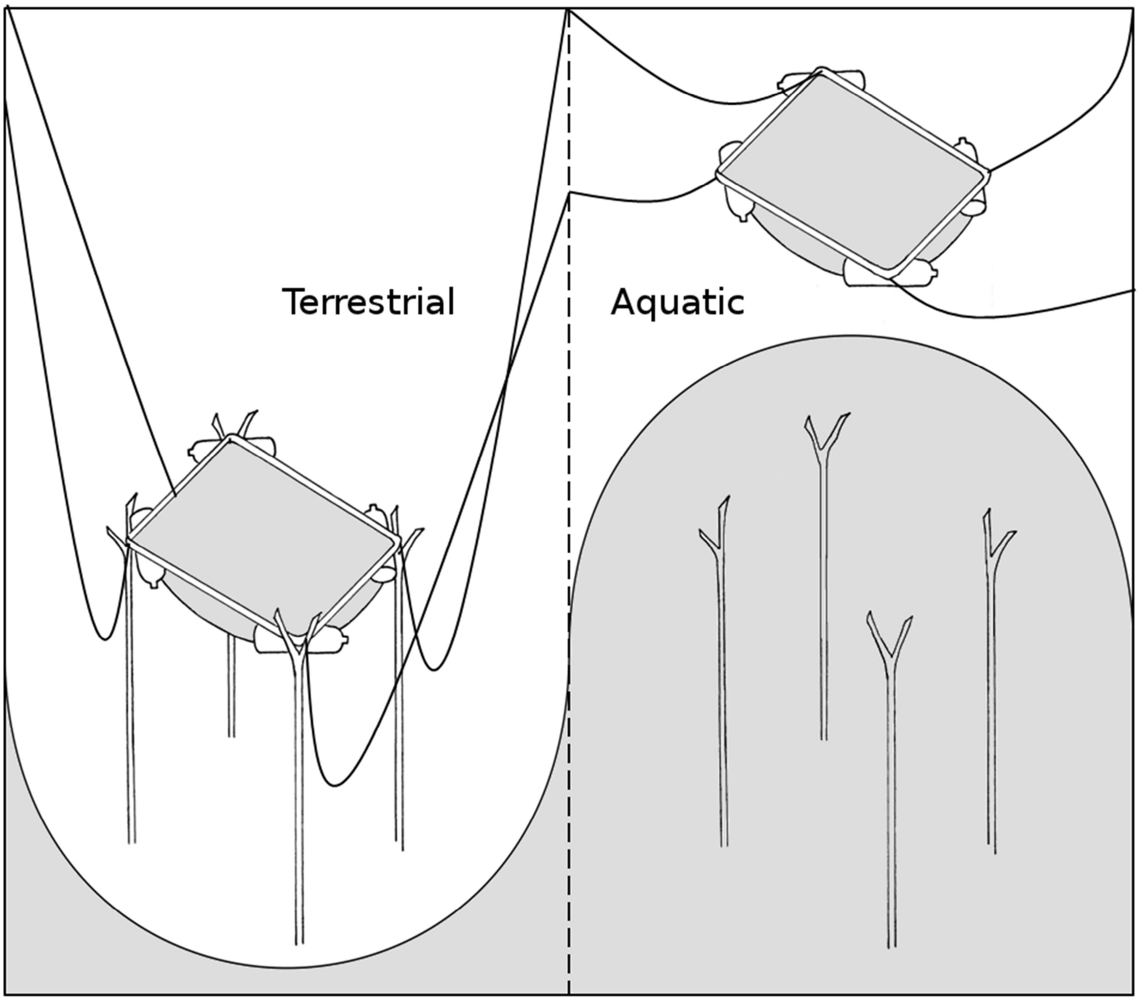


Figure 3.2. *Diagram of floating fruit/seed trap used in* várzea *forest, supported at a height of 1m during the terrestrial phase but free to float with the fluctuating floodwaters during the prolonged aquatic phase.*

Fruit traps were employed for twelve consecutive months (May 2009 – April 2010) within two 100-ha plots (1 TF, 1 VZ), each plot consisting of a grid of 1-km transects at 200-m intervals (Figure 3.1). Traps were located along all transects at 100-m intervals, resulting in a total of 96 traps in each plot (total collection area = 48 m^2). All material was collected from the traps twice a month (by canoe during the aquatic phase in *várzea*), dried to a constant weight, and separated by plant part into fruits and seeds, flowers, leaves, and twigs. Each fraction was then weighed separately (using an electronic scale with a 0.01 g resolution error) and all fruits and seeds were retained for collection and identification. Mean monthly litterfall collections were estimated as Mg ha^{-1} and trap collections were summed to provide annual estimates, standardising for any variation in number of days per collection period and the occasional omission of individual damaged traps.

3.2.4. Residual ground surveys

We conducted monthly ground surveys for residual fruit-fall in three 100-ha plots (2 TF, 1 VZ), as described above. Surveys were completed between April 2008 and July 2010 (TF: total 18 months, 15 consecutive; VZ: total 26 months, 13 consecutive). All transects were surveyed slowly over the course of four days (3 transects per day), recording the presence of all patches of fallen fruit detected along a 1-m wide strip of transect (total length of transects per plot = 12 km, total survey area per plot = 1.2 ha). For each fruit patch encountered we recorded its position along the transect, and took a specimen for our reference fruit collection. In each case we also located the source fruiting stem, and measured its DBH and perpendicular distance from the transect. During the aquatic phase in *várzea* forest, floating fruits/seeds were also recorded, but unless their source crowns could be located overhead, these were assumed to have been water-dispersed and thereby excluded from the analyses.

3.2.5. Tree and fruit identification

Number-tagged phenology trees were identified by a trained technician from the Botany Department of the Instituto Nacional de Pesquisas da Amazônia (INPA, Manaus), which maintains the largest herbarium of central-western Amazonian flora. Additional identification of trees and fruits was aided by van Roosmalen (1985), Gentry (1993), Ribeiro et al. (1999), Cornejo & Janovec (2010), and Wittmann et al. (2010a), which were also used to assign each genus recorded to the appropriate seed dispersal mode: anemochory, hydrochory, barochory/boleochory, synzoochory or endozoochory. All specimens of fruits and/or seeds were deposited at the Herbarium of the Instituto Federal de Educação, Ciência e Tecnologia do Amazonas (IFAM, Manaus).

3.2.6. Data analyses

Phenophase activity was calculated for each of the three methods employed: canopy observations were quantified as the percentage of stems or genera observed in a given phenophase (which was further partitioned by seed dispersal mode for unripe and ripe fruit), and as the FAI index of fruit production. Trap collections were used to derive the monthly mean dry weight (Mg ha^{-1}) across all traps or the overall mean per trap across all months. Finally, fruit/seed collections from ground surveys were used to estimate the basal area of fruiting stems (m^2 ha^{-1}). Seasonal variation in phenological and climatic/abiotic patterns are presented in radial form, in addition to traditional linear plots, using circular methods with the angular representation of annual cycles as 0-360° (Morellato et al. 2000). We used Spearman’s rank correlations to test the temporal correlation between plant phenology and climate and water-level, and between different estimates of fruit production and different plant parts. All analyses were conducted in R (R Development Core Team 2010).

3.3. Results

3.3.1. Climate and water-level

The Médio Juruá region experiences a marked seasonal variation in rainfall, temperature, humidity, and flood waters (Figure 3.3). Although hot and humid throughout the year, the hottest months are August-November, and humidity peaks in January-April. The precipitation pattern (rainy season: November-April, dry season: May-October) is asynchronous with the flood pulse generated by the variation in river water-level, so that the flood pulse lags approximately 6 weeks behind rainfall (aquatic phase: January-June, terrestrial phase: July-December) (Figure 3.3).

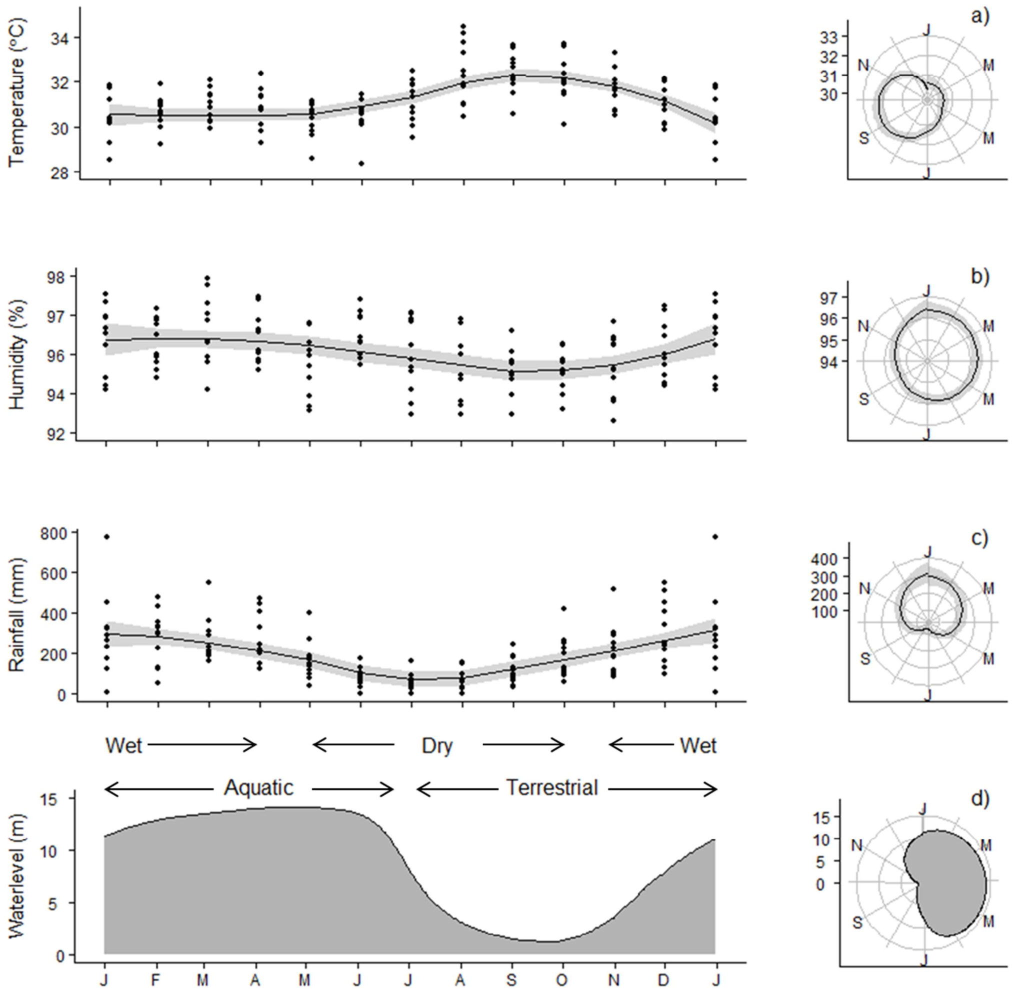


Figure 3.3. *Seasonal variation in climate and river water-level of the Médio Juruá region of western Brazilian Amazonia. Mean monthly records for (a) temperature, (b) humidity, and (c) rainfall from the Eirunepé meteorological station (2000-2010, source: INMET); mean daily records for (d) water-level of the Juruá river at Porto Gavião, Carauari (1972-1994, source: Petrobrás S.A.).*

3.3.2. Canopy observations

The 1,056 stems (874 trees, 182 lianas) monitored during canopy observations comprised 120 genera belonging to 45 families (Table 3.2). On the basis of this sample, the Fabaceae, Lecythidaceae, and Sapotaceae were the most abundant families in both *terra firme* and *várzea*. The Chrysobalanaceae and Moraceae were particularly abundant in *terra firme* relative to *várzea*, whereas the Annonaceae and Malvaceae had comparatively higher abundance in *várzea*.

Table 3.2. *Taxonomic composition of woody stems (trees and lianas) included in the phenological monitoring using canopy observations in* terra firme *and* várzea *forest.*

	Terra firme		*Várzea*		Total	
Family	No. genera	No. stems	No. genera	No. stems	No. genera	No. stems
Anacardiaceae	2	3			2	3
Annonaceae	4	6	4	23	5	29
Apocynaceae	5	11	2	9	6	20
Bignoniaceae	1	2	1	1	2	3
Boraginaceae			1	2	1	2
Burseraceae	1	13			1	13
Capparaceae			1	1	1	1
Caryocaraceae	1	4	1	1	1	5
Celastraceae	1	7	1	2	1	9
Chrysobalanaceae	3	61[a]	1	10[a]	3	71
Clusiaceae	5	31	3	22	7	53
Combretaceae	1	7	1	5[a]	1	12
Convolvulaceae			1	5	1	5
Dichapetalaceae	1	1			1	1
Dilleniaceae	2	4			2	4
Ebenaceae	1	1			1	1
Elaeocarpaceae	1	8	1	4	1	12
Euphorbiaceae	5	12	4	14[a]	7	26
Fabaceae	20	72[a]	16	114[a]	25	186
Goupiaceae	1	7			1	7
Humiriaceae	2	6			2	6
Icacinaceae	1	2[a]			1	2
Lauraceae	5	17	2	12	5	29
Lecythidaceae	4	60	4	48	6	108
Malpighiaceae	1	2[a]	2	6[a]	2	8
Malvaceae	5	11	7	28	9	39
Marcgraviaceae	1	1			1	1
Melastomataceae	1	1			1	1
Meliaceae	3	10			3	10
Menispermaceae	1	5	1	1	1	6
Moraceae	6	50	4	27	6	77
Myristicaceae	2	35	2	30	2	65
Myrtaceae	1	2	2	8[a]	2	10
Nyctaginaceae	1	1			1	1
Olacaceae	1	1			1	1
Piperaceae	1	1			1	1
Polygalaceae		1[a]				1
Rubiaceae	1	1	1	1	2	2
Salicaceae			1	3[a]	1	3
Sapotaceae	5	55[a]	4	59[a]	5	114
Simaroubaceae			1	1	1	1
Urticaceae	2	26	2	38	2	64
Verbenaceae			1	1	1	1
Violaceae		1[a]	2	7[a]	2	8
Vochysiaceae	3	5			3	5
Unidentified		12		17		29
Total	102	556	74	500	120	1056

[a] Includes one or more individuals not identified to the level of genus.

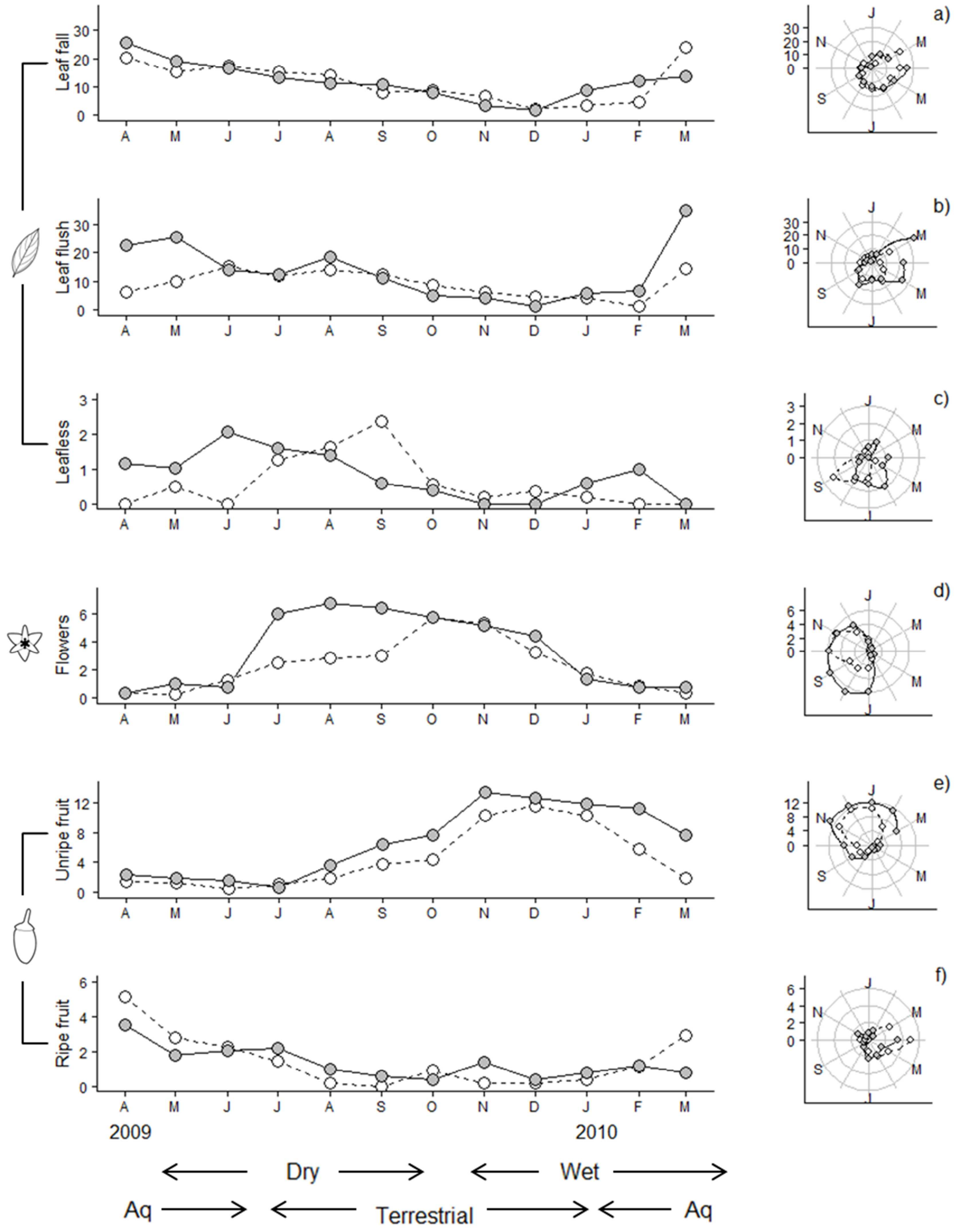


Figure 3.4. *Percentage of stems for each phenophase recorded during monthly canopy observations in* terra firme *(open circles, dashed line) and* várzea *forest (solid circles, solid line).*

Both *terra firme* and *várzea* forests were typically evergreen, with leaf fall and leaf flush recorded at low levels continuously throughout the year but with peaks in March-April. Deciduous species occurred in both forest types, although peaks in leaflessness occurred towards the end of the aquatic phase (June) in *várzea* forest, and at the end of the dry season (September) in *terra firme* (Figure 3.4). Flowering reached maximum levels shortly after peaks in leaflessness and leaf flush in both forest types, with a *várzea* peak in July-September and a *terra firme* peak in October-November. Flowering in *várzea*, however, was prolonged until December, with subsequent fruit production and maturation appearing much more synchronous between the two forest types than for other phenophases (Figure 3.4). Production of immature fruits peaked in November-January, whereas that of mature fruits peaked in March-April.

3.3.3. Trap collections

Mean total fine litterfall in *várzea* forest was not significantly different from that in *terra firme* (Table 3.3). Although leaf fall was significantly lower, the amount of small branches, bark and trash was higher. The proportion of total fine litterfall comprising leaves was 80.4% and 74.7% in *terra firme* and *várzea* forest, respectively, with litterfall fractions consisting of fertile material making the smallest contributions (Table 3.3, Appendix 3.2).

Leaf fall collections appeared to peak during the middle of the aquatic phase (March-May) in *várzea* forest, compared to a major peak during the dry season (August) in *terra firme*. Peak flower fall in *várzea* forest was recorded in June with peak for *terra firme* forest in September-November. Peak fruit fall was recorded in January for both *várzea* and *terra firme* forest (Figure 3.5).

Table 3.3. *Annual fine litterfall fractions (Mean ± SD, Mg ha^{-1} yr^{-1}) sampled by 96 traps in each forest type from April 2009 to March 2010. P-values are represented by * $P < 0.05$, ** $P < 0.005$, *** $P < 0.001$.*

	Terra firme	*Várzea*	*t*	*P*
Leaves	8.27 ± 0.96	7.43 ± 1.04	-5.76	<0.001 ***
Small branches, bark and trash	1.69 ± 0.39	2.36 ± 0.51	10.16	<0.001 ***
Flowers	0.15 ± 0.24	0.05 ± 0.07	-4.09	<0.001 ***
Fruits	0.18 ± 0.20	0.12 ± 0.24	-1.94	0.054
Total	10.29 ± 1.18	9.95 ± 1.33	-1.84	0.068

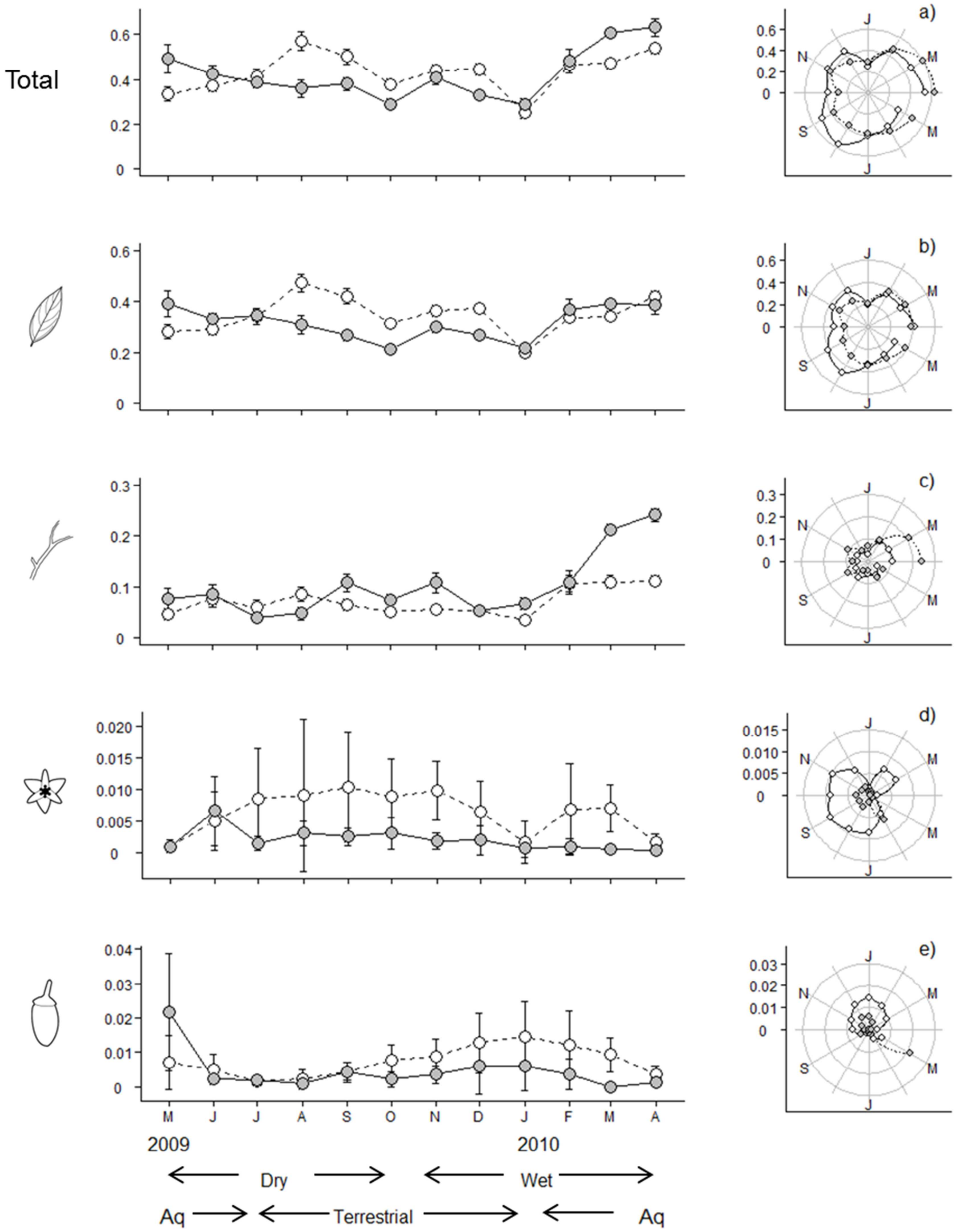


Figure 3.5. *Mean monthly values for (a) total fine litterfall (Mg ha*$^{-1}$*), recorded from bi-monthly collections of 96 traps in both* terra firme *(open circles, dashed line) and* várzea *forest (solid circles, solid line), and for individual vegetative and reproductive fractions: (b) leaves, (c) fine woody litter (small branches, bark, trash) , (d) flowers, and (e) fruits.*

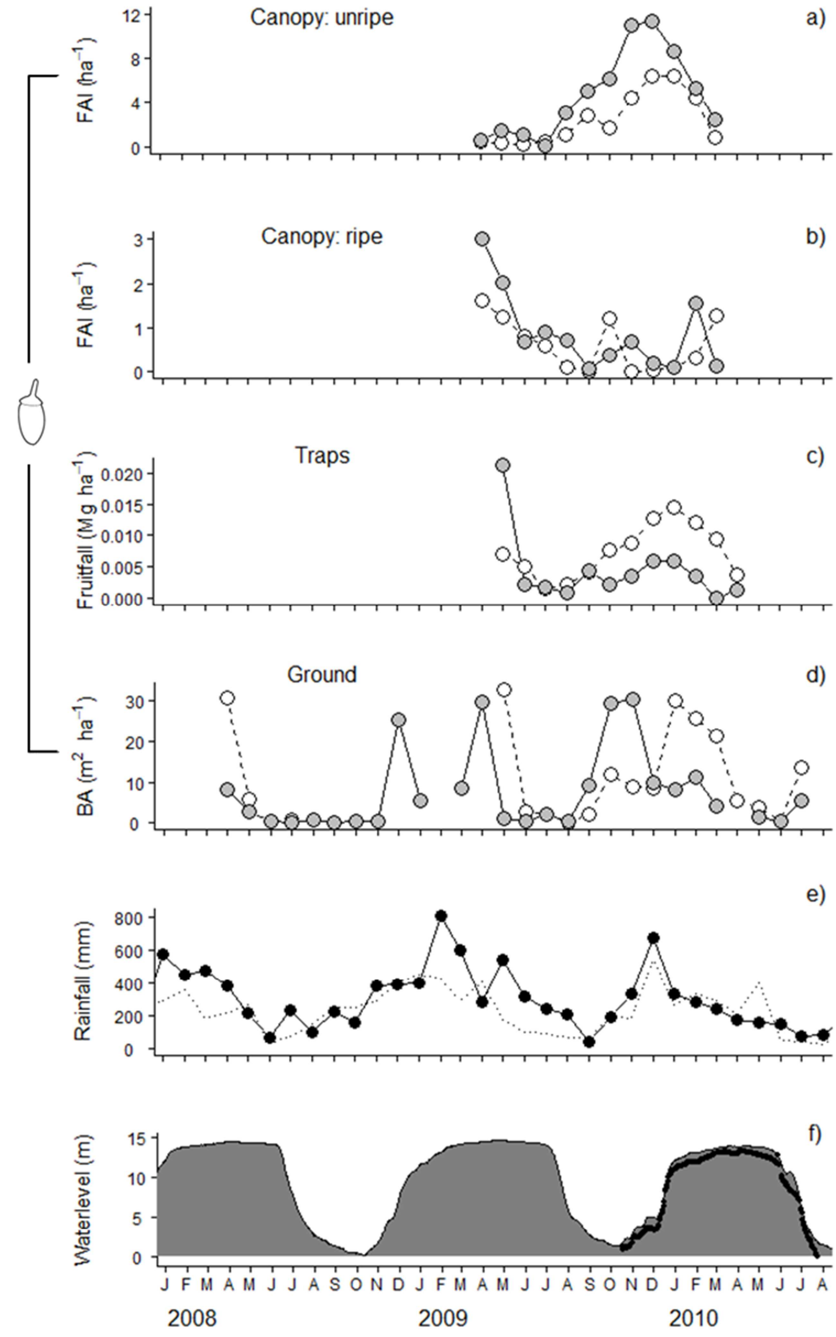


Figure 3.6. *Fruit production estimates in* terra firme *(open circles, dashed line) and* várzea *forest (solid circles, solid line) using three complementary sampling methods: canopy observations of (a) unripe and (b) ripe fruit, (c) trap collections of the fruit fraction in litterfall, and (d) ground surveys of residual fruit patches (stem basal area: m^2 ha^{-1}). Seasonal variation in (e) rainfall: black points represent total monthly values from daily records at the Bauana field station; dotted line represents records from the Eirunepé meteorological station (source: INMET), and (f) water-level: black points represent daily measurements at the Bauana field station; grey fill represents records obtained at Porto Gavião, Carauari (source: Petrobrás, S.A.).*

3.3.4. Ground surveys

Surveys for residual fruit-fall showed the considerable inter-annual variation but do suggest a unimodal pattern in *terra firme* forest and a peak associated with maximum rainfall. Temporal fruit availability in *várzea*, in contrast, appear to be more complex with the largest peaks during the aquatic phase, but smaller secondary peaks during the terrestrial phase (Figure 3.6).

3.3.5. Seasonality of seed dispersal modes

While the overall pattern in fruit production appeared similar in both *terra firme* and *várzea* forest, there were noticeable differences when considering different seed dispersal modes (Figure 3.7). There was a larger number of plant genera exhibiting abiotic dispersal modes (wind, water and ballistic) in *várzea* forest than in *terra firme*, which was dominated by animal-dispersed plants. The fruiting peak in *terra firme* forest was initiated during the mid-rainy season exclusively by animal-dispersed plants, with wind-dispersed and ballistic genera bearing fruit from the onset of the dry season. In *várzea* forest, wind-dispersed genera bore fruits most frequently during the terrestrial phase between May and September, whereas water-dispersed genera were restricted to the aquatic phase. Finally, a secondary fruiting peak during the terrestrial phase in *várzea* was dominated by endozoochorous plants (Figure 3.7).

3.3.6. Phenological and environmental correlates

Correlations were detected between different plant phenophases and between different phenology monitoring methods. Temporal correlations were also present between plant phenology and climate variables, as well as water-level. Correlations with rainfall and flood water-level are shown in full across lag periods of up to 12 months (Appendix 3.3). A summary of peak correlations demonstrates the likely role of water-level as a trigger in *várzea* forest, as opposed to rainfall in *terra firme* (Table 3.4).

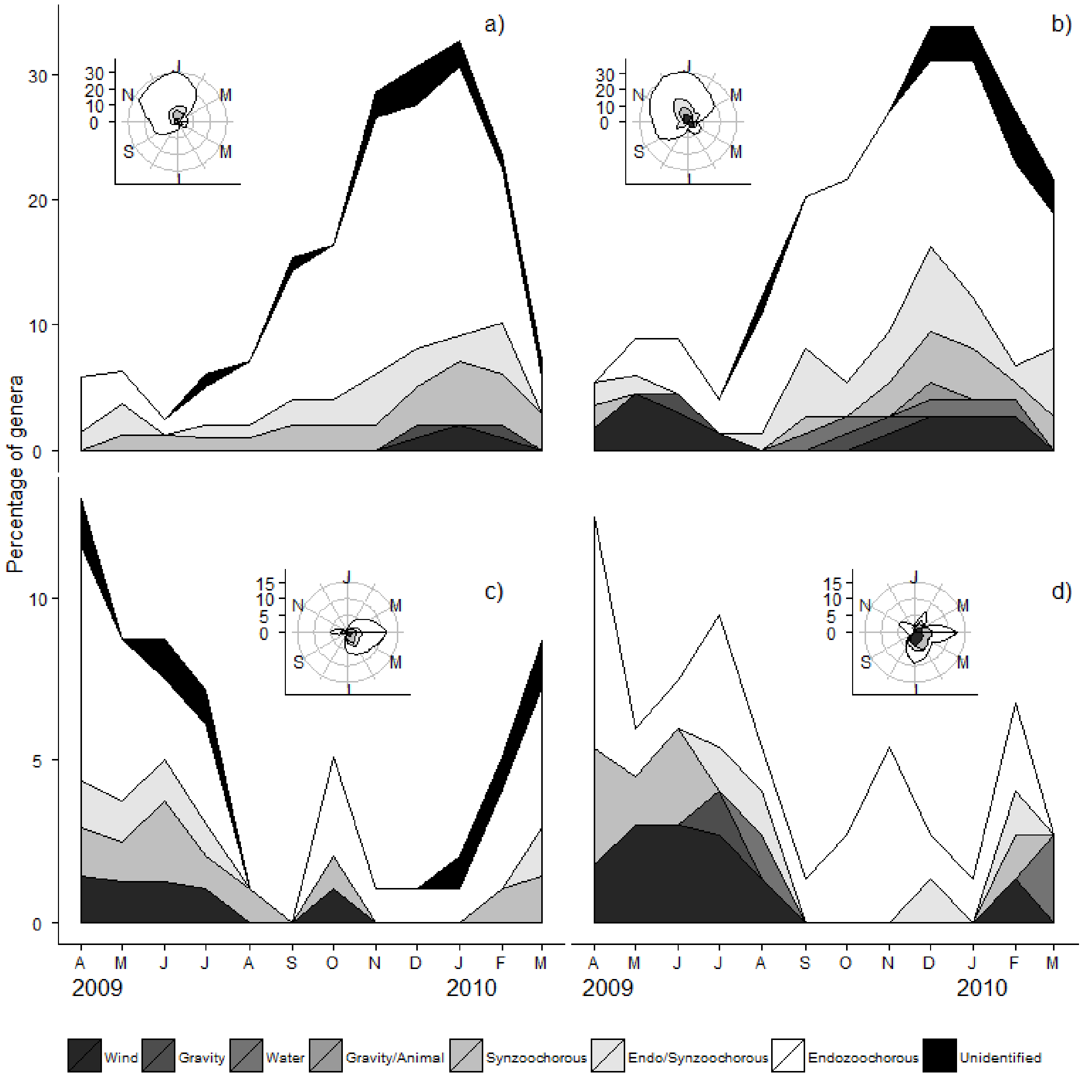


Figure 3.7. *Percentage of genera with (a-b) unripe or (c-d) ripe fruit, recorded during canopy observations in* terra firme *(a,c) and* várzea *forest (b,d) and partitioned by seed dispersal modes. Circular plots do not show unidentified stems.*

Table 3.4. *Summary of peak correlation coefficients (r) within a lag of four months between sequential plant phenophases (listed in chronological order) recorded from canopy observations in* terra firme *and* várzea *forests, and rainfall and water-level. P-values are represented by * P < 0.05, ** P < 0.005, *** P < 0.001, followed by the respective lag period in months.*

	Terra firme						*Várzea*					
Phenophase	Rainfall			Waterlevel			Rainfall			Waterlevel		
Leaf fall	-0.608	*	0	0.741	**	3	0.902	***	4	0.916	***	2
Leaf flush	-0.657	*	1	0.643	*	3	0.874	***	4	0.783	**	3
Leafless	-0.692	*	3	-0.756	**	0	-0.783	**	0	0.861	***	3
Flowers	-0.886	***	4	-0.907	***	1	-0.804	**	3	-0.895	***	0
Unripe fruit	-0.683	*	4	-0.967	***	3	0.888	***	0	-0.951	***	3
Ripe fruit	0.873	***	4	0.838	**	1	0.581	*	1	0.687	*	2

3.4. Discussion

This study provides a multi-faceted examination of the differences in plant phenology patterns between seasonally flooded and unflooded forest along the Rio Juruá, a major, yet poorly known, white-water tributary of the Amazon. Our use of three complementary methods, including a novel floating trap designed to cope with the fluctuating flood levels in *várzea* forest, enabled us to quantify litterfall and fruit production throughout the year. This year-round community-wide assessment represents one of the most extensive efforts conducted in *várzea* forest, making a substantial contribution to understanding phenological patterns and processes within this forest type. Our study reports several important observations: (1) in *várzea* forests, abiotic seed dispersal modes are more prevalent than in *terra firme* forest, where trees and lianas are primarily dispersed by animal seed-dispersal vectors; (2) both vegetative and reproductive phenological cycles show strong seasonality in both forest types, and these appear to be primarily triggered by flood waters in *várzea* and rainfall in *terra firme*; and (3) different sampling techniques, including floating litter traps in várzea as successfully used in this study, provide complementary information on plant phenology to account for systematic biases of each technique in isolation.

3.4.1. Vegetative phenology

Phenological studies often focus on flowers and fruits although leaf production and abscission, which affects the overall photosynthetic machinery, is potentially a key stage in the timing of other phenophases. Fine litterfall is strongly seasonal in Amazonian floodplains (Chave et al. 2009) but the proportions of individual fractions are not always reported, since this is typically studied as a measure of primary productivity. In the *várzea* forests of the Médio Juruá, leaves comprised 74.5% of total fine litterfall, in close agreement with records for central Amazonia (Schöngart et al. 2010) but higher than in Peruvian *várzea* forests (Nebel et al. 2001a). Absolute values for total fine litterfall in our study were slightly higher than the regional average and, in contrast to regional analyses (Chave et al. 2009), we found no evidence for significant differences in total fine litterfall between flooded and unflooded forests.

Leaf fall, recorded as a fraction of fine litterfall in traps, showed a peak during the aquatic phase in *várzea* (February-May), but during the dry season (August) in *terra firme*. Canopy observations failed to clearly detect this pattern but captured corresponding patterns in leaf flush and leaflessness. Both methods support evidence from previous studies (Ayres 1986, Worbes 1997, Schöngart et al. 2002, Haugaasen & Peres 2005, Schöngart et al. 2010) that leaf fall in *várzea* is related to cambial dormancy induced by the onset of the aquatic phase, with leaflessness peaking around the maximum flood pulse. In contrast, leaflessness in *terra firme* peaks during the height of the dry season and is inversely correlated with rainfall, although we failed to find evidence for differing degrees of deciduousness between forest types (but see Parolin 2001, Haugaasen & Peres 2005).

3.4.2. Reproductive phenology

The timing of flowering in the Juruá, using records from both canopy observations and litter-traps, again concurs with previous findings that peak levels in *várzea* forest occurs towards the end of the aquatic phase, but can extend into the terrestrial phase once floodwaters recede (Ayres 1986, Schöngart et al. 2002, Haugaasen & Peres 2005). However, while Haugaasen & Peres (2005) report no difference between peak flowering in *terra firme* and *várzea*, we find flowering in *terra firme* to peak later than in *várzea*, and going beyond the dry season into the onset of the rainy season. These patterns are clearer for canopy observations than for trap collections, where records of flowering events for *várzea* were notably sparser than those for *terra firme*. From canopy observations it is also noteworthy that community-wide flowering extends for a period of almost six months, indicating a wide range of strategies for individual species.

Fruiting in humid tropical forests typically occurs during the early to mid rainy season (Zhang &Wang 1995, van Schaik et al. 1993). Our data from *terra firme* forest were consistent with this pattern, especially considering trap collections which showed a January peak in fruit-fall (mid-rainy season). Canopy observations showed a peak in immature fruits in the preceding month, as would be expected, but the apparent peak for mature fruit was as late as April. However, observations of ripe fruit may be less accurate since they become effectively detectable for a much shorter period of time than unripe fruit (Ayres 1986). In practice, ripe fruiting events are so ephemeral that they can be more easily missed by monthly surveys; immature fruits often succumb to the reverse bias whereby individual fruits may be repeatedly scored within the same plant in consecutive months. Traps, by providing a continuous record of fruit-fall between canopy observations, may therefore be considered more reliable in this sense, despite other drawbacks of this method including a bias against rare plant species or plants producing few large fruits or seeds (Milton et al. 2005).

At first glance, patterns in fruit availability were apparently similar in *várzea* and *terra firme*, despite preceding differences in the phenology of leaves and flowers. Likewise, fruiting peaks at Lago Uauaçú were observed in December-March (early-mid rainy season) and January (start of the aquatic phase) in *terra firme* and *várzea* forest, respectively (Haugaasen & Peres 2005). However, on closer inspection, this pattern seems more complex in *várzea* forest than merely a lag behind *terra firme*. While our trap collections indicate a peak in December-January (early-rainy season) as in *terra firme*, the amplitude is much lower and a much more pronounced peak occurs during maximum flood levels in April-May. This is supported by ground surveys for residual fruit fall, which suggest a bimodal distribution in fruit production in *várzea* forest in contrast to a unimodal pattern in *terra firme*. This is similar to the *várzea* forest at Lago Teiú, Mamirauá (Ayres 1986), where a first fruit peak follows the peak rainfall but precedes peak water levels, and a secondary peak precedes the start of the rainy season, coinciding with the submergence of low-lying *várzea* (*chavascal*). In this study the secondary peak occurred during the terrestrial phase (onset of the rainy season), and was notably comprised of fleshy fruits such as *Byrsonima* spp. and *Manilkara* spp.

3.4.3. Fruiting seasonality and seed dispersal modes

Animal-dispersed plants bearing fleshy fruits are well represented in Amazonian forests, and tropical humid forests in general (Fleming & Kress 2011). Abiotically dispersed plants, including wind (anemochory) and gravity (boleochory) dispersal, are more common in dry forests (Griz & Machado 2001), and are expected to fruit during the driest and windiest period of the year within humid forests (van Schaik et al. 1993). Desiccation is also an essential requirement for fruit maturation in many plants exhibiting explosive seed-dispersal strategies, such as rubber trees (*Hevea* spp.), in contrast with the humid conditions that may be required for the maturation of fleshy fruits (Lieberman 1982). Our results from *terra firme* are consistent with these expectations, in terms of the high proportion of plant taxa during the early wet season bearing fleshy fruits consumed by vertebrate frugivores and, conversely, the dry-season maturation of fruits and seeds dispersed by abiotic agents.

In seasonally-inundated forests such as *várzea*, which are intensively regulated by the abiotic influence of the flood pulse, a higher proportion of plants bearing seeds dispersed by abiotic agents are expected and water, in particular, is expected to be the principal dispersal vector (Kubitzki & Ziburski 1994). Bouyancy, however, represents just one of a range of strategies employed by plants with fruits or seeds falling during flood conditions (Ferreira et al. 2010). Others alternatively sink, remaining dormant on the forest floor until the water-levels recede (Kubitzki & Ziburski 1994) where they provide a resource for returning terrestrial frugivores. During the aquatic phase moreover, many zoochorous fruits are consumed and potentially dispersed by fish, rather than mammals or birds (Goulding 1980, Kubitzki & Ziburski 1994, Correa et al. 2007, Horn et al. 2011). Thus, while we documented a surprisingly low proportion of hydrochorous plant genera, seed dispersal in several plants classified as anemochorous or zoochorous may in fact be additionally assisted by the floodwaters.

The greater prevalence of anemochorous trees and lianas within *várzea* forest is also likely related to the lower stature and less continuous nature of the canopy, as well as the history of plant colonisation of the floodplains from adjacent *terra firme* forest communities (Wittmann et al. 2010b). While it is unsurprising not to find any hydrochorous plants bearing mature fruits during the terrestrial phase, it is interesting to note that fruiting in anemochorous *várzea* forest plants appears more tightly aligned to the dry season *per se* than to the terrestrial phase.

3.4.4. Phenological triggers

Phenological triggers are best determined from the examination of long-term datasets, which allow the identification of patterns in relation to anomalies in climatic variables or other environmental gradients. The importance of multi-year studies is highlighted by the supra-annual reproductive cycles in many species (Newstrom et al. 1994, Haugaasen & Peres 2005) and the wide inter-annual variation in climatic conditions resulting in substantial oscillations in flood pulses. In the absence of multi-year data from all our datasets, other than residual fruit-fall, we are unable to examine the occurrence of supra-annual patterns. Further caution in defining the environmental triggers of plant phenology is necessary due to the difference between proximate triggers (environmental events correlated with phenology) and the ultimate factors actually driving evolutionary scale selection pressures (Hamann 2004).

Although seasonality in wind velocity has been recognised as an important factor in South-East Asian forests frequented by typhoons (Hamann 2004), varying levels of precipitation have more often been considered the most significant environmental trigger for plant phenology in the tropics (van Schaik et al. 1993). The key proximate cue is usually assumed to be the period of water stress, although evidence has not always supported this hypothesis (Wright & Cornejo 1990). Dry conditions were found to be important in East African riverine forests (Kinnaird 1992), but in relation to river level as opposed to rainfall. The role of water-level has also received attention within Amazonian flooded forests where, paradoxically, the greatest degree of water stress is a result of anoxia from the extended period of water-logging and deep submersion (Parolin 2009).

The significant correlations of plant phenophases with rainfall and flood water-level in both forest types in our study show the high degree of seasonality and the auto-correlation between environmental variables. By examining the lag between phenophases and their environmental correlates, it is possible to determine the relevance of these correlations. In *terra firme* forest, the chronological sequence of phenophases is consistent only for correlations with rainfall (Table 4) and any correlations with floodwaters in adjacent *várzea* forests should be considered coincidental, as would be expected. In contrast the most significant temporal correlations with rainfall in *várzea* forest bear little relation to the chronological sequence of plant phenophases, in contrast to those for water-level.

3.5. Conclusions

Both seasonally-flooded and unflooded forests of the Médio Juruá region of western Brazilian Amazonia exhibit strong seasonal patterns in plant phenology that can be clearly linked to climatic variables. In *várzea* forest, the extreme annual flood cycle, with waterlogging and submersion in a water column of up to 10-15 m for as long as half of the year, results in perhaps the most seasonal low-latitude environments anywhere. Our study provides a useful comparison between adjacent flooded and unflooded forests, and tentatively supports the hypothesis for the primary role of the flood pulse as a primary trigger for plant phenology in *várzea* forests. Other environmental variables, however, may potentially contribute as proximate triggers (Parolin et al. 2010) and, given the wide variety of plant strategies, different triggers may be relevant for different species in both *terra firme* and *várzea* forests (Wright & Cornejo 1990, Parolin et al. 2010). This is shown by the variation in phenological schedules between plants with different seed dispersal syndromes, where fruiting events in wind-dispersed species in *várzea* forest appears more closely related to the dry season than to the flood pulse.

Within any single study, however, it is likely to remain difficult to disentangle the relationship between phenology and various environmental variables. Clarification of the relative roles of environmental triggers in the phenology of flooded forests would be aided, not just by a multi-year studies, but by a systematic effort to increase the spatial distribution of phenology studies. Rainfall patterns vary greatly across the Amazon basin and to a large degree this is independent of the flood regime. By monitoring plant phenology in flooded forests with contrasting lag periods between peaks in rainfall and flood pulses, a more robust assessment of their relative roles may be possible. *Várzea* forests remain vastly understudied, in terms of both sampling effort and the distribution of study sites across Amazonia, partly as a result of the practical difficulties associated with fieldwork in such a dramatically unstable habitat. While recent advances have been made in digital and remote phenology monitoring (Pennec et al. 2011, Zhao et al. 2012), there remains no replacement for field surveys. Our successful use of three complementary field methods to monitor plant phenology illustrates the possibilities for long-term studies in *várzea* and other flooded forests.

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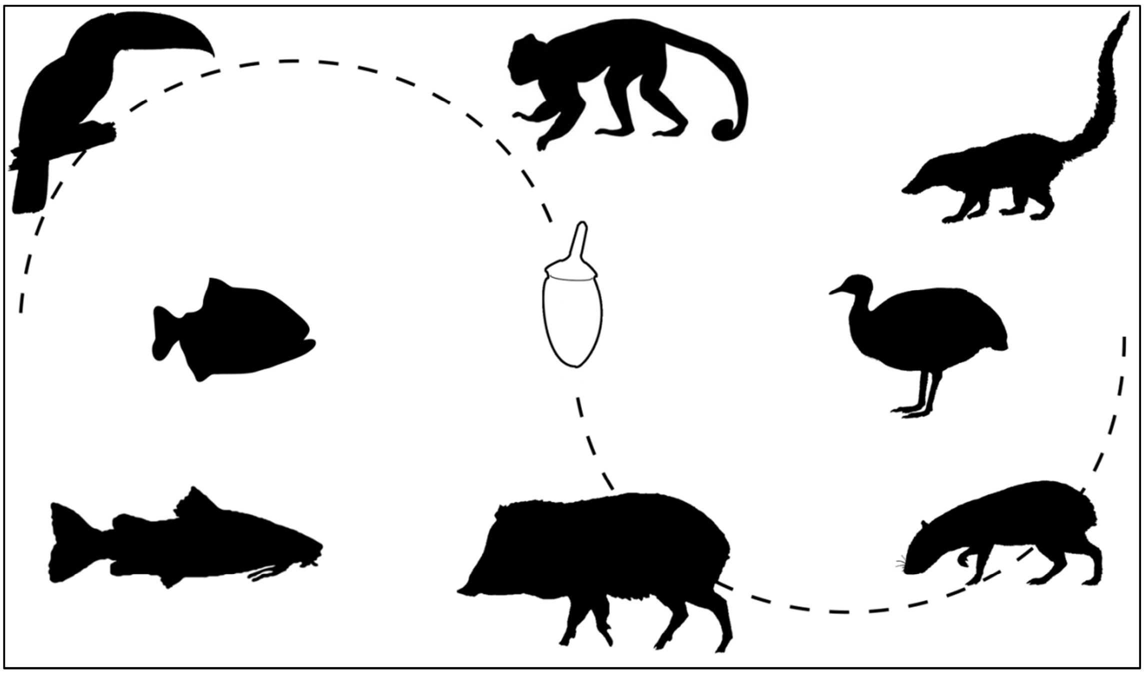
Chapter 4

Fruit-frugivore interactions in Amazonian seasonally flooded and unflooded forests



To be submitted to *Oecologia* as:

Hawes, J.E., & Peres, C.A. Fruit-frugivore interactions in Amazonian seasonally flooded and unflooded forests.

Abstract

Construction of empirical fruit-frugivore networks for an entire frugivore assemblage at a tropical forest site has proved challenging to date. Of the few ecological studies that have successfully examined a broad coterie of co-existing frugivores, there is a conspicuous absence of research in lowland Amazonia, the tropical region hosting the highest diversity of frugivorous vertebrates and the widest spectrum of morphological fruit types worldwide. We assessed the fruit resources, the frugivore assemblages, and corresponding fruit-frugivore networks of two contrasting forest types along the Rio Juruá region of western Brazilian Amazonia: seasonally-flooded *várzea* (VZ) and the adjacent unflooded *terra firme* forest (TF). Monthly surveys of fruit patches and medium- to large-bodied vertebrate frugivores were conducted within three 100-ha plots (two in TF and one in VZ), supplemented by fruit surveys conducted along 67 transects of 5 km in length distributed across two contiguous forest reserves (41 in TF; 26 in VZ). Observations of feeding interactions from these surveys were further supplemented by semi-structured interviews with experienced long-term local residents, including hunters and fishermen, from 16 local communities in the two reserves. Interviews incorporated local knowledge of fish frugivory, and expanded our frugivore assemblages to include primates, ungulates, rodents, terrestrial and canopy birds, bony and cartilaginous fish, and freshwater turtles. We constructed binary matrices of trophic interactions for each forest type independently, which contained low proportions of all potential interactions (TF: 25.7%; VZ: 19.4%). NMDS and ANOSIM analysis showed significant partitioning of fruit resources among broad frugivore guilds in both forest types but recursive partitioning analysis failed to clearly match differences in fruit selection to fruit traits. The dramatic annual flood pulse in *várzea* forests had an overriding influence on the species turnover of fruit resources and frugivores between the two forest types, with higher-order effects on network structure.

4.1. Introduction

The mutualistic interactions between frugivorous vertebrates and the fleshy-fruited angiosperms, which have undergone a co-evolutionary process over 90 Ma (Fleming & Kress 2011), have received an ever-increasing amount of research attention due to the importance of seed dispersal (Howe & Smallwood 1982) and the maintenance of functional integrity in degraded ecosystems (Cordeiro & Howe 2003). Recent focus is now moving from an organism-based approach (typically focused on either consumer or resource species) to a more complete understanding of community networks and the mechanistic processes driving the fabric of interactions (Carlo & Yang 2011, Jordano et al. 2011), as more frequently achieved for pollination networks (Olesen et al. 2007).

The most comprehensive assessments of fruit-frugivore networks to date have often been conducted in temperate environments (e.g. Herrera 1998), or focused on birds and bird-dispersed plants (e.g. Snow 1981). However, frugivores are particularly ubiquitous in tropical forests, where both unripe and ripe fruit represent a key resource for a wide range of vertebrate taxa (Fleming & Kress 2011). In addition to birds (Kissling et al. 2009), frugivory has evolved independently within bats (Muscarella & Fleming 2007), carnivores (Ray & Sunquist 2001), fish (Goulding 1980, Correa et al. 2007, Horn et al. 2011), primates (Chapter 6), reptiles (Valido & Oleson 2007), and ungulates (Bodmer 1990). Attempts to produce regional scale compilations of observed trophic interactions from fruit-frugivore studies to date have been largely restricted to a single taxon (e.g. figs: Shanahan et al. 2001; hornbills: Kitamura 2011; spider monkeys: González-Zamora et al. 2009; tapirs: Hibert et al. 2011), with few networks assembled across multiple frugivore taxa (e.g. bats and birds: Mello et al. 2011).

Efforts to construct networks across an entire frugivore assemblage at single tropical forest sites have also proved difficult, perhaps partly due to their high diversity of both fruiting plants and fruit consumers. Some studies have compared the diets of a select set of coexisting frugivores within a community (e.g. Poulsen et al. 2002), but few studies have examined the degree of dietary overlap or partitioning of available fruit resources among all members of a large coterie of phylogenetically independent co-occurring frugivores (e.g. Kitamura et al. 2002, Donatti et al. 2011, Schleuning et al. 2011). Indeed, Gautier-Hion et al.’s (1985) study in Makokou, Gabon — which identified distinct fruit morphology partitioning amongst frugivores — remains one of the most comprehensive assessments of the trophic interactions within a broad guild of tropical forest frugivores.

Fruit morphology is frequently proposed as one of the trait complexes that determines the consumers and potential seed-dispersal agents of particular plants. A suite of plant traits, including fruit size, mode of presentation, colour and nutritional content, are suggested to collectively create a ‘dispersal syndrome’ that matches a functional group of fruit consumers (Janson 1983, Jordano 1995, van der Pijl 1969). However, whether or not dispersal syndromes actually operate in the real-world remains a contentious hypothesis (Fischer & Chapman 1993, Lomáscolo & Schaefer 2010) and the role of frugivores in the evolution of fruit traits thus remains obscure. In contrast to plant-animal pollination networks, fruit-frugivore interactions tend to be diffuse and characterised by a low degree of specialisation, whereby individual fruiting species may be attended by a large number of generalist frugivores (Bascompte & Jordano 2007).

Elucidating the variation in fruit trait selection and degree of dietary overlap in co-existing consumers is critical to understand frugivore resilience to disturbance. For example, large frugivores are more at risk from selective hunting, which could threaten the status of large-fruited or large-seeded plants (Wheelwright 1985, Peres & van Roosmalen 2002) unless alternative frugivores can effectively provide substitutional roles as dispersal agents. Several tropical forest studies have examined differences in the selection of fruit traits within a single frugivore assemblage (Kitamura et al. 2002, Bollen et al. 2004, Voigt et al. 2004, Flörchinger et al. 2010). Surprisingly, however, few studies have been attempted in lowland Amazonia (Link & Stevenson 2004), even though this region holds both the highest diversity of terrestrial and aquatic frugivorous vertebrates (Fleming et al. 1987) and the widest spectrum of morphological fruit types (van Roosmalen 1985, Gentry 1996) anywhere in the world.

The dearth of community-wide Amazonian fruit-frugivore studies is compounded by the marked differences between Amazonian forest types sharing the same regional scale biota. One of the clearest such cases is the distinction between unflooded (*terra firme*) and seasonally-flooded (*várzea*) forests. *Várzea* forests, occupying the white-water floodplains of the Amazon (=Solimões) river and its tributaries (Prance 1979), account for >200,000 km^2 of Brazilian Amazonia alone (Junk 1997) and can be inundated for up to 210 days per year, rising to a depth of 10-15m (Parolin et al. 2004). Such extreme environmental conditions results in substantial differences between *terra firme* and *várzea* forests in terms of plant composition, forest structure (Chapter 2: Hawes et al. 2012), plant phenology and fruit production (Chapter 3). The resident frugivore assemblage in *várzea* forests is also strongly affected by the seasonal flood pulse (Haugaasen & Peres 2005, 2008), which physically excludes terrestrial vertebrates during the aquatic phase, but remains accessible to arboreal and scansorial mammals and canopy birds and bats. This frugivore assemblage, however, is further boosted by the highly predictable seasonal incursion of frugivorous fish, including characids and catfish, which abandon the river channel and oxbow lakes with the rising flood waters to take advantage of canopy resources, including seeds, fruit pulp and arthropods (Goulding 1980).

Our study landscape, in the Rio Juruá region of western Brazilian Amazonia, provides the ideal opportunity to examine differences between *terra firme* (TF) and *várzea* (VZ) forests, which diverge markedly in environmental gradients and plant life-history traits, and yet typically co-occur side-by-side. We aimed to compare the plant diet of terrestrial, arboreal and aquatic frugivorous vertebrates in both *terra firme* and *várzea* forest, and examine the relative contribution of fruit traits, including fruit morphology and colour, to their diet selection in terms of fruit resources. To our knowledge, this represents the first systematic attempt to document the complete tropical fruit-frugivore networks of two adjacent, yet radically different, forest types. We do not attempt to infer the demographic consequences of fruit-frugivore interactions to the fate of seeds, and thereby define frugivory (*sensu lato*) as simply feeding on fruit parts, including immature/mature seeds consumed by granivores and ripe fruit pulp consumed by frugivores (*sensu stricto*).

4.2. Methods

4.2.1. Study area

This study was conducted within two contiguous sustainable-use forest reserves in the State of Amazonas, Brazil, namely the Médio Juruá Extractive Reserve (*ResEx Médio Juruá*, 253,227 ha) and the Uacari Sustainable Development Reserve (*RDS Uacari*, 632,949 ha) (Figure 4.1). These reserves border the Juruá river, a major white-water tributary of the Solimões (=Amazon) river, and contain large expanses of upland unflooded *terra firme* forest (80.6% of combined reserve area) and, closer to the river channel, seasonally-flooded *várzea* forest (17.9%) (Chapter2: Hawes et al. 2012).

The Juruá region has a wet, tropical climate with a mean annual temperature of 27.1°C and annual rainfall, calculated from daily records over three consecutive years (2008 - 2010) at the Bauana Ecological Field Station (S 5°26’19”, W 67°17’12”), averaging 3,679 mm. The elevation range within the reserves is 65 - 170 m above sea level. *Terra firme* soils are typically heavily leached and nutrient poor in comparison to the eutrophic alluvial soils of pre-Andean origin in *várzea* forests. All sites surveyed consisted of primary forest, although commercially valuable timber species along the Juruá river had experienced small-scale selective logging from 1970 to 1995, especially in *várzea* forest (Scelza 2008).

4.2.2. Frugivore surveys

We conducted surveys for medium- to large-bodied diurnal vertebrates (birds and mammals) in three 100-ha plots (two in TF and one in VZ), each consisting of a trail grid of twelve 1-km transects at 200-m intervals (Figure 4.1). Monthly surveys were conducted in accordance with a standardised line-transect census protocol (Peres and Cunha 2011), between 0630h and 1100h, and were discontinued whenever necessary during rain. The 100-ha plots were surveyed during the first two weeks of every month (April 2008 – July 2010), over the course of four consecutive days (three 1-km transects per day, depending on weather conditions). Transects in *várzea* forest were surveyed by dugout canoe during the aquatic phase. For all encounters, we recorded species, detection cue, distance along the transect, perpendicular distance from the transect, and animal group size. We also recorded any observations of fruit feeding behaviour, including identification and/or collection of plant vouchers of whole fruits or fruit parts. Target species of frugivores in our surveys included primates, ungulates, caviomorph rodents, squirrels, some frugivorous Carnivora, terrestrial birds and larger-bodied canopy birds. However, small-bodied frugivorous birds, including Cotingidae, Pipridae and Tyranidae, were excluded from our surveys.

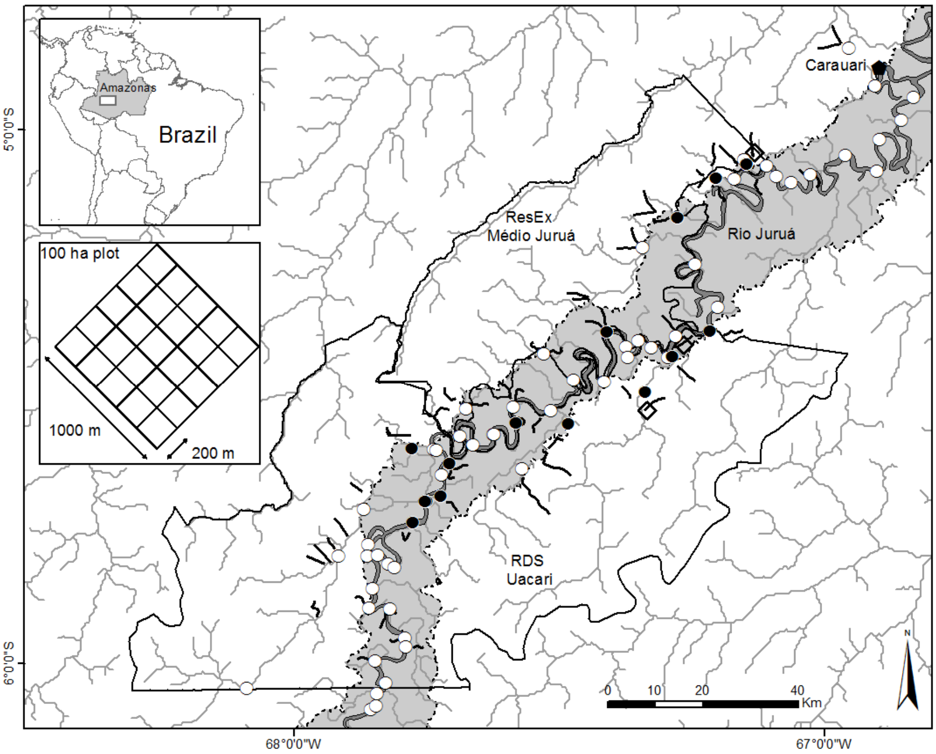


Figure 4.1. *Map of the Médio Juruá region of western Brazilian Amazonia showing locations of 67 transects of 5 km in length (lines) and three 100-ha plots (squares) in* terra firme *(no shading) and* várzea *forest (grey shading). Local communities within the two forest reserves are indicated by solid circles (where interviews were conducted) and open circles (where interviews were not conducted). Solid black and grey lines represent reserve boundaries and perennial streams, respectively; dashed lines represent the total extent of the* várzea *floodplainin this region as measured by ALOS ScanSAR images © JAXA/METI 2009 (Hawes et al. 2012).*

4.2.3. Fruit surveys

We conducted monthly ground surveys of residual fruit-fall in three 100-ha plots (two TF, one VZ), as described above. Surveys were completed concurrently with frugivore surveys, recording the presence of all patches of fallen fruit occurring within a 1-m wide strip along the transect (total transect length = 12 km per plot, total survey area = 1.2 ha per plot). For each fruit patch encountered we recorded its location along the transect, and collected a fresh specimen for our reference fruit collection. In each case we also located the fruiting stem bearing fruits, including both trees and high-climbing woody lianas, and measured its DBH and perpendicular distance from the transect. Similar ground surveys were also conducted on an intermittent monthly basis by 22 trained local field assistants who walked a network of 67 transects of 5 km in length (41 TF, 26 VZ; Figure 4.1) which were widely distributed across the two study reserves.

4.2.4. Fruit identification and traits

Further voucher collections were made of fallen fruit from tagged trees monitored for phenology records (see Chapter 3), which were identified *in situ* by a trained technician from the Botany Department of the Instituto Nacional de Pesquisas da Amazônia (INPA, Manaus). All fruit and seed specimens were also identified at INPA before being deposited at the EAFM Herbarium of the Instituto Federal de Educação, Ciência e Tecnologia do Amazonas (IFAM, Manaus). Additional identification of trees and fruits was aided by the following sources: van Roosmalen (1985), Gentry (1996), Ribeiro et al. (1999), Cornejo & Janovec (2010), and Wittmann et al. (2010). Fruits and seeds were weighed using a 0.01g electronic scale and their length, width and depth were measured using callipers (10 fruits/seeds per sample where possible). Fruit type, colour, dehiscence and number of seeds were also recorded. Fruit type was reduced from an initial formal botanical classification including 15 morphological categories (e.g. Spjut 1994) to only four functional groups (van der Pjil 1982, Fleming & Kress 2011): i) berries and berry-like fruit, ii) drupes, iii) pulpa, and iv) dry fruits. Fruit colour was also reduced following an initial classification, from 16 to only five categories: green, brown, yellow, red and purple/black. The number of seeds per fruit was assigned into four classes as single-seeded, several (2-5), numerous (6-15) and many seeds (>15).

4.2.5. Fruit-frugivore interactions

In addition to feeding observations made during the course of frugivores surveys within the 100-ha plots and along the 5-km transects, we include all feeding observations recorded opportunistically by JEH during the course of other field activities over an 18-month period. To supplement these records with local knowledge of fruit-frugivore interactions, we conducted eighteen semi-structured interviews in sixteen local communities located within the two study reserves (Figure 4.1), during July-August 2011. Interviewees were selected non-randomly in each community to target the most knowledgeable informants, typically experienced hunters, fishermen, and older women who had examined stomach contents of hundreds/thousands of fish. Colour photographs of fruits with known identity from our reference collection were shown to two or three interviewees simultaneously who were invited to list their respective vertebrate consumers whenever those were known. Colour photographs of frugivorous mammal, bird and fish species were available as a prompt in all cases. Local informants interviewed were free to contribute jointly, and records were made for the combined group. A total of 188 photographs of fruit species/genera were shown (103 from *terra firme* and 79 from *várzea* forest), including six additional photographs of non-native (exotic) fruit to check for any tendency to report type II errors (i.e. false feeding interactions), with interviews typically lasting 90 min. Finally, an unstructured portion of the interview invited informants to list all known food sources for resident fish species.

4.2.6. Data analyses

Data from monthly frugivore surveys were pooled across the two *terra firme* plots and converted into number of sightings per 10 km walked to compare between forest types. Sightings of closely related species were typically pooled at the genus level, including for *Cebus* spp., *Mazama* spp., and *Saguinus* spp., although ambiguous identifications also necessitated the pooling of observations across genera for parrots, pigeons, and tinamous.

Fruit-frugivore interactions recorded from all methods (direct observations from 100-ha plots and transects, and local knowledge) were combined to create a single binary matrix of frugivore consumers and fruit resources, with a value of 1 representing the confirmed presence of a positive interaction and 0 representing an undocumented interaction. We examined the number of positive interactions recorded per fruit resource and per frugivore consumer as an indication of community-wide richness of interactions or degree (*sensu* Jordano et al. 2003); more sophisticated analyses of specialisation/generalisation would require a standardized metric of interaction frequencies across the different methods (Blüthgen et al. 2006) which is unavailable in this study. Independent networks were generated for each forest type using Pajek 2.05 (Batagelj & Mrvar 1998), and presented as bipartite graphs, excluding consumers with fewer than 10 trophic resources identified in both forest types. Non-metric multidimensional scaling (NMDS) ordinations, based on the Bray-Curtis similarity index, were produced from the same binary matrices, and we used ANOSIM to further explore the differences in dietary composition between functional groups of frugivores.

All plant species and genera were assigned mean values for fruit and seed mass, length, width and depth, with field measurements of at least 10 fruits/seeds supplemented by values from the literature where necessary (van Roosmalen 1985, Cornejo & Janovec 2010, Wittmann et al. 2010a). This approach is appropriate as both fruit type (Casper et al. 1992) and seed size (Kelly 1995, ter Steege & Hammond 2001) tend to be morphologically conservative and consistently uniform within Amazonian tree and woody liana genera, so that most of the variation in these traits occurs between genera. As a result of strong correlations between morphometric variables, we used only fruit and seed mass in the following analyses, predicting missing values where necessary from fruit and seed width and length measurements (see Appendix 4.1).

In addition to the continuous variables fruit and seed mass, we used fruit type, fruit colour, a ranked classification of number of seeds as categorical variables, and whether or not fruits were dehiscent (as a binary variable) to examine the role of fruit traits on the relative partitioning of fruit genera across all functional groups of frugivores. We used a classification and regression tree (CART) approach (Breiman et al. 1984, Loh 2011) that successfully incorporates the combination of continuous, categorical and binary variables, which is not conducive to ordination techniques. All analyses were conducted in R (R Development Core Team 2010): NMDS and ANOSIM used the ‘vegan’ package (Oskanen et al. 2011); CART analysis used the ‘rpart’ package (Therneau & Atkinson 2012).

4.3. Results

4.3.1 Frugivores

Total survey effort of the 100-ha plots was 552 km in *terra firme* (Plot 1 = 24 months: 11 wet season, 13 dry; Plot 2 = 22 months: 7 wet season, 15 dry) and 312 km in *várzea* forest (26 months: 13 aquatic phase, 13 terrestrial). We detected 36 functional groups of medium to large-bodied non-aquatic frugivorous vertebrates, typically equivalent to genus level classification, including 9 primates, 4 ungulates, 5 rodents, 2 carnivores, 9 canopy birds, 6 terrestrial birds and 1 reptile (Table 4.1). These surveys failed to detect the Wattled Currasow (*Crax globulosa*) or the nocturnal primates (night monkey, *Aotus nigriceps*), and two arboreal procyonids (kinkajou, *Potos flavus* and olingo, *Bassaricyon gabbii*), although their presence was confirmed in the Médio Juruá region outside of surveys. The complete list of the medium-large bodied frugivore assemblage of the Médio Juruá region also includes aquatic frugivores represented by 12 bony fish, 6 cartilaginous fish, and 3 freshwater turtles (Appendix 4.2). We do not report on the interactions of frugivorous bats.

There are clear differences between the frugivore assemblages in *terra firme* and *várzea* forests (Figure 4.2). Primates such as woolly monkeys (*Lagothrix*), saki monkeys (*Pithecia*) and tamarins (*Saguinus* spp.) were absent from *várzea* forest. Uacaris (*Cacajao*) and spider monkeys (*Ateles*) are known to occur in *várzea* forest but, apart from a solitary spider monkey sighting, were patchy in their distribution across the Médio Juruá region and absent from our *várzea* study plot. In contrast, howler monkeys (*Alouatta*) and squirrel monkeys (*Saimiri*) were much more frequently sighted in *várzea* than *terra firme* forest. Within the ungulates, lowland tapir (*Tapirus*) and collared peccary (*Pecari*) were absent from *várzea* forest, while within the rodents, agoutis (*Dasyprocta*) and acouchis (*Myoprocta*) were also almost exclusively sighted in *terra firme*. Conversely, arboreal echimyiad rodents (*Dactylomys* and *Isothrix*) and squirrels (*Sciurus*) were largely restricted to, or far more common in *várzea*, respectively. This strong turnover in community composition is enhanced when considering the additional inclusion of frugivorous fish and turtles during the prolonged aquatic phase when floodwaters invade the *várzea* forest.

Table 4.1. *Sightings (N) and encounter rates (ER, expressed as sightings per 10 km walked) of frugivorous vertebrates during monthly line-transect surveys within three 100-ha plots in* terra firme *and* várzea *forest.*

	Frugivore species	N		ER	
		TF	VZ	TF	VZ
Mammals					
Primate	*Alouatta seniculus*	1	48	0.02	1.54
	Ateles chamek	41	1	0.74	0.03
	Cacajao calvus	33		0.60	
	Callicebus spp.	8	7	0.14	0.22
	Cebus apella, C. albifrons	72	49	1.30	1.57
	Lagothrix spp.	25		0.45	
	Pithecia spp.	41		0.74	
	Saguinus mystax, S. fuscicollis	34		0.62	
	Saimiri sciureus	3	80	0.05	2.56
Rodent	*Cuniculus paca*	4	1	0.07	0.03
	Dasyprocta fuliginosa	61	1	1.11	0.03
	Myoprocta acouchy	30		0.54	
	Sciurus spp.	15	24	0.27	0.77
	Echimyidae		24		0.77
Ungulate	*Mazama americana, M. nemorivaga*	36	21	0.65	0.67
	Pecari tajacu	46		0.83	
	Tapirus terrestris	6		0.11	
	Tayassu pecari	18	4	0.33	0.13
Carnivore	*Eira barbara*	11	2	0.20	0.06
	Nasua nasua	13	4	0.24	0.13
Birds					
Canopy bird	*Amazona spp.*	9	33	0.16	1.06
	Ara spp.	18	35	0.33	1.12
	Cacicus spp.		3		0.10
	Clypicterus, Ocyalus, Psarocolius	8	9	0.14	0.29
	Ibycter americanus	13		0.24	
	Pionities, Pionopsitta, Pionus		5		0.16
	Pteroglossus spp.	4	4	0.07	0.13
	Ramphastos spp.	40	12	0.72	0.38
	Trogon spp.	12	31	0.22	0.99
Terrestrial bird	Columbidae	14	18	0.25	0.58
	Crypturellus spp., Tinamus spp.	119	79	2.16	2.53
	Mitu tuberosa	30	28	0.54	0.90
	Ortalis guttata		1		0.03
	Penelope jaquacu	85		1.54	
	Psophia leucoptera	54	1	0.98	0.03
Reptiles					
Tortoise	*Chelonoidis denticulata*	12	2	0.22	0.06

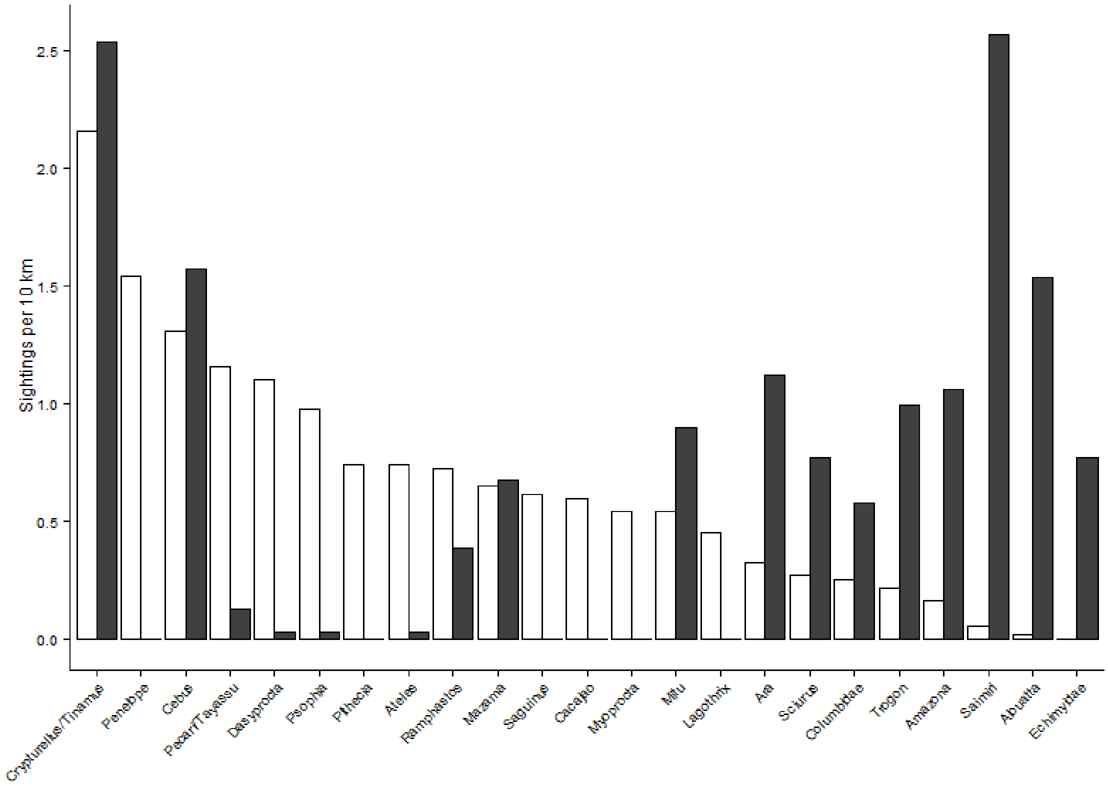


Figure 4.2. *Encounter rates of frugivorous vertebrates (> 10 sightings per plot in at least one forest type, mean per 10 km) during line transect surveys conducted within 100-ha plots in* terra firme *(open bars) and* várzea *forest (solid bars).*

4.3.2 Fruits

In addition to the survey effort within the three 100-ha plots, information on fruit resource availability was supplemented by fruit surveys along the 5-km transects. Total effort comprised 498 surveys (312 TF, 186 VZ) over 29 months and an average of 78.9 km walked along transects per month (50.5 TF, 28.4 VZ). Of the 152 plant genera considered in the remainder of this study, 50 and 54 genera were detected only in either *terra firme* or *várzea* forest, respectively, whereas the other 48 genera occurred in both forest types.

Fruit and seed mass were measured or compiled for over 75% of sampled plant genera in both *terra firme* and *várzea* forests (Table 4.2). Fruit and seed dimensions and mass did not differ significantly between plant genera occurring in *terra firme* and *várzea* forest, but fruit mass and size were more evenly distributed over a wider range in *várzea* forest (Appendix 4.3). The proportion of plant genera within mutually exclusive categories of fruit type, fruit colour, fruit dehiscency, and number of seeds per fruit were also comparable across the two forest types (Table 4.2).

Table 4.2. *Summary of fruit morphology measures per plant genus (mean ± SD) and other fruit traits (% of plant genera) in* terra firme *(TF) and* várzea *(VZ) forest.*

Traits	TF	N	VZ	N	t-test	p
Morphology						
Fruit mass (g)	27.84 ± 48.45	83	34.67 ± 107.44	78	-0.5144	NS
Fruit length (cm)	5.52 ± 6.62	93	5.51 ± 9.00	98	0.0073	NS
Fruit width (cm)	3.08 ± 1.81	92	3.04 ± 2.63	92	0.1177	NS
Seed mass (g)	3.7 ± 9.21	82	3.51 ± 7.60	84	0.1391	NS
Seed length (cm)	2.04 ± 1.56	91	1.77 ± 1.32	95	1.3092	NS
Seed width (cm)	1.36 ± 1.03	91	1.30 ± 1.10	95	0.4122	NS
Dehiscence						
Dehiscent	37.8		37.8			
Indehiscent	62.2		66.3			
Fruit type						
Berries	19.4		25.5			
Drupes	35.7		33.7			
Arrilate	9.2		7.1			
Dry	35.7		37.8			
Fruit colour						
Brown	34.7		32.7			
Green	17.3		15.3			
Yellow	20.4		19.4			
Red	13.3		22.4			
Purple/black	13.3		13.3			
No. seeds						
Single	40.8		45.9			
Several (2-5)	24.5		18.4			
Numerous (6-15)	9.2		15.3			
Many (>15)	25.5		24.5			

4.3.3. Fruit-frugivore interactions

The compilation of fruit-frugivore interactions, excluding functional groups with insufficient data (<10 interaction records), yielded a sample of 55 frugivore consumers targeting 152 fruit resources across the two forest types (TF: 38 x 98; VZ: 48 x 103). We recorded an almost equal number of positive interactions in each forest type (TF: 956; VZ: 958), resulting in the overall filling or connectance (*sensu* Jordano 1987) of 25.7% and 19.4% of all potential interactions in the fruit-frugivore matrices in *terra firme* and *várzea* forest, respectively.

These fruit-frugivore interactions were distributed very unevenly between both fruit resources and fruit consumers (Figure 4.3). Mammals were the principal consumers for most fruit genera in *terra firme* forest, in contrast to *várzea* where more fruit genera were consumed by a combination of mammals, birds and fish. Primates featured prominently amongst both terrestrial and arboreal mammals with the highest number of unique interactions, especially in *terra firme*. With the exception of four primate (*Cebus* spp., *Cacajao*, *Saimiri*, *Alouatta*) and three canopy bird taxa (*Ara* spp., *Amazona* spp., *Pionus* spp. etc), almost all frugivores occurring in both forest types had a lower number of interactions in *várzea* forest than in *terra firme* forest. Six bony fish were recorded as consumers for as many plant genera as primates in *várzea* forest.

Bipartite graphs (Figure 4.4) show that fruit-frugivore networks in both *terra firme* and *várzea* forest were highly diffuse, with most frugivores exhibiting a generalised diet including fruit resources from a wide range of plant genera. Similarly, most plant genera bear fruits consumed by a diverse coterie of frugivores. Beyond these general observations, however, the networks appear to differ substantially between the two forest types. The interactions in *terra firme* forest were heavily dominated by arboreal frugivores, and primates in particular. Primates remained important in *várzea* but in, addition to a number of plant genera common to *terra firme*, their fruit resources were notably comprised of plant genera unique to *várzea* forests, which were also heavily consumed by frugivorous fish. Accordingly, there was a notably smaller contribution to the *várzea* forest network from terrestrial frugivores, including ungulates, rodents and terrestrial birds, as these taxa are not year-round residents in this forest type.

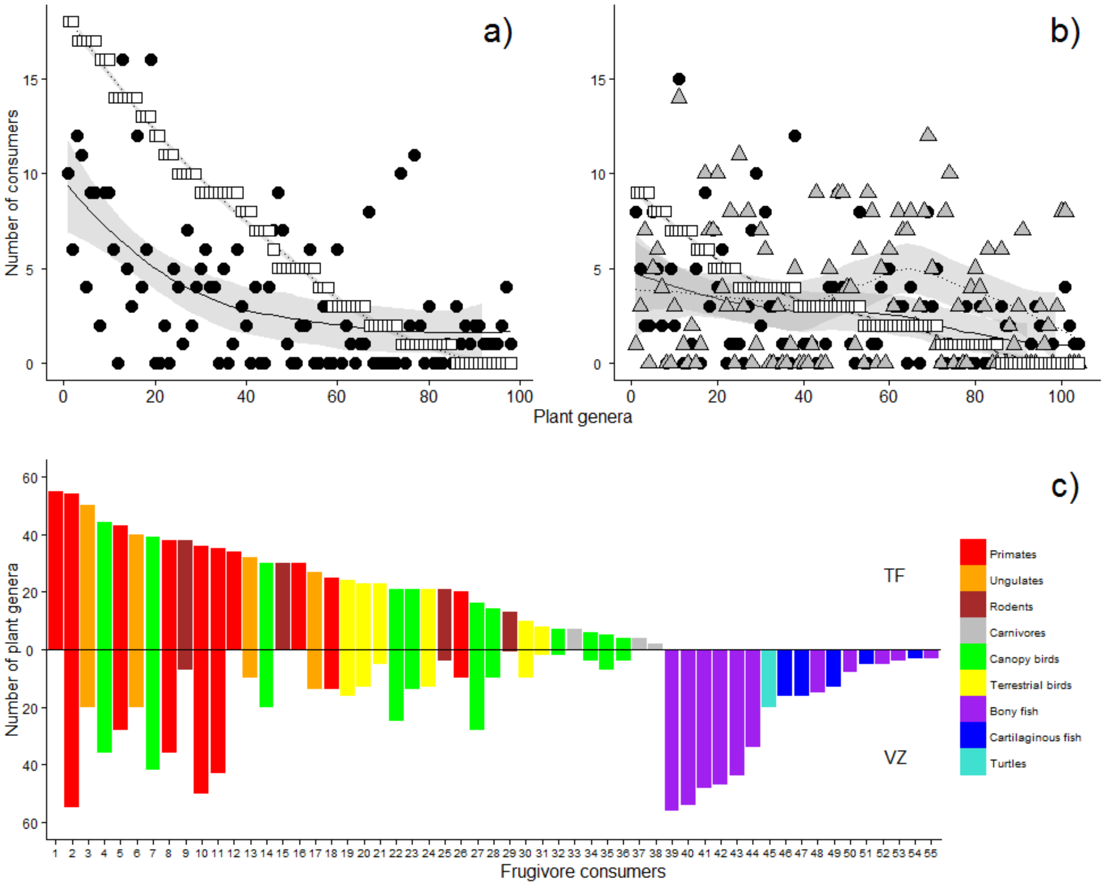


Figure 4.3. *Numbers of fruit consumers identified per plant genus in (a) terra firme and (b) várzea forest, and (c) corresponding numbers of plant genera identified as fruit resources per frugivore consumer in* terra firme *and* várzea *forest (bars above and below the zero line, respectively). Symbols in (a) and (b) represent mammals (squares), birds (circles) and fish (triangles); plant genera are ranked by number of mammalian consumers; curves represent smoothed means; grey shading represents 95% confidence intervals. Numbers along the x-axis in (c) refer to frugivore codes listed in Appendix 4.2.*

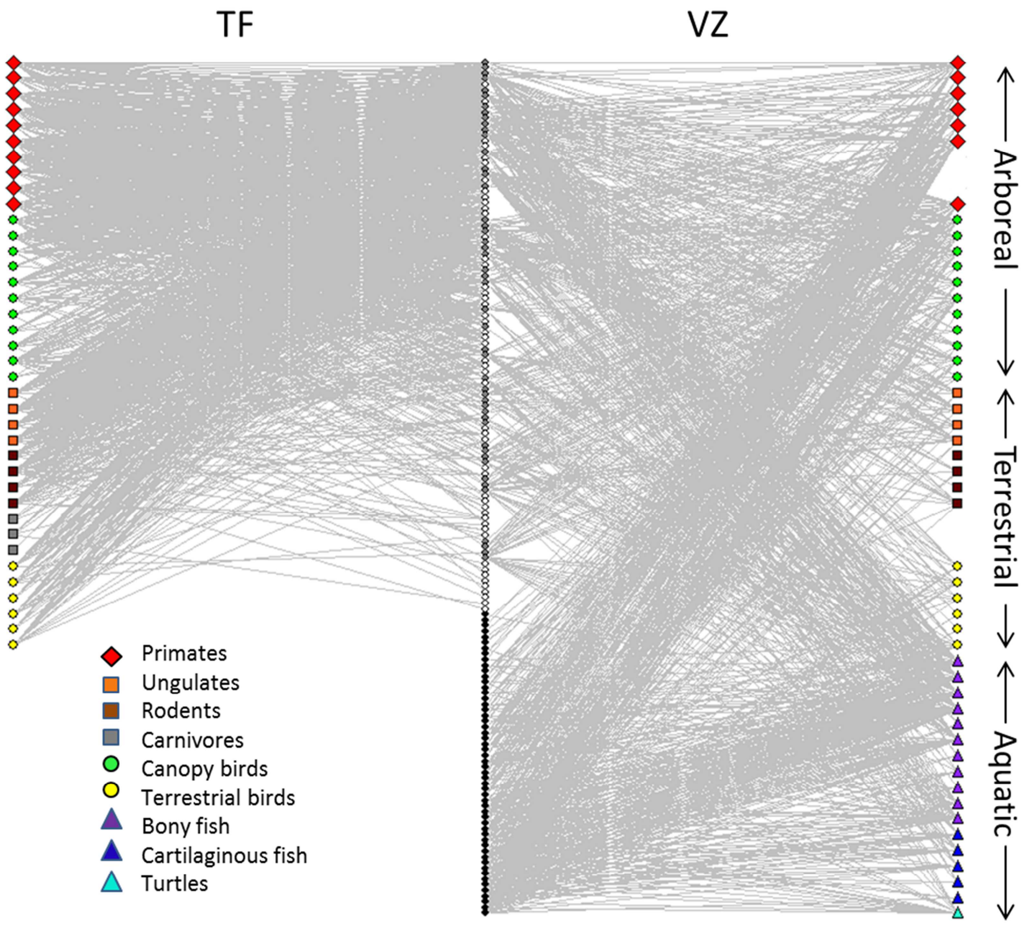


Figure 4.4. *Bipartite networks of fruit-frugivore interactions in terra firme and várzea forests. Fruit consumers are ordered by taxonomic group. Fruit resources are plotted in descending order of the number of interactions detected in* terra firme *forest. White, black and grey circles represent plant genera occurring in* terra firme, várzea, *and both forest types, respectively.*

Despite such apparent overlap in fruit resources across frugivorous vertebrates of widely different life histories, the two-dimensional NMDS ordination plots, based on the binary interaction matrices, show a distinct grouping of frugivores according to major functional groups (Figure 4.5; ANOSIM, TF: $R = 0.6968$, $p < 0.001$, VZ: $R = 0.6597$, $p < 0.001$). Variation in the composition of fruit diets is generally lower within functional groups than between pairs of frugivore groups (Table 4.3). There was also a noticeable separation between arboreal and terrestrial frugivores in *terra firme* forest, and between arboreal, terrestrial and aquatic frugivores in *várzea* forest. The partitioning of fruit resources amongst frugivores was not clearly explained by the CART analysis of fruit traits (Appendix 4.4), although the relative importance of fruit traits indicate that fruit and seed size, and to some degree fruit dehiscency, were the most importart traits in the overall partitioning of fruit genera across the frugivore assemblages in both *terra firme* and *várzea* forest. In contrast, other categorical traits, such as fruit colour and fruit type, explained the least amount of the variation in trait partitioning. Finally, forest type was the most important dichotomous variable when included in the analysis, likely because of the high degree of turnover in fruit genera available in either *terra firme* or *várzea* forest.

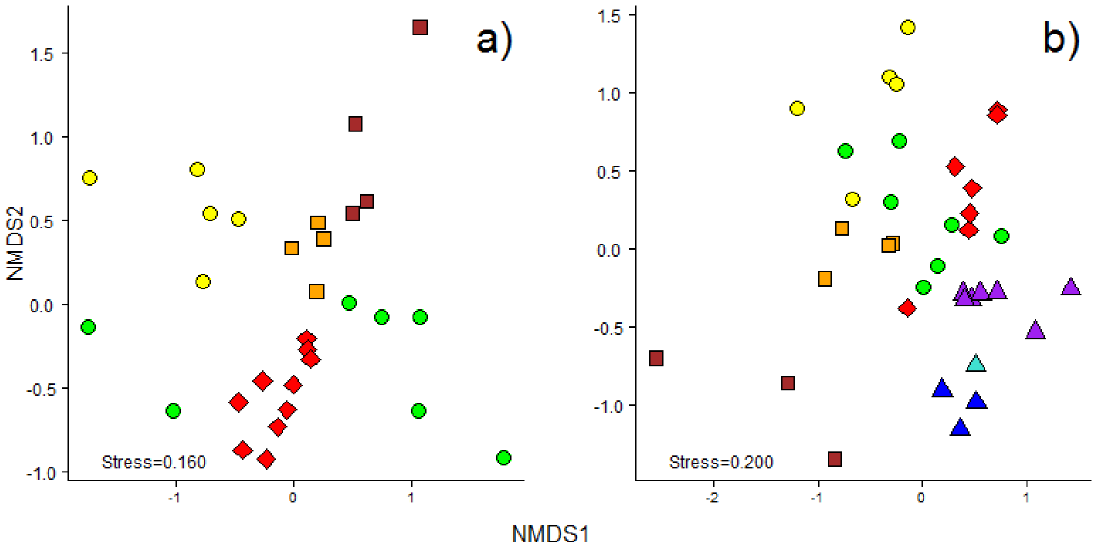


Figure 4.5. *NMDS ordinations based on binary matrices describing the genus-level plant composition of fruit diets in (a)* terra firme *and (b)* várzea *forest. Symbols represent major classes of frugivores as in the legend for Figure 4.4.*

Table 4.3. *ANOSIM results showing partitioning of fruit resources between frugivore consumer groups. Below the diagonal: R, above the diagonal: p.*

	TF					VZ							
	Primates	Ungulates	Rodents	Canopy birds	Terrestrial birds	Primates	Ungulates	Rodents	Canopy birds	Terrestrial birds	Bony fish	Cartilaginous fish	Turtles
Primates	-	0.0009	0.0009	0.0001	0.0001	-	0.0029	0.028	0.0027	0.0017	0.0004	0.0085	0.1171
Ungulates	0.74	-	0.2001	0.0779	0.0075	0.72	-	0.0674	0.0835	0.0445	0.0032	0.0286	0.1905
Rodents	0.93	0.1	-	0.0114	0.0092	0.97	0.75	-	0.0258	0.0466	0.026	0.0984	0.3302
Canopy birds	0.71	0.26	0.46	-	0.0052	0.38	0.24	0.92	-	0.0098	0.0005	0.0076	0.3757
Terrestrial birds	1	0.89	1	0.48	-	0.86	0.37	1	0.48	-	0.0014	0.0183	0.1721
Bony fish	-	-	-	-	-	0.66	0.9	1	0.54	0.91	-	0.0098	0.2541
Cartilaginous fish	-	-	-	-	-	0.92	1	0.92	0.66	0.9	0.74	-	0.2477
Turtles	-	-	-	-	-	0.85	0.92	1	0.17	1	0.67	1	-

4.4. Discussion

This study provides one of the first assessments of two complete tropical fruit-frugivore networks from adjacent but highly contrasting forest types. Our use of direct feeding observations from extensive frugivore and fruit surveys, coupled with knowledge of interactions obtained through interviews with long-term residents, allowed us to construct binary matrices for seasonally-flooded and unflooded forest from the Rio Juruá region of western Brazilian Amazonia. Our study reports three important observations: (1) taxonomic turnover was high between *terra firme* and *várzea* forests, in terms of both vertebrate consumers and fruit resources available; (2) fruit-frugivore networks in both forest types consisted of a large and diffuse set of interactions whose structure varied markedly between forest types; and (3) partitioning of fruit resources among functional consumer groups was clear but not well explained by our data on fruit morphology and presentation.

4.4.1. High turnover in frugivore assemblages and fruit resources

Even without considering the seasonal occupancy of fish (Horn et al. 2011) and freshwater turtles (Balensiefer & Vogt 2006) in *várzea* forests during the aquatic phase, we recorded considerable differences in the vertebrate assemblages of flooded and unflooded forests. In addition, frugivores common to both forest types also differed substantially in their abundance expressed as encounter rates. These findings are consistent with previous studies comparing the vertebrate communities of flooded and unflooded forests (Ayres 1986, Peres 1997, Patton et al. 2000, Haugaasen & Peres 2005, 2008), which tend to report a relatively depauperate fauna in *várzea* in comparison to *terra firme*, although mammal biomass is higher in the former (Peres 1999, Haugaasen & Peres 2005).

These differences owe much to the physical barrier to terrestrial frugivores imposed by the seasonal floodwaters. Most arboreal and scansorial vertebrates, including primates, squirrels, generalist carnivores such as tayra (*Eira barbara*) and coati (*Nasua nasua*), and canopy birds retain accessibility to *várzea* forests all year-round. In contrast, caviomorph rodents, ungulates, terrestrial birds and tortoises are almost completely excluded from this forest type during the aquatic phase for up to half the year. The annual lateral migration patterns between flooded and unflooded forests have not yet been comprehensively explored but the seasonal use of flooded forests by a range of terrestrial rodents and marsupials, ungulates, primates and birds has been documented (Bodmer 1990, Fragoso 1998, Peres 1996, Boubli 1999, Malcolm et al. 2005, Haugaasen & Peres 2007). In particular, those terrestrial frugivores excluded during the aquatic phase are potentially attracted to the renewed supply of fruits and seeds exposed or deposited on the forest floor by the receding floodwaters, in addition to the burst of fresh undergrowth foliage (Haugaasen & Peres 2007), all of which are sustained by the nutrient-rich soils of várzea forests.

The species composition of fruit resources are similarly divergent between flooded and unflooded forests. The plant communities of Amazonian floodplain forests have received less research attention than their upland counterparts, but have consistently been shown to have lower species richness (Campbell et al. 1986, ter Steege et al. 2000, Haugaasen & Peres 2006) as a result of the extreme conditions of stress imposed by the flood pulse. Yet Amazonian *várzea* forests are the most species-rich floodplain forests worldwide (Wittmann et al. 2006), partly as a result of their internal habitat heterogeneity, the relentless process of natural forest succession, and the relative geoclimatic stability of Amazonian floodplains over recent geological history (Hoorn & Wesselingh, 2010, Wittmann et al. 2010b).

The high species richness of *várzea* forests can also be partly attributed to the ability of some *terra firme* plant species to tolerate varying degrees of inundation and thus expand their ecological distribution into floodplain forests on high ground (Wittmann et al. 2010b). However, the unique environmental pressures within *várzea* forests are reflected in very low levels (10 - 30%) of floristic similarity with *terra firme* forests (Wittmann et al. 2010b). These general patterns are consistent with the composition of fruit genera in our surveys that were unique to either *terra firme* or *várzea* forests, with a smaller fraction occurring in both forest types. Moreover, this floristic dissimilarity further increases at the species level as many parapatric congeners are restricted to either *terra firme* or *várzea* forest (Junk, 1989).

4.4.2. Forbidden or missing interactions

The high species diversity in the frugivore and fruit resource assemblages in our study area results in a large number of potential interactions. Our field observations, combined with repeatedly verified cognitive information from local informants, suggest that a large proportion of these interactions are not realised. It is important to understand that these unobserved interactions may truly not occur (forbidden), or alternatively may just have passed undetected during sampling (missing) (Olesen et al. 2011). This issue of unobserved interactions is of general concern to network studies as the problem in discerning forbidden from missing links makes it difficult to assess the degree of completion in the matrix, and any number of sampling artefacts resulting in incomplete matrices will affect a variety of network metrics (Blüthgen et al. 2008).

Our networks, however, are likely to contain both sorts of unobserved interactions. Incomplete sampling from field observations is supplemented by in-depth knowledge from local residents with decades of personal experience from hunting, fishing and examining gut contents of terrestrial and aquatic game vertebrates, particularly from frugivorous fish which are typical of the local subsistence diets. However, there are biases in this approach as local knowledge is likely to favour those frugivore species most targeted by hunters and fishers, and fruits from the best known plant species. For example, the diet of primates, ungulates and caviomorph rodents are likely to be more comprehensively reported than that of non-game mustelids and procyonids, which have broadly omnivorous diets that can include high levels of frugivory (Kays 1999, Alves-Costa & Eterovick 2007). Similarly, consumers are likely to be more readily reported for plant species that are prominent in the local ethnobotany, including those that are abundant, large-girthed or more heavily used by people as valuable extractive resources, such as fruits, seeds, latex, and timber (Peterson 2010). The patchy distribution and rarity of many plant species in tropical forests, and the often ephemeral nature of their fruiting strategies, means that some rare interactions are much more unlikely to be observed than others. In our study area, we also note the possibility that local knowledge may be more extensive within *várzea* forests, which lie in closer proximity to most reserve communities and are potentially more heavily exploited (Figure 4.1).

Despite the high likelihood of many missing links in our dataset, it is also certain for a number of reasons that a large proportion of zero values in our matrix represent forbidden interactions. Firstly, the spatial turnover of fruits and frugivores between *terra firme* and *várzea* simply prohibits certain interactions from taking place. Secondly, any asynchrony between the temporal cycles of fruit production and accessibility of flooded forests to terrestrial or aquatic frugivores (at diametrically opposite times of year) precludes otherwise possible interactions. Finally, the repeated absence of any given interaction in the aggregate data pool from 2,288 km of census walks along 371 km of transects, sampled over 29 months by 25 local field assistants likely reflects either forbidden or very rare interactions, which are unlikely to be ecologically important. We are therefore confident that the networks presented here effectively portray the broad patterns of frugivory in both flooded and unflooded forests.

4.4.3. Partitioning of large, diffuse networks

Whilst networks in both forest types showed a large number of diffuse interactions, overall connectance (the proportion of total potential links realised) and the degree (number of links) was higher in *terra firme* for almost all frugivores occurring in both forest types. Primates in *várzea* forest exhibited ecological plasticity in retaining a large number of links, including interactions with plant genera unique to this forest type, but the overall dominance of primates in the *várzea* network was weaker than that in *terra firme.* This was in part due to the absence of three major *terra firme* fruit consumers (*Lagothrix*, *Pithecia*, and *Saguinus*). The high number of interactions associated with frugivorous fish also provided a major contribution to the more even distribution of fruit resources among *várzea* consumers. Despite their wide recognition as important frugivores (Goulding 1980), we still have little detail on the diet of many fish species including their relative generalisation/specialisation (Correa et al. 2007, Horn et al. 2011).

The suggestion that the diet of frugivorous fish may overlap substantially with other consumers (Horn et al. 2011) is supported by evidence from *várzea* forest that fish consume fruits that are widely used by both mammals and birds. This overlap could potentially reduce the selective pressure on fruit traits; with trait matching being hardly detectable compared to more specialised networks such as many flowering plants and their pollinators (Blüthgen et al. 2007). While we found clear partitioning of fruit resources among major frugivore groups in both forest types, this could not be immediately attributed to particular fruit traits, which may be related to the considerable levels of overlap recorded. We also note the overriding influence of forest type in our study, demonstrating the important role of the annual flood pulse in partitioning fruit resources between arboreal, terrestrial and aquatic frugivores in *várzea* forests.

4.5. Conclusions

Both seasonally-flooded and unflooded forests of the Médio Juruá region of western Brazilian Amazonia contain large and complex assemblages of frugivorous vertebrates, although turnover is high and the temporal sequence of frugivores and their fruit resources in *várzea* forests are strongly determined by the annual flood pulse. Terrestrial vertebrates are excluded by the prolonged inundation of the aquatic phase, when access is permitted to frugivorous fish and freshwater turtles. In combination with the variable fruit resources available in *terra firme* and *várzea* forests throughout the year, the binary networks of fruit-frugivore interactions we constructed from field observations and local knowledge differed substantially in structure between the two forest types. Fruit resources were clearly partitioned among broad taxonomically coherent groups of frugivores but we did not identify a clear explanation for these differences on the basis of fruit traits.

Our networks were characterised by a large proportion of unobserved potential interactions, suggesting a high probability of missing data due to sampling effects in addition to the identification of truly ‘forbidden links’. However, we hope that this study will highlight the importance of community-wide assessments of fruit-frugivore networks, particularly in tropical forests where such a large proportion of the vertebrate species richness and biomass is sustained by immature and mature fruits and seeds as a resource. We also hope to highlight the potential roles of poorly studied frugivores, particularly frugivorous fish in flooded forests. Finally, we emphasize the valuable role that local knowledge can play in ecological studies in species-rich ecosystems, including the assembly of complex fruit-frugivore networks.

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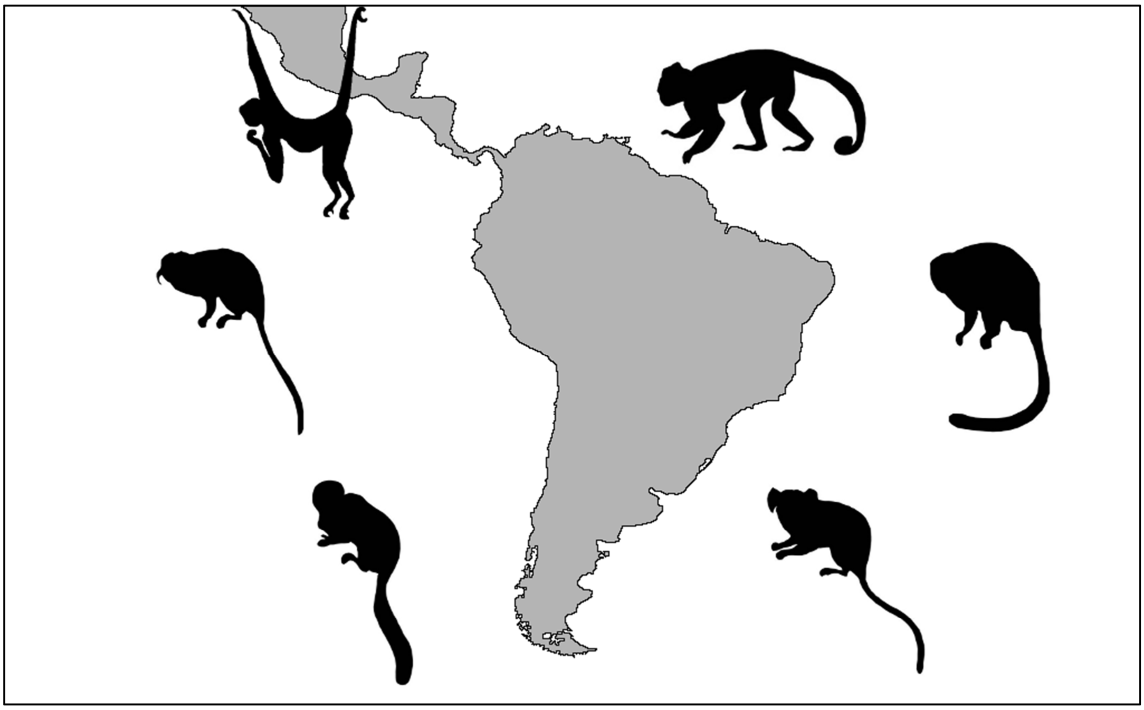
Chapter 5

Sampling effort in neotropical primate studies: geographic and taxonomic biases



To be submitted to *International Journal of Primatology* as:

Hawes, J.E., Calouro, A.M., & Peres, C.A. Sampling effort in neotropical primate studies: geographic and taxonomic biases.

Abstract

Primates comprise the most observable and best studied order of mammals, yet the distribution of sampling effort by primatologists has inevitably focused on a few genera, and a limited number of study sites. Here, we present the first systematic review of such biases in research on wild primate populations, by investigating effort allocated to primate dietary studies across the entire Neotropics. Primate diets, particularly in this region of the world have been extensively studied over the last few decades, since primates are widely recognised as the most important frugivores in tropical forests, with vital roles as seed dispersal agents for many tropical plants. We use a standardised measure of sampling effort to assimilate datasets derived from multiple methodologies and attempt to understand the distribution of effort based on a combination of geographic variables and primate species traits. By identifying primate taxa and geographic regions that have been particularly poorly investigated in terms of total sampling time and density of research effort in relation to species geographic range size and country size, we hope to redirect future research effort towards current knowledge gaps. In addition, we show a collective failure by primatologists to investigate the full primate assemblage occurring at any given study site. We therefore advocate that primate ecologists should focus on the most undersampled geographic regions and improve sampling coverage across taxa at existing study sites. Finally, we propose the creation of a common data library of primate feeding records (including currently unpublished datasets), complete with associated metadata and full details of study sample effort, in the interest of increasing our understanding of community-wide fruit-frugivore interaction networks.

5.1. Introduction

Non-human primates comprise the most intensively studied order of mammals. Many species traits in tropical forest primates — including their diurnal habits, arboreality, tolerance of habituation by human observers, and relatively cohesive social groups occupying stable home ranges — render them highly amenable to long-term observational field studies. This has predisposed diurnal primates to the continuous close scrutiny of field observers worldwide (Kappeler & Watts 2012), both in the Paleotropics (Whitehead & Jolly 2000) and the Neotropics (Garber et al. 2009). Field research effort on non-human primate populations has concentrated on various aspects of primate social behaviour (Smuts et al. 1987, Strier 2010) and ecology, with noticeable attention paid to their diets and feeding ecology (Clutton-Brock 1977, Hohmann et al. 2006). This compares favourably to other highly observable, charismatic, and well-studied vertebrate taxa, such as birds, where high levels of observation effort have not necessarily focused on detailed data acquisition on their trophic ecology.

The distribution of this impressive observation effort by primatologists is highly unequal, however, both in terms of the geographic and taxonomic focus of studies, as previously reported for field botanists (Nelson 1994) and ornithologists (Reddy & Davalos 2003). Data on primate behavioural ecology appear heavily skewed towards certain species, particularly at a few well-studied localities, yet consideration of the impact of these biases remains conspicuously absent in the literature. For example, reviews of primate feeding ecology have glossed over variation in sampling effort to provide broad and simplified overviews of diets (National Research Council 2003) or are restricted to summaries of the nutritional benefits of different dietary profiles (Felton et al. 2009). Yet it is critically important to account for such incomplete datasets in community ecology (Kodric-Brown & Brown 1993), and to clearly appreciate their inherent sampling biases. In the case of feeding ecology, this approach can help identify the ecological requirements of poorly studied threatened species and encourage a more integrated understanding of complex feeding networks. For example, geographic and taxonomic gaps in our knowledge of primate feeding ecology may severely affect which species can be defined as important hubs or connectors in interaction networks (Olesen et al. 2007).

To compare the relative effort employed by primatologists, in terms of both its spatial and taxonomic distribution, requires a standardised unit of study effort. Comparative analyses to date has been problematic, particularly due to the inconsistent nature of reporting effort; feeding studies varyingly report the number of contact or feeding hours, the number of feeding bouts, the number of food items or food species consumed, the number of observations or group scans, or merely the total duration of a study (e.g. number of days or months). In addition, sampling effort in some primate dietary studies is quantified only indirectly, for example by the number of faecal samples collected or stomach contents analysed. This disconcerting diversity of quantitative metrics clearly stems, at least in part, from the variety of methods employed by field primatologists to provide different insights into primate feeding ecology (Dew 2003), comprising both direct observations and alternative techniques.

The most common methodology in orthodox primate field studies is to monitor a study group that has been previously habituated to observers, recording the food items observed during feeding bouts, usually over ‘dawn-to-dusk’ group follows. Additional sources of dietary observations are often derived from systematic vigils of key food trees visited by primates, and brief, opportunistic observations during the course of line-transect surveys or other fieldwork. Systematic observations during ‘group follows’ and ‘tree vigils’ typically use focal-animal (continuous or instantaneous) or all-animal (usually scans) observational sampling (Altmann 1974, Lehner 1996), whereas population censuses and other opportunistic encounters tend to record any feeding observations *ad libitum*. Alternative methods (including examination of stomach contents of specimens killed by hunters and museum collectors, and analyses of faecal samples) are either used independently or to supplement direct observations. Finally, an important contribution to our understanding of primate diets comes from indirect evidence based on reliable signs of specialized feeding activity (e.g. inspection of holes gouged into tree trunks, exploited for exudates), but more frequently via interviews with local informants, often highly experienced hunters (e.g. Voss & Fleck 2011).

All these methods have been used by primate dietary studies in the Neotropics, the biogeographic domain containing the largest remaining tracts of tropical forest and the highest primate species richness worldwide (Rylands & Mittermeier 2009). Primate studies have recently been summarised for each country in Mesoamerica (Estrada et al. 2006) and South America (Garber et al. 2009), but with a limited focus on feeding ecology. Within the Neotropics, detailed dietary data have been reviewed for a restricted number of taxa within smaller subregions (e.g. *Ateles* in Mesoamerica: González-Zamora et al. 2009; Atelines: Peres 1994a). However, a comprehensive quantitative review of primate diets across the entire neotropical region — building on earlier anecdotal attempts to review dietary information (Coimbra-Filho & Mittermeier 1981, Mittermeier et al. 1988) — is still required. In particular, it is important to compile data on a wide range of plant species in order to understand the close relationships between primates and plants, and the degree to which diets overlap among both sympatric taxa sharing the same flora and ecologically equivalent taxa that may not.

The geographic distribution of extant neotropical primates spans from southern Mexico to northern Argentina, but some genera are much more widely distributed than others. For example, the range of howler monkeys (*Alouatta*) extends across the entire distribution of neotropical primates (Peres 1997). At the other extreme, woolly spider monkeys (*Brachyteles*) and lion tamarins (*Leontopithecus*) are endemic genera to remnant fragments of the Brazilian Atlantic Forest, following a vast reduction of their historical geographic ranges (Pinto & Rylands 1997, Kierulff & Rylands 2003, Cunha et al. 2009). This results in marked variation in the spatial availability of any given taxon for potential studies, with wide-ranging and relatively abundant taxa much more likely to occur at any given study site (Peres & Janson 1999). This variation in geographic availability could clearly contribute to biases in the study effort logged by primatologists towards different species, although other traits such as body size, behaviour and conservation status, and directed financial resources may also render some species more or less amenable or attractive to study.

The distribution of primates may also influence the spatial variation in aggregate study effort by all primatologists. Neotropical primates are markedly arboreal and thus generally restricted to closed-canopy forest habitat, although some species persist in forest fragments and tolerate close proximity to human populations (Cristóbal-Azkarate & Arroyo-Rodríguez 2007). Primate species richness varies substantially in relation to continental scale variation in environmental factors such as forest cover and total rainfall, peaking at mid latitudes in western Amazonian forest sites with up to 14 sympatric species (Peres & Janson 1999). However, few primate diet studies cover the entire species assemblage coexisting at any given site and logistical considerations, such as accessibility (Schulman et al. 2007), undoubtedly affect study site selection criteria.

Here, we provide a quantitative review of the geographic and taxonomic distribution of ecological sampling effort allocated to wild primate populations across the New World tropics, which contain the world's most diverse primate fauna (140 species in 19 genera: IUCN 2011). By standardising existing metrics of sampling effort in primate feeding studies conducted using a variety of techniques, we aim to highlight the inherent discrepancies and poor comparability in the distribution of feeding ecology sampling effort accumulated over decades by field primatologists. We then examine the main factors that drive the selectivity of study sites and study species. Finally, we inform future research agendas by pinpointing the most conspicuous knowledge gaps in terms of severely undersampled taxa and regions.

5.2. Methods

5.2.1. Data compilation

We performed a comprehensive literature review of all published and unpublished sources of neotropical primate diet studies reporting primate-plant feeding interactions in natural settings. We therefore exclude all captive and semi-free ranging primate populations. Individual studies are defined as a survey effort covering a single or multiple primate species over a discrete sampling period at a single study site. For each study we recorded the primate species, geographic coordinates of the study site, observation methods used, and the total sampling effort realised.

Our literature review of neotropical primate studies reporting primate-plant feeding interactions, returned 423 references for consideration spanning 42 years (1969 - 2011). These references comprised published sources (336 peer-reviewed articles, 30 book sections), grey literature (36 dissertations, 15 reports, 3 conference proceedings), and three additional datasets (C.A. Peres, unpubl. data, M. van Roosmalen, unpubl. data, TEAM 2011). This excludes unsubstantiated references to feeding interactions and reviews of multiple sources where original sources were otherwise available. Of these sources, 92 represented multiple publications based partly or entirely on a single original dataset, resulting in a final set of 331 unique references, corresponding to 289 individual studies using a variety of field methods (Table 5.1).

Table 5.1. *Summary of references included and field methods employed in this review of neotropical primate diet studies.*

Type	Method	Total references considered	Unique references included	Studies
Observations	Group follow	313	332	206
	Tree vigil	34	30	29
	Transects	26	22	21
	Opportunistic	38	36	35
	Total observations	408	317	274
Alternative	Local knowledge	8	6	5
	Stomach contents	7	7	9
	Faecal samples	33	23	25
	Tree examination	2	1	1
	Total alternative	48	35	38
Total		423	331	289

The final reference compilation reported on the plant diets of 24 functional groups (or ‘ecospecies’) belonging to 17 neotropical primate genera (Table 5.2), from 163 study sites across 17 neotropical countries (Figure 5.1; Table 5.3). A full list of references, studies and study sites are available from the authors upon request.

5.2.2. Standardised sampling effort

Sampling effort was calculated by standardising different observation methods and metrics of observation effort. To achieve this, we assumed a 10-min opportunistic observation bout per group encounter during multi-species line-transect surveys, and 3 h of observations per faecal sample or examination of digesta (e.g. in seed-dispersal and stomach content studies), based on the approximate mean gut passage time across all species. Where study effort in terms of sampling time was not reported directly for group follows, effort could be calculated from the number of scan samples obtained or estimated from the number of days or months of study based on the typical daily/monthly effort of comparable studies, accounting for the total dawn-to-dusk activity period of different primate species. Where only the number of feeding

Table 5.2. *Key traits of neotropical primate ecospecies and taxonomic distribution of effort in feeding ecology studies.*

Code	Functional ecospecies	Activity	Body mass (kg) [a]	Range (km^2) [b]	Countries	Sites [c]	Studies [c]	References [c]	Months [d]	Hours [d]	Site density (per 1,000,000 km^2)
Al	Howler monkeys	Diurnal	6.32	13095330	15	74	108	151	893	47236.5	5.65
At	Spider monkeys	Diurnal	8.56	6784000	13	29	44	71	419	18328.3	4.27
Br	Woolly spider monkeys	Diurnal	8.84	267800	1	5	9	11	83	3643.5	18.67
La	Woolly monkeys	Diurnal	8.46	3351007	4	11	16	29	185	8714.7	3.28
Cf	White-fronted capuchins	Diurnal	2.92	4057250	7	17	30	34	149	21291.6	4.19
Ca	Brown capuchins	Diurnal	3.09	11193082	8	40	50	64	412	13152.5	3.57
Co	Wedge-capped capuchins	Diurnal	2.91	1944175	3	4	4	6	45	1424.5	2.06
Sa	Squirrel monkeys	Diurnal	0.81	6417552	5	15	19	21	146	4956.3	2.34
Sf	Saddle-back tamarins	Diurnal	0.51	2436081	4	12	18	39	169	13585.1	4.93
Sx	Moustached tamarins	Diurnal	0.50	827714	3	8	13	29	115	12297.5	9.67
Sm	Midas tamarins	Diurnal	0.55	1574740	3	8	8	11	36	568.1	5.08
So	Bare-faced tamarins	Diurnal	0.44	216323	3	6	6	8	27	2033.3	27.74
Cx	Atlantic marmosets	Diurnal	0.37	2745620	1	14	22	20	162	6540.7	5.10
Mi	Amazonian marmosets	Diurnal	0.38	1256621	1	3	4	6	26	1868.4	2.39
Cb	Pygmy marmosets	Diurnal	0.12	1579650	4	6	6	9	63	3351.5	3.80
Le	Lion tamarins	Diurnal	0.58	85208	1	4	8	10	81	12244.9	46.94
Cg	Goeldi's monkeys	Diurnal	0.48	2745620	1	2	4	7	32	2505.5	0.73
Pi	Saki monkeys	Diurnal	2.31	3677870	5	12	17	26	182	6208.8	3.26

cont.

Table 5.2. cont.

Code	Functional ecospecies	Activity	Body mass (kg) [a]	Range (km^2) [b]	Countries	Sites [c]	Studies [c]	References [c]	Months [d]	Hours [d]	Site density (per 1,000,000 km^2)
Ch	Bearded saki monkeys	Diurnal	2.86	3006600	3	10	18	24	139	5124.0	3.33
Cj	Uakaries	Diurnal	3.05	764586	3	8	9	18	68	1881.7	10.46
Cm	Amazonian dusky titi monkeys	Diurnal	0.96	3741840	4	7	8	10	32	1272.3	1.87
Cp	Atlantic dusky titi monkeys	Diurnal	1.33	896493	1	4	6	8	44	2649.5	4.46
Ct	Collared titi monkeys	Diurnal	1.25	1752351	3	4	4	6	25	750.3	2.28
Ao	Night monkeys	Nocturnal	0.93	7711498	5	11	12	14	47	1661.3	1.43
					17	163	289	423	3579	193291.0	

[a] Source: Smith & Jungers (1997)

[b] Source: Patterson et al. (2007)

[c] All sites, studies, and references, including duplicate references and sites/studies with only tree vigils or local knowledge.

[d] Total excluding effort from tree vigils and local knowledge.

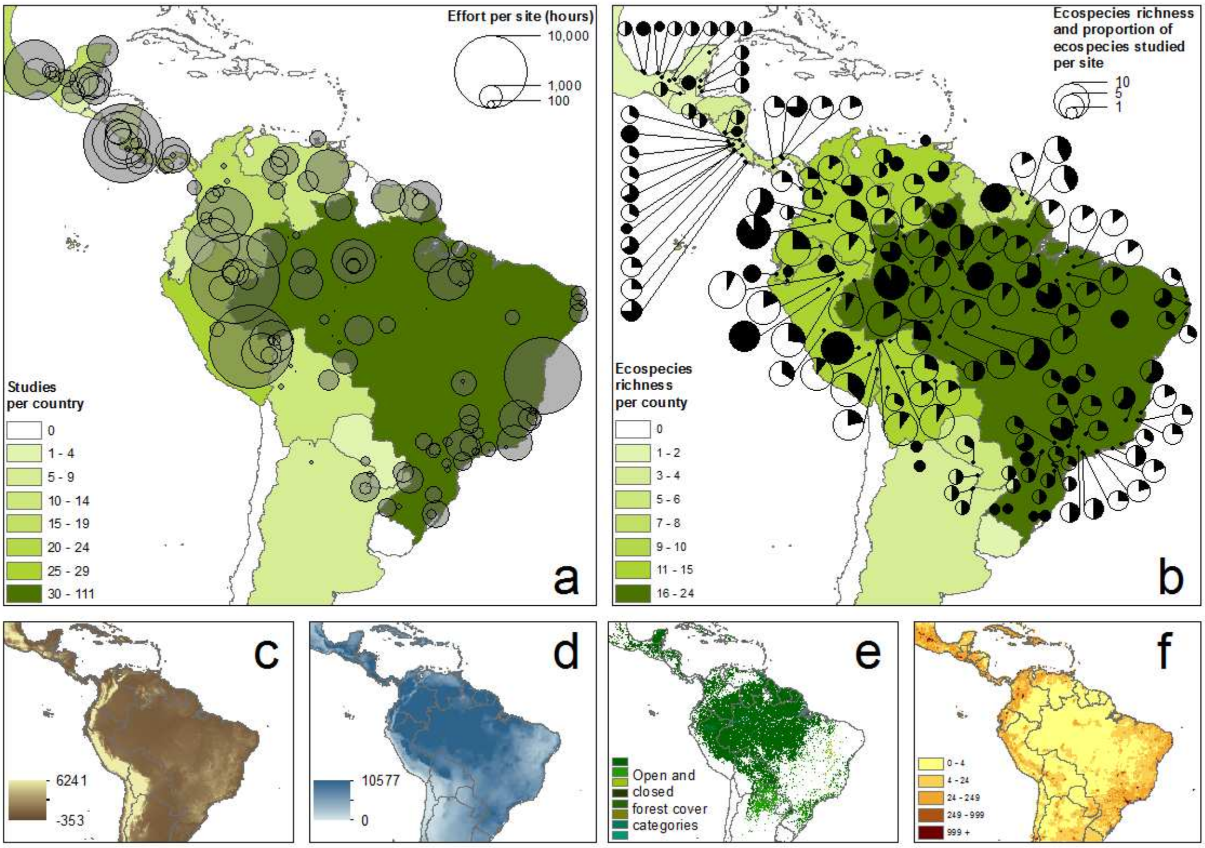


Figure 5.1. *Map of primate diet studies at 148 field sites across 17 neotropical countries showing (a) sampling effort (circle size represents effort per site (hours), country colour represents number of studies per country) and (b) ecospecies richness (circle size represents ecospecies richness, shading represents proportion of ecospecies studied, country colour represents ecospecies richness per country). Smaller maps show (c) elevation above sea level (m), (d) total annual precipitation (mm), (e) distribution of forest cover and (f) human population density (persons per km^2)*

Table 5.3. *Occurrence of primate ecospecies across neotropical regions and countries, and distribution of effort in feeding ecology studies. Dark grey and light grey shading represents ecospecies studied and resident ecospecies that are yet to be studied within that country, respectively.*

Code	Country	Sites [a]	Studies [a]	Refs [a]	Months [b]	Hours [b]	Al	At	Br	La	Cf	Ca	Co	Sa	Sf	Sx	Sm	So	Cx	Mi	Cb	Le	Cg	Pi	Ch	Cj	Cm	Cp	Ct	Ao	ER [c]	ES [c]	PS [c]
Mesoamerica																																	
BZ	Belize	3	6	7	61	5795	•	░																							2	1	0.5
CR	Costa Rica	11	22	29	208	26140	•	•			•			•																	4	4	1
SV	El Salvador	2	2	3	6	12	•	•																							2	2	1
GT	Guatemala	1	2	3	16	1728	•	•																							2	2	1
HN	Honduras						░	░			░																				3	0	0
MX	Mexico	9	17	28	238	13101	•	•																							2	2	1
NI	Nicaragua	3	4	6	32	2649	•	░			•																				3	2	0.67
PA	Panama	4	13	15	58	4033	•	•			•			░				•												░	6	4	0.67
Amazon																																	
BO	Bolivia	9	13	20	131	7270	•	•		░	•	•		░	•	•				░			•	░			•			░	13	8	0.62
BR	Brazil	28	47	75	522	21650	•	•		•	•	•	•	•	•	•	•	•		•	•		░	•	•	•	•		•	•	20	19	0.95
CO	Colombia	12	19	30	390	12539	•	•		•	•			•	•			•			•		░	•		•	░		•	•	14	12	0.86
EC	Ecuador	3	7	8	92	7249	░	•		•		•		░	░						•			░			•		░	░	11	5	0.45
FG	F. Guiana	5	7	15	117	4223	•	•				•	░	░			•							░	░				░	░	8	4	0.5
PE	Peru	14	29	64	619	38320	•	•		•	•	•		•	•	•					•		░	•		•	•		•	•	15	14	0.93
SR	Suriname	2	4	14	134	2226	•	•				•	•	•			•							•	•						8	8	1
VE	Venezuela	7	14	17	172	8913	•	•			░	•	•	░										•	•	•			░	░	11	7	0.64
GY	Guyana						░	░				░	░	░			░							░	░						8	0	0
TT	Trin. & Tob.						░				░																				2	0	0

cont.

Table 5.3. cont.

Code	Country	Sites[a]	Studies[a]	Refs[a]	Months[b]	Hours[b]	Al	At	Br	La	Cf	Ca	Co	Sa	Sf	Sx	Sm	So	Cx	Mi	Cb	Le	Cg	Pi	Ch	Cj	Cm	Cp	Ct	Ao	ER[c]	ES[c]	PS[c]
Atlantic																																	
AR	Argentina	8	10	11	74	4341	•					•																		•	3	3	1
BR	Brazil	41	72	85	706	32863	•		•			•							•			•						•			6	6	1
PY	Paraguay	1	1	1	4	240	░					░								░							░			•	5	1	0.2
UY	Uruguay						?																								1?	0	0
N/A																																	
CH	Chile[d]																														0	0	0
	Brazil	69	119	160	1228	54513	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	░	•	•	•	•	•	•	•	24	23	0.96
	Mesoamerica	33	66	91	619	53457	•	•			•			•				•												•	6	5	0.83
	Amazon	80	140	243	2177	102390	•	•		•	•	•	•	•	•	•	•	•		•	•		•	•	•	•	•		•	•	20	20	1
	Atlantic	50	83	97	784	37444	•		•			•							•	•		•					•	•		•	9	7	0.78
Total		163	289	423	3579	193291	21 17	17 13	1 1	5 4	10 7	11 9	5 3	11 5	5 4	3 3	4 3	3 3	1 1	3 1	4 4	1 1	4 1	9 5	5 3	4 4	6 4	1 1	5 3	9 5	24	24	1

[a] All sites, studies, and references, including duplicate references and sites/studies with only tree vigils or local knowledge.

[b] Total excluding effort from tree vigils and local knowledge.

[c] ER = Ecospecies richness, ES = Ecospecies studied, PS = Proportion studied.

[d] Chile falls outside the range of neotropical primates.

observations or feeding bouts was reported, we derived approximations of study effort on the basis of comparable studies. In this manner, despite the wide range of observation methods and the inconsistent reporting of study effort, we were able to standardise sampling effort in terms of observation time (hours) across 91.0% (263/289) of studies. In addition to observation time, we also recorded the duration of each study (months) and the proportion of the annual cycle covered by the study.

5.2.3. Taxonomy

The alpha-taxonomy of neotropical primates (Parvorder Platyrrhini: New World monkeys) is not universally agreed upon. Several taxonomic arrangements are proposed on the basis of distribution and behaviour (Rylands & Mittermeier 2009), genetics (Wildman et al. 2009), and morphology (Rosenberger 2011). The general consensus, however, is of a monophyletic group of approximately 140 extant species (IUCN 2011) belonging to 16 to 19 genera. Despite recent trends towards taxonomic inflation, Rosenberger (2011) sees no justification for splitting *Oreonax* from *Lagothrix*, *Callibella* from *Cebuella*, or *Mico* from *Callithrix*. Uncertainty also remains surrounding the placement of *Aotus*, variously assigned to Pithecidae or its own family, Aotidae. Since we are primarily interested in functional diversity we use an updated version of Peres & Janson's (1999) functional classification, which recognises 24 species groups, hereafter 'ecospecies' (Appendix 1). These generally correspond to genus level taxonomy (Rosenberger 2011), with the exception of *Callicebus*, *Cebus* and *Saguinus*, where we recognise multiple ecospecies based on the degree of intra-genus ecological divergence; indeed, only these genera exhibit sympatric congeners coexisting in stable assemblages. In addition, we consider Atlantic Forest populations separately from Amazonian populations to enable comparisons of ecological analogues in different geographic regions (i.e. distinguishing the marmoset genera *Mico* from *Callithrix*, and the titi monkey *Callicebus personatus* group from other *Callicebus spp.*). For each ecospecies we compiled data on mean adult body mass (Smith & Jungers 1997), total geographic range size (from NatureServe and IUCN polygons: Patterson et al. 2007, IUCN 2011), and mean extinction risk [based on the IUCN Red List status per species (LC=1, NT=2, VU=3, EN=4, CR=5): Purvis et al. 2000, Mace et al. 2008).

5.2.4. Geography

Site locations were recorded by extracting geographic coordinates from publications or, where these were missing, by estimates from other available mapping resources, including Google Earth. Sites were assigned into one of three broad regions containing distinct assemblages of both primates and plants: (1) Amazonia, including the WWF ecoregions of the Andes, Choco, and Llanos (Olson et al. 2001); (2) the Atlantic region, including the Atlantic Forest, Caatinga, Cerrado, Chaco, and Pantanal; and (3) Mesoamerica. The total number of primate ecospecies co-occurring at each site (i.e. the potential species richness available to be studied) was calculated from NatureServe range distributions (Patterson et al. 2007), incorporating necessary adjustments due to inaccuracies in range polygons (Palminteri et al. 2011). We were thus able to estimate the total number and proportion of ecospecies studied at each site. Using threat status scores per ecospecies, we also calculated a mean threat value per site, as a metric of potential level of assemblage-wide conservation concern.

Finally, we used a geographic information system (GIS) to extract values within 100-km buffers around each site for the following variables: mean human population density (GPW v3: CIESIN/CIAT 2005), degree of forest cover (GlobCover: ESA 2008/Arino et al. 2008), mean elevation (masl), standard deviation of elevation, and climatic data including total annual rainfall (mm) and mean annual temperature (WorldClim: Hijmans et al. 2005). We performed the buffer analysis at distances of 10, 25, 50, 100, and 250 km, using the Hawth’s Tools extension (Beyer 2004) within ArcGIS 9.2. Extracted values for each variable were strongly positively correlated across buffer distances so we used only those values from 100-km buffers in all further analyses.

5.2.5. Data analyses

We used generalized linear models (GLM) to assess the distribution of sampling effort across the 148 study sites with known geographic coordinates and standardised effort (hours). We relate variation in study effort to the biophysical and climatic variables extracted within 100-km buffers for each study, in addition to the primate species richness and an aggregate score of IUCN conservation threat for all species co-occurring at each site. Finally, country identity was included as a categorical variable. All analyses were conducted in R (R Development Core Team, 2010).

5.3. Results

5.3.1. Standardised sampling effort

The vast majority of primate diet studies we reviewed consisted of direct observations, mainly via systematic group follows (Table 5.1). The remainder of direct dietary observations consisted of vigils of focal trees, transect walks, and other opportunistic observations. In addition, a small number of studies provided diet information through alternative methods including analyses of stomach contents or faecal samples, collation of local informants' knowledge, and examination of tree trunks for evidence of exudate consumption. Compiling data from all studies to date across all ecospecies at all sites — and standardising to account for variable methods — yielded a cumulative sampling effort on neotropical primate diets equivalent to 193,291 h of observation.

Regardless of this volume of sampling effort, most sites have been severely under-sampled in terms of the proportion of coexisting taxa studied at each site, with only a few notable exceptions (e.g. Cocha Cashu, Peru; Pacaya-Samiria, Peru; Raleighvallen-Voltzberg, Suriname; and Urucu, Brazil) (Figure 5.1b). The vast majority of sites have only hosted a diet study on a single primate ecospecies despite the far higher species-richness of most assemblages (57% of study sites had at least four species and only <8% had a single species) (Figure 5.2). Although less pronounced, there are similar patterns at a national level; many countries have failed to study their entire primate fauna and most ecospecies are yet to be studied across all countries in which they occur (Table 5.3). In addition to widespread species undersampling in many countries and most local assemblages, the available sampling effort has been distributed very unevenly, both across primate taxa and neotropical regions (Tables 5.2-5.3).

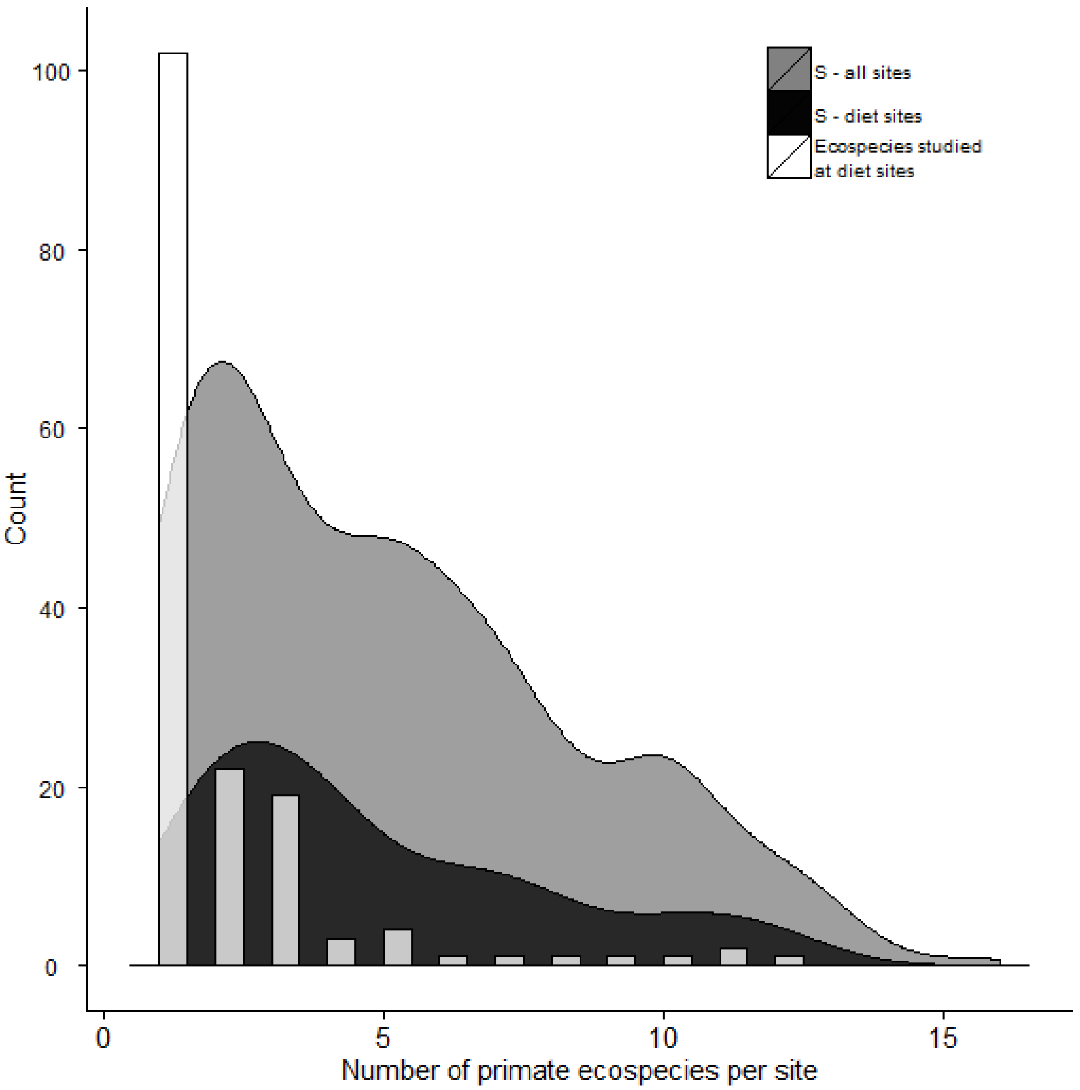


Figure 5.2. *Frequency of observed ecospecies in primate diet studies at 158 neotropical sites (white bars), in relation to true primate species richness at those sites (dark shading), and to all 490 neotropical sites including at least one primate species for which species richness is known (light shading; C.A. Peres, unpublished data).*

5.3.2. Taxonomic distribution of sampling effort

There is a clear bias in sampling effort towards large-bodied species (i.e. the Atelidae, and howler monkeys in particular), followed by Cebinae (white-fronted and brown capuchins) and Callitrichinae (saddle-back and moustached tamarins) (Figure 5.3a). This bias is apparent in both the number of sites where primate diets have been investigated, and the total amount of time effort allocated. In contrast, other ecospecies that are now restricted to a small portion of their former ranges such as lion tamarins

(*Leontopithecus*) have been heavily studied at few sites in comparison to night monkeys (*Aotus*), for example, which have received very little attention throughout their vast geographic range (Figure 5.3c). Adjusting for differences in geographic range size of each ecospecies, highlights the relatively intensive effort on Goeldi's monkeys (*Callimico goeldii*) and, conversely, the low effort allocated to midas tamarins and collared titi monkeys, for example (Figure 5.3e).

There was a weak positive effect of both geographic range size and mean body mass on sampling effort per ecospecies (Figure 5.4), with broadly distributed ecospecies receiving greater attention than range-restricted ecospecies ($R^2 = 0.08$, $p = 0.184$) and large-bodied ecospecies receiving greater attention than small-bodied ecospecies ($R^2 = 0.08$, $p = 0.186$). However, body mass and geographic range size are also positively related ($R^2 = 0.08$, $p = 0.187$). The mean threat score per species based on the IUCN Red List status was apparently unrelated to the amount of sampling effort per ecospecies ($R^2 = 0.002$, $p = 0.823$).

5.3.3. Geographic distribution of sampling effort

In terms of spatial distribution of sampling effort, the broad pattern shows comparable levels in each of the three major neotropical regions (Amazonia, Atlantic and Mesoamerica), with particularly large total effort allocated to Brazil, Peru and Costa Rica (Figure 5.3b). Brazil is unique in encompassing large amounts of primate habitats in both the Amazon and the Atlantic Forest regions, although the amount of effort per site is lower throughout Brazil than in either Peru or Costa Rica (Figure 5.3d). Adjusting for country area emphasises the relatively intensive sampling effort in Costa Rica, Belize, Peru, Ecuador and Suriname, especially in comparison to severely understudied El Salvador and Paraguay (Figure 5.3f). Four countries in tropical South America (excluding Chile, where nonhuman primates do not occur) and Mesoamerica had no primate diet studies, namely Guyana, Honduras, Trinidad and Tobago (populations of *Alouatta* and *Cebus albifrons*), and Uruguay (unconfirmed population of *Alouatta*: Villalba et al. 1995).

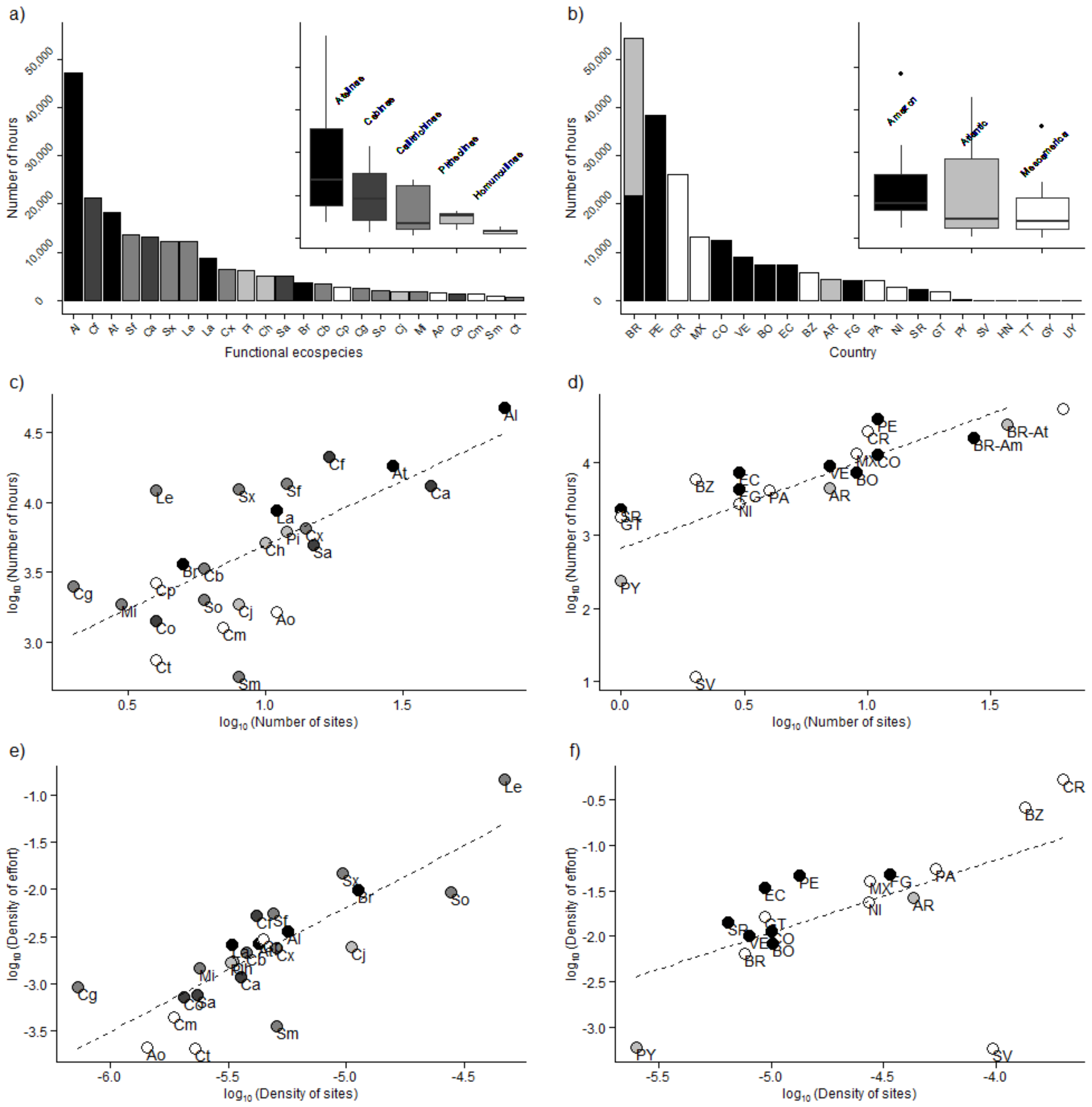


Figure 5.3. *Sampling effort in neotropical primate dietary studies (a) per ecospecies and (b) for different countries. Scatter plots show the relationship between the number of sites surveyed and total hours effort by (c) ecospecies and (d) country, and the analogous relationship adjusted by (e) ecospecies geographic range size and (f) country area including the range of at least one primate species. Grey shading represents (a,c,e) taxonomic subfamily and (b,d,f) geographic subregion according to insets in (a) and (b). Ecospecies and country codes correspond to Tables 5.2 and 5.3, respectively. Dashed lines represent linear regressions.*

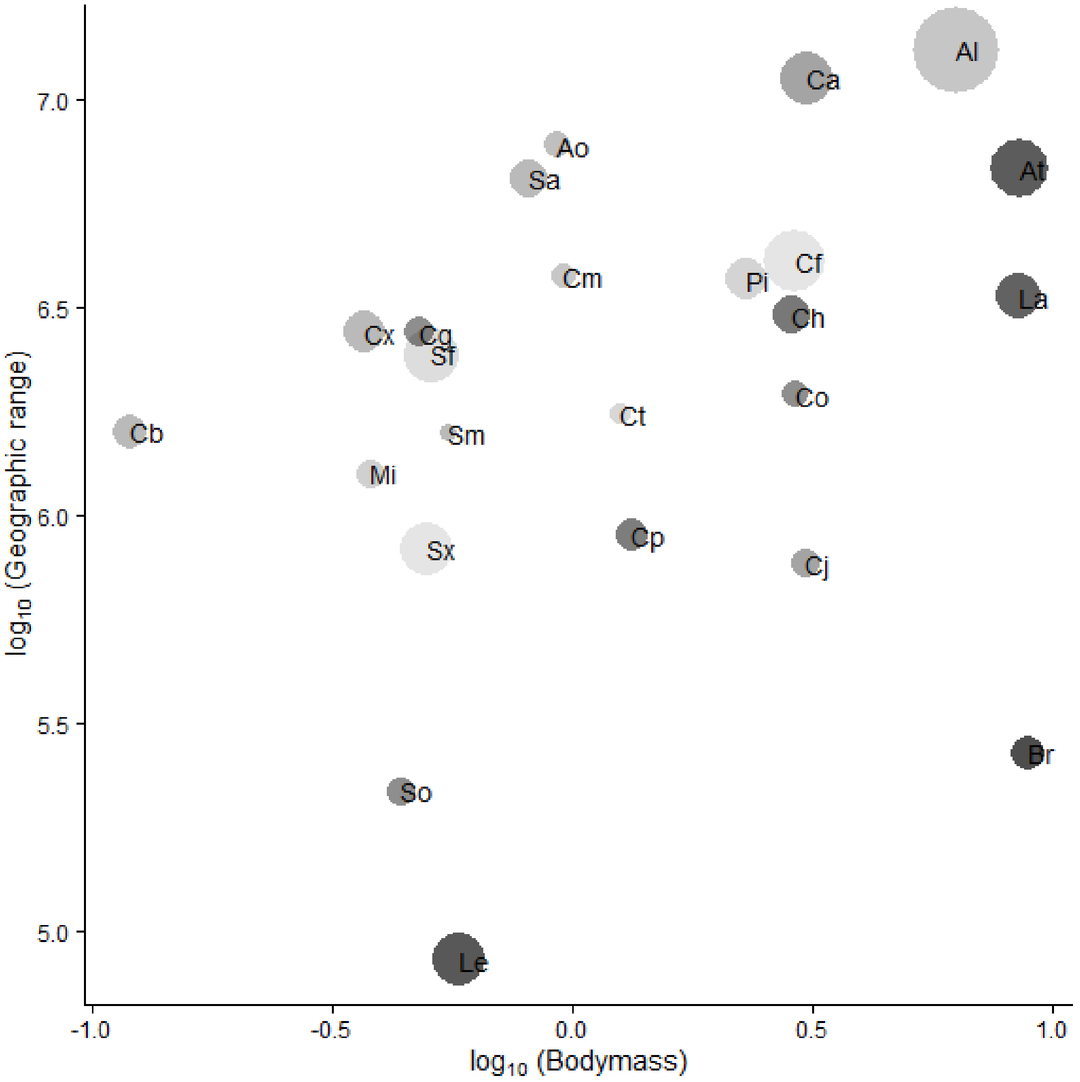


Figure 5.4. *Distribution of sampling effort (hours), represented by circle area, in relation to geographic range size and mean body mass per neotropical primate ecospecies. Degree of grey shading represents the mean conservation threat score per ecospecies, based on the IUCN Red List status per species (Appendix 2).*

The spatial distribution of effort is also highly uneven when considered in more detail at the locality scale (Figure 5.1a). Most sampling effort has been heavily skewed to relatively few sites (e.g. Quebrada Blanca, Peru; Cocha Cashu, Peru; Lomas Barbudal, Costa Rica; Lemos Maia, Brazil; and Los Tuxtlas, Mexico), with most sites elsewhere experiencing relatively low effort. Broad gaps in study effort are obvious in vegetation biomes lacking large areas of closed-canopy forest cover, such as the Brazilian *cerrado* and *pantanal* and the Bolivian and Paraguayan *chaco* (Figure 5.1e). However, there is also a low density of study sites and relatively low total effort right across the Brazilian Amazon, compared to a high density of sites in highly fragmented forest landscapes of Mesoamerica and the Brazilian Atlantic Forest, which are densely settled and benefit from improved accessibility (Figure 5.1f).

GLM modelling, used to examine the amount of research effort (expressed as the $\log_{10}$ hour-equivalent) allocated across the 148 neotropical forest sites for which both effort and geographic coordinates were available, indicates that mean human population density within a 100-km radius had a significant positive effect on research effort ($p = 0.0463$), whereby more heavily-settled regions were better investigated. High elevation, however, was a significant inhibitor of research effort ($p = 0.0126$), and country identity also had a significant effect ($p = 0.0313$). Surprisingly, the richness of primate species ($p = 0.6375$), the aggregate IUCN conservation status of those species ($p = 0.3764$), and landscape-scale degree of forest cover ($p = 0.2337$) had little or no effect on the overall distribution of research effort.

5.4. Discussion

This study provides a timely summary of the highly skewed sampling effort conducted by field primatologists in documenting neotropical primate diets. This represents the first large-scale assessment of the cumulative sampling effort allocated to primate feeding ecology anywhere, which is critical in identifying knowledge gaps in terms of severely undersampled taxa and geographic regions. In particular, we highlight some key emergent patterns: (1) Almost all study sites have been hugely undersampled in terms of the proportion of co-occurring primate taxa; (2) The taxonomic distribution of effort has generally been skewed towards large-bodied species occupying large geographic ranges; (3) The geographic distribution of effort allocated by both habitat-country and expatriate primatologists has been concentrated at relatively few ‘primatology hubs’ in specific regions, particularly in Costa Rica, southeastern Peru and the Brazilian Atlantic Forest.

5.4.1. Severe undersampling of primate assemblages

Only a tiny minority of sites have had the diet of their entire resident primate assemblage investigated, even to a minimal degree. This is illustrated by the small number of synecological dietary studies successfully conducted to date, notably in Cocha Cashu, Peru (Terborgh 1983), Pacaya-Samiria, Peru (Soini 1986), Raleighvallen-Voltzberg, Suriname (Mittermeier & van Roosmalen 1981), and Urucu, Brazil (Peres 1994b). Conversely, most sites have only hosted a single or a few autoecological studies, meaning that any comparative analyses of dietary composition would rest on cross-site comparisons, which are plagued by potential compositional differences in plant communities and food sources available. Primate species richness is highest at mid-latitudes and especially in the western Amazon (Peres & Janson 1999), suggesting that primate assemblages in this region are frequently less well studied proportionately. Beyond this pattern of community-level undersampling across virtually all studies, there are also conspicuous gaps amongst certain primate ecospecies and in certain regions.

5.4.2. Taxonomic biases

Both the extent of geographic ranges and body size explain to a limited degree the amount of sampling effort received by neotropical primate ecospecies, although the relationships were weak and other factors likely affect the spatial distribution of research effort by primatologists. Larger geographic ranges clearly increase the spatial availability of a species in different regions, and larger species often attract more attention and research funding than smaller species (Martín-López et al. 2009). However, these factors are not independent of each other, as large-bodied ecospecies are frequently associated with large geographic ranges (Gaston & Blackburn 1996).

The overwhelming focus of dietary studies on howler monkeys (*Alouatta*), which accounts for 37.4% of all studies and 24.4% of the aggregate observation effort, seems best explained by a combination of these and other factors. Howlers represent one of the largest bodied and occupy by far the largest geographic range of any neotropical primate. They are also forest habitat generalists occurring in both evergreen and deciduous forest and from sea level to cloud forests over 3200 m in elevation (Peres & Janson 1999). In fact, the dominance of howler monkey studies over that of other larger-bodied atelids is best explained by its geographic and ecological distribution. In addition to their large body size and wide distribution, however, howler monkeys are highly amenable to systematic observations in being relatively sedentary, highly folivorous, and consistently exhibiting small spatial requirements, often persisting even in small isolated forest fragments.

Following the Atelidae, cebine primates have received the largest amount of sampling effort, particularly white-fronted and brown capuchins. This can similarly be explained by their ubiquitous distribution and large body size; the smaller effort dedicated to wedge-capped capuchins matches a correspondingly smaller geographic range. Squirrel monkeys (*Saimiri*), however, have been relatively poorly sampled given their wide geographic distribution. In contrast, much more attention to date has been allocated to some Amazonian callitrichids at patchy localities, such as saddle-back tamarins and moustached tamarins, than would be expected in relation to their size and geographic range, perhaps because they provide excellent models for studies of mixed-species groups in primates (Peres 1993). Conversely, other callitrichids have generally experienced lower research effort, with the notable exception of lion tamarins which have been relatively well studied despite their highly restricted contemporary geographic ranges (Rylands et al. 2002). The threat status and accessibility of the few extant populations of lion tamarins has encouraged high research effort, yet similarly threatened woolly-spider monkey populations have not been studied to the same extent, even though they are also endemic to Atlantic Forest remnants (Brito et al. 2008).

In general, pitheciids (tribes Pitheciinae, Callicebini, and Aotini) have been remarkably undersampled in relation to other taxa. Sakis monkeys (*Pithecia*) and bearded saki monkeys (*Chiropotes*) have received the most amount of research attention but even these ecospecies are poorly sampled in relation to their size and relatively large ranges. This is potentially due to observational difficulties posed by the remoteness of extant Amazonian populations, the cryptic behaviour of saki monkeys (Palminteri et al. 2012) and the rapid locomotion of bearded saki monkeys in the highest forest strata (Silva & Ferrari 2009). The ecology of uakaries (*Cacajao*) has been studied even less than other pitheciids (but see Bowler & Bodmer 2011), but this ecospecies is often patchily distributed in relatively inaccessible and poorly studied Amazonian seasonally-flooded forests (Ayres 1986).

Compared with collared titi monkeys and Amazonian dusky titi monkeys, Atlantic Forest titi monkeys have been slightly better sampled, likely because their smaller geographic range is both more accessible and much closer to heavily settled metropolitan areas, and they persist in even small forest fragments. Finally, the total sampling effort dedicated to date to the ecology of night monkeys, is particularly low considering their continental scale distribution from Panama to northern Argentina. This can be easily explained by their nocturnal habits, unique among all primates other than prosimians, which widely discourages research effort from visually oriented observers.

5.4.3. Geographic biases

Spatial variation in sampling effort was best explained by variables relating to the physical accessibility of study sites. In contrast, species-rich sites do not necessarily attract greater attention from primatologists. Sites closer to large urban centers received higher levels of research effort than remote sites in sparsely-settled areas and high-elevation sites were undersampled compared to lowland forests. That we detected no effect from the degree of forest cover within each landscape suggests that vast areas of continuous lowland forest remain severely undersampled in relation to highly fragmented forest landscapes. The effect of country identity emphasises the clear disparities in research effort across international political borders. Belize, Guatemala, Peru and Suriname received relatively high levels of effort per study site. This contrasts with Brazil, the largest neotropical country, which is host to a relatively large number of study sites, although the density of research effort within those sites tends to be low. Within this context, we concentrate primarily on describing the variation in effort between regions, countries and key study sites.

Mesoamerica has long been recognised as the source of most science outputs in modern tropical ecology (Stocks et al. 2008). This general overdominance in ecological sampling is extended at least to some degree to primate field studies despite the relatively species-poor primate fauna north of the Panamanian isthmus. Although most Mesoamerican primate assemblages include only *Alouatta* and *Ateles*, *Aotus* and *Saguinus* extend their much larger South American ranges into Panama, while *Cebus* and *Saimiri* reach slightly farther north at least into Costa Rica. The cumulative sampling effort in relatively affluent Mesoamerican countries, such as Mexico and Costa Rica, is disproportionately large in relation to South America, with only Brazil and Peru surpassing these countries in terms of either number of studies or total observation load. This becomes even more impressive once we consider relative country areas within the distribution of neotropical primates (which excludes only Chile); virtually all Mesoamerican countries have a higher density of study sites than their South American counterparts.

Greater physical accessibility of forest sites to researchers, in combination with stronger investment in ecological research facilities and infrastructure, may contribute to the disproportionately large effort in Mesoamerica. However, the main driver is more likely to be the greater accessibility to North American and European investigators, including easier political access in terms of research permits for expatriate primatologists (Antonelli and Rodriguez 2009). Mexican primate research, traditionally centred primarily at Los Tuxtlas Biological Station, is unique in having produced a strong cadre of Mexican primatologists (Estrada et al. 2006). In contrast, logistical convenience for foreign researchers has been a decisive factor in shaping the spatial distribution of research effort throughout the rest of Mesoamerica (cf. Stocks et al. 2008) and, conversely, inhibiting research in several South American countries.

Within the Amazon region, Peru has hosted by far the greatest sampling effort, although French Guiana has a comparable density of effort, followed by Ecuador, accounting for the relatively small country area within the range of neotropical primates. Again, this is largely explained by sampling effort by researchers from North America and Europe (Pitman et al. 2011). In contrast, while over 20,000 hours of effort have been invested in primate diet studies across the Brazilian Amazon, the density of both study sites and research effort across this vast inaccessible region are relatively low. Moreover, this is considerably less than the total research effort allocated to Peru, even though Peruvian Amazonia is only ~16% the size of Brazilian Amazonia. Brazil, like Mexico, has successfully cultured a well developed community of in-country primatologists and a strong tradition in field primatology. However, with the exception of Manaus and Belém, the vast majority of Brazilian academic institutes are based well outside Amazonia.

In contrast, many of these research communities are based in urban centers within the highly fragmented Atlantic Forest, which extends from northeastern Brazil into northern Argentina and western Paraguay. Ease of physical access and close proximity to wild primate populations are clearly attractive to primatologists, corresponding to the high density of study sites and total research effort in this region. The severe threats facing primate habitat in the Atlantic Forest, the imperilled conservation status of many resident primate species (Galetti et al. 2009), and favourable funding allocated to endangered species likely represent additional contributing factors. Conversely, the physical and political inaccessibility and poorly developed research infrastructure of vast forest tracts across the Brazilian Amazon contribute towards a failure to i) encourage field studies by primatologists from other parts of Brazil, ii) attract foreign researchers, or most importantly iii) develop the currently small community of resident Amazonian primatologists. The Amazon region supports both the highest primate richness (Peres & Janson 1999) and the highest plant diversity (ter Steege et al. 2006), emphasizing the severe undersampling of the lowland Amazon (and Brazilian Amazonia in particular) in relation to the rest of the Neotropics, especially in terms of species diets.

In addition to comparing total observation load across countries and regions it is also useful to assess the proportion of ecospecies studied at a country scale. For example, despite a relatively high density of investigation effort, dietary studies in Ecuador and French Guiana have only included around half of their primate ecospecies (Table 5.3). We found no primate dietary studies in Guyana, Honduras and Trinidad & Tobago, whereas only night monkeys had been studied in Paraguay despite the occurrence of four other primate ecospecies (Stallings 1985), including the only *Mico* marmoset species occurring outside Amazonia (Rylands et al. 2009). In terms of taxonomic breakdown, the ecology of night monkeys and squirrel monkeys remain unstudied in almost half of the countries in which they occur, and the diet of the monotypic Goeldi's monkey has only been studied at single site in northern Bolivia (Porter et al. 2007). Although these observations are crude given the varying degree of effort between studies and countries, they complement a more detailed analysis of relative effort and can inform research priorities at a national level.

5.4.4. Data quality and sampling completeness

Data quality is important in addition to data quantity. Study duration is of particular importance in dietary studies, since food sources are ephemeral and highly variable over the course of the year, and even a continuous year-round study will miss food species that become available on a supra-annual basis (Strier & Mendes 2009). The methods used in a study will also affect the findings; indirect methods such as stomach contents and faecal samples are biased towards fruits containing seeds passed intact through digestive tracts, and towards primates that are more likely to ingest whole seeds. However, some food sources are less reliably recorded during direct observations, particularly for certain primates, and indirect methods can therefore provide useful complementary data to systematic observations of habituated groups.

That primate species richness is not a significant predictor of sampling effort emphasizes the point that the full assemblage of primates is rarely studied in its entirety at most individual study sites. This degree of completeness at the site level represents one opportunity to increase effort of undersampled taxa. In addition to encouraging increased effort in the taxonomic and geographic gaps in our current knowledge of primate diets across the Neotropics, we also highlight the importance of reporting complete datasets and accompanying metadata for all studies conducted. In particular, perhaps partly due to inadequate botanical expertise, studies conducted to date have frequently failed to report complete annotated checklists of food species, including plant parts consumed at different times of the year, and the relative importance of these items in the overall diet (for instance, in terms of time spent feeding, number of feeding bouts, and number of food patches). Moreover, a clear description of methods used in feeding ecology studies is critical, and we were surprised by the number of previous studies omitting site co-ordinates and key measures of study effort, including the study dates, the number of months and days of observation, total observation hours, amount of feeding time observed, and number of feeding bouts.

Finally, despite attempting to be as extensive as possible, there may be further studies, particularly from inaccessible grey literature sources and unpublished datasets, which could improve the overall picture presented in this review on what we know about primate feeding ecology in the Neotropics. We would encourage all researchers to contribute such datasets (full plant species diet list including plant parts consumed, and with associated metadata including full details of study sample effort) to a common data library of feeding records even if these studies are not formally published.

5.5. Conclusions

This review represents the first comprehensive assessment of the sampling biases inherent in the aggregate field effort allocated to ecological studies targeting an entire continental scale primate fauna. As the most intensively studied mammalian order, primates provide an unparalleled opportunity to represent the inconsistencies and sampling biases that potentially plague other much less well studied taxa. We focus on feeding ecology studies of New World primates, with the neotropical region representing the highest global levels of both primate richness and plant diversity. By standardising effort across methodologies we were able to compare total sampling effort (in hours between primate taxa and between study sites) across the countries and regions of the Neotropics. In this manner we highlight biases in sampling effort and the resulting geographic and taxonomic gaps in our current knowledge of neotropical primate ecology. We further pinpoint major geographic gaps where it is important to increase the coverage of study sites, and which ecospecies have been most poorly sampled to date. In addition, we highlight the collective failure by primatologists to ensure that the full complement of species co-occurring at any given site are investigated, which could be used to address a wide range of community ecology questions. In practical terms, improving the quality of datasets on full primate assemblages at existing sites is potentially a useful starting point to allow meaningful comparisons of ecological traits such as feeding behaviour.

Although the biases discussed in this review have been poorly considered to date, they remain central to our understanding of the dietary and spatial requirements of non-human primates, especially as they face mounting conservation threats from habitat loss and fragmentation. In a wider context, the variation in sampling effort among neotropical primate ecological studies has serious implications for the degree of completeness in the continental-scale knowledge of the feeding ecology of each species or functional group, and thus for determining the relative importance of primate species as seed dispersal agents in network analyses of feeding interactions. We hope this review will encourage greater consideration of these biases in network studies of both primate and non-primate consumers.

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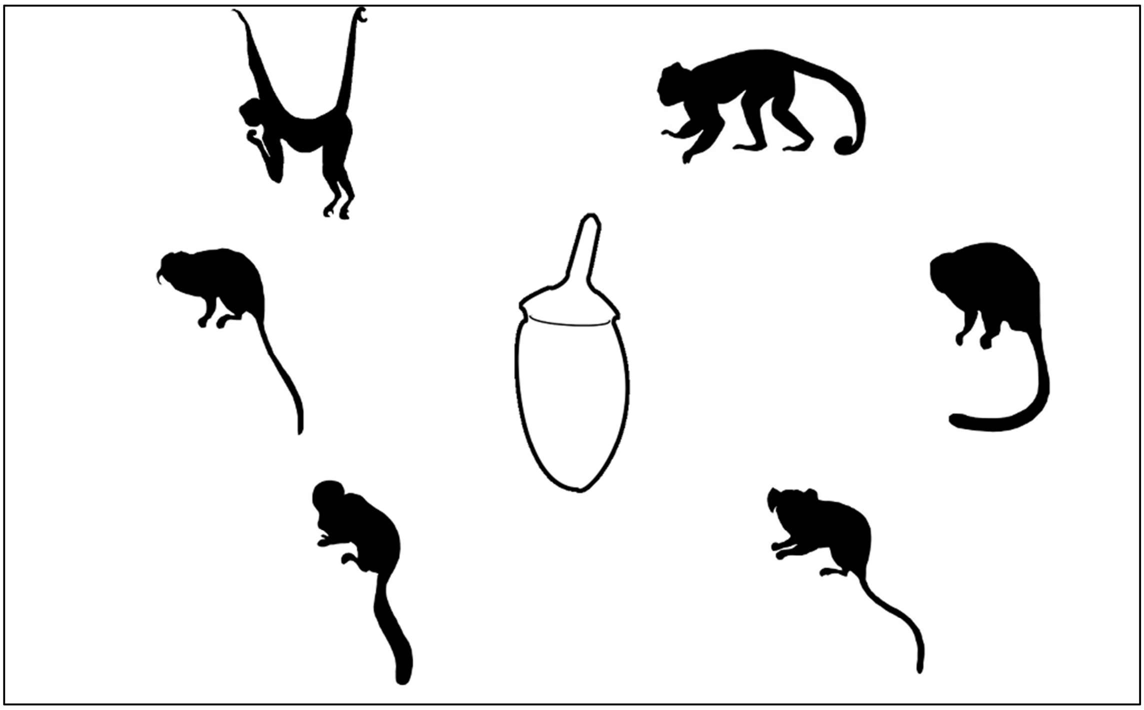
Chapter 6

Frugivory in neotropical primates:

trophic status and ecological correlates



To be submitted to *Oikos* as:

Hawes, J.E., & Peres, C.A. Frugivory in neotropical primates: trophic status and ecological correlates.

Abstract

Primates comprise the most observable and best studied mammalian order in tropical forests, with widespread attention dedicated to the feeding ecology of wild populations. In particular, primates play a key role as frugivores and seed dispersal agents for a myriad of tropical plants. Sampling effort by primatologists, however, has been unequally distributed, hampering quantitative comparisons of primate diets. Here, we provide the first systematic review of primate diets, with an emphasis on frugivory, using a comprehensive compilation of 289 unique primate dietary studies from 163 localities across the entire Neotropics. We account for sampling effort (standardised as hours) in comparing the richness of fruiting plants recorded in primate diets, and the relative contribution of frugivory to the overall diet in relation to key life-history traits, such as body mass. We find strong support for the long-held hypothesis, based on Kay's Threshold, that body size imposes an upper limit on insectivory and a lower limit on folivory, and therefore that frugivory is most important at intermediate body sizes. However, the truncation in the upper body mass limit of extant neotropical primates, induced by the post-Pleistocene megafaunal overkill, has implications for the extent of the frugivory-folivory continuum in extinct lineages. Contemporary threats faced by the largest primates serve as a further warning that the diets of all neotropical primates remain severely undersampled with regard to the richness of fruit consumed. Indeed, frugivorous primates expected to have the most species-rich diets are amongst those most poorly sampled, exposing implications for our understanding of primate-plant interaction networks.

6.1. Introduction

Fruit represents a key dietary resource for most tropical forest vertebrates, and most tropical forest plants depend on fruit-eating vertebrates as seed dispersal vectors (Howe & Smallwood 1982, Fleming 1987). This mutualism, developed over a long evolutionary history, means frugivores are ubiquitous in a wide range of taxa (Smythe 1986, Oleson & Valido 2003, Correa et al. 2007, Muscarella & Fleming 2007), particularly in birds and mammals (Fleming & Kress 2011). Within mammals, frugivory has evolved independently on multiple occasions and is especially well represented amongst prosimians and anthropoids, with most primate families worldwide being moderately to highly frugivorous. New World monkeys (Primates: Platyrrhini) are markedly arboreal, yet inhabit a variety of tropical-subtropical forest habitats, and differ substantially in terms of population dynamics, social organization, and locomotion, in addition to diet (Garber et al. 2009). However, the entire radiation of platyrrhine primates routinely include fruit in their diets, although there is wide variation in the degree of frugivory across taxa, forest types, and geographic regions.

Ecological differences between extant neotropical primates appear to reflect evolutionary changes in body size since the Late Eocene or Early Oligocene arrival of their common Old World ancestor (Fleagle & Christopher 2006), with a predicted body size of ~1kg. Freed from competition with smaller strepsirrhines, New World monkeys diverged in both directions filling most available niches (Ford & Davis 1992), to result in a present-day size range spanning two orders of magnitude (0.12 – 10kg). This contributed significantly to the diverse range of observed life-history traits. Dietary composition, for example, has long been recognised to be influenced by body size (Ford & Davis 1992, Fleagle 1998), with particular respect to protein requirements (Felton et al. 2009a, 2009b). Although fruit are widely consumed in the tropics, they represent a patchy resource in space and time (Fleming et al. 1987, Levey 1988, Herrera 1998), that is typically of poor nutritional value compared to both animal prey (e.g. arthropods) and foliage (Oftedal et al. 1991). Insects provide a high-quality source of nutrients and calories, ideal for the high metabolic requirements of small primates (Kleiber 1947). Large primates require a greater bulk food intake but have lower basal metabolic rates (BMR) and lower energy demands per unit of body mass, thus enabling a diet based on lower energy sources (Fleagle 1998). Moreover, large primates can exploit foliage because of the greater complexity of their larger guts, which can tolerate high levels of (hemi)cellulose and toxins that render this widely available resource either unpalatable or undigestible to smaller primates (Chivers 1994). Large-bodied primates are also rarely able to consume large amounts of arthropods because of either prohibitive pursuit-and-handling time involved in capturing widely dispersed small prey or anatomical and locomotor constraints on arthropod predation (e.g. Terborgh 1983, Peres 1994b). Body size constraints therefore appear to impose both upper limits on insectivory and lower limits on folivory, leading to the proposed dichotomy between frugivore-insectivores and frugivore-folivores (Rosenberger 1992) as predicted by Kay’s Threshold (Kay 1984).

The general profile of most primate diets is relatively well understood, following long-term observational field studies in all tropical land masses (Garber et al. 2009, Kappeler & Watts 2012). However, these studies have been heavily skewed towards certain lineages, typically large-bodied and widely-distributed species (Chapter 5). For example, howler monkeys (*Alouatta* spp.) are by far the best studied neotropical primate genus, having received almost one quarter of the aggregate dietary sampling effort (Chapter 5). Such sampling biases have unforeseen consequences in our understanding of primate diets. While a summary of the overall trophic strategy of a primate species may remain relatively accurate despite a low sample effort, the implications are more severe when considering dietary details. Elementary metrics such as the number of food species consumed by a primate population or the degree of frugivory or folivory of a primate species are greatly affected by the overall distribution of sampling effort.

This is compounded by the highly variable food-species richness (e.g. of fruiting plants) of a primate population, which will depend upon the overall floristic diversity of the surrounding habitat. In addition to taxonomic biases, primate sampling effort is plagued by geographic biases with the distribution of effort concentrated at relatively few sites in specific regions (Chapter 5). For example, a high proportion of the overall effort from neotropical studies have been conducted in Mesoamerica or the Atlantic Forest, which are relatively poor in terms of both woody plant and primate diversity compared to the lowland Amazon. Perhaps more importantly, range-restricted primates have a smaller plant meta-community from which to potentially sample their diets than widespread genera, such as howler monkeys, whose range spans the entire distribution of neotropical primates, from southern Mexico to northern Argentina (Peres 1997). A markedly skewed sampling effort then clearly has implications for any comparative analyses of vertebrate diets, particularly given that more ubiquitous, large-bodied species typically receive the most attention from investigators (Chapter 5).

We first amassed a comprehensive survey of both the dietary data and sampling effort allocated to feeding ecology studies of neotropical primates (Chapter 5). Given a more accurate understanding of the geographic and taxonomic biases inherent in our present knowledge, we are able to examine in more detail how the dietary profiles of all neotropical primates actually diverge, particularly in relation to frugivory. Two orthodox methods have been used to quantify fruit consumption by highly observable frugivores, such as diurnal primates: 1) estimates of the total biomass of fruit consumed, and 2) duration/frequency of fruit feeding bouts as a proportion of feeding time or observation events. We do not consider the first method, more popular in the field of metabolic ecology, but focus instead on the second, favoured by behavioural primatologists, and a third method, quantifying the degree of frugivory given the richness of fruiting plants observed in primate diets. Our assessment considers the inherent variation in observational sampling effort, to test long-held hypotheses regarding the relationships between vertebrate body size, geographic distribution, and diet.

We therefore provide the first comprehensive quantitative review of the feeding ecology of wild primate populations across the New World tropics, which contain both the world’s most diverse primate fauna and the highest diversity of plants and fruit morphological design. Comparable reviews are available for only a limited number of frugivore taxa (e.g. hornbills: Kitamura 2011; tapirs: Hibert et al. 2011), or the frugivore assemblage attending a single plant taxon (e.g. *Ficus* spp.: Shanahan et al. 2001). Instead we have identified primates as a large and important group of frugivores in neotropical forests that are long overdue a systematic review, despite the strong tradition of observational field studies dedicated to these charismatic vertebrates. We aim to 1) quantify the degree to which neotropical primates rely on fruit pulp and other fruit parts to meet their basic metabolic requirements, considering differences in sampling effort allocated to date across taxa, and 2) attempt to explain trophic status in relation to the body size and geographical range of different species. Finally, we hope to inform future research priorities by pinpointing the most urgent gaps in our current knowledge of the plant diets of neotropical primate, and encourage similar reviews in other taxa and regions worldwide.

6.2. Methods

6.2.1. Data compilation

We performed a comprehensive literature review spanning 42 years of research (1969 – 2011), from published and unpublished sources, of neotropical primate diet studies reporting primate-plant feeding interactions in wild populations (Chapter 5). From a total of 423 references, we included 331 unique references corresponding to 289 individual studies, defined as a survey effort covering a single or multiple primate species over a discrete time period at a single study site. These sources reported on the plant diets of 24 functional groups or 'ecospecies' (*sensu* Peres & Janson 1999) belonging to 17 neotropical primate genera distributed across 163 study sites in 17 Meso and South American countries (Figure 6.1; Table 6.1). A full list of references and study sites is available from the authors upon request.

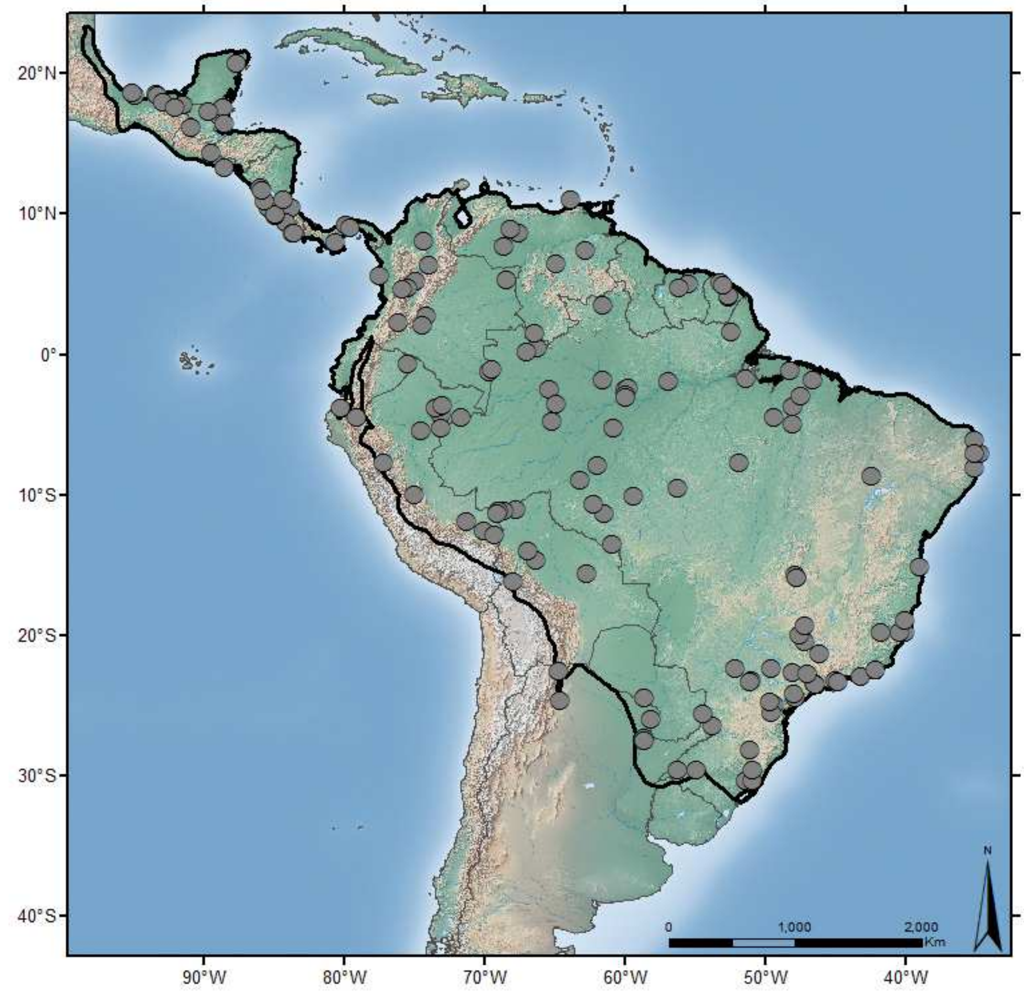


Figure 6.1. *Map of primate dietary studies at 149 sites compiled in this review, showing the composite range of extant platyrrhines (dark line) across 17 neotropical countries.*

Table 6.1. *Taxonomy and corresponding ecospecies classification of neotropical primates used in this analysis.*

Subfamily: Tribe [a]	Code	Ecospecies [b]	Taxonomic species included	Body mass (kg) [c]	Range (km^2) [d]
Atelinae	Al	Howler monkeys	*Alouatta* spp.	6.32	13095330
	At	Spider monkeys	*Ateles* spp.	8.56	6784000
	Br	Woolly spider monkeys	*Brachyteles* spp.	8.84	267800
	La	Woolly monkeys	*Lagothrix* spp., *Oreonax flavicauda*	8.46	3351007
Cebinae	Cf	White-fronted capuchins	*Cebus albifrons*, *C. capucinus*	2.92	4057250
	Ca	Brown capuchins	*C. apella* + *Cebus* spp. [e]	3.09	11193082
	Co	Wedge-capped capuchins	*C. kaapori*, *C. olivaceus*	2.91	1944175
	Sa	Squirrel monkeys	*Saimiri* spp.	0.81	6417552
Callitrichinae: Saguinini	Sf	Saddle-back tamarins	*Saguinus fuscicollis*, *S. inustus*, *S. melanoleucus*, *S. nigricollis*, *S. tripartitus*	0.51	2436081
	Sx	Moustached tamarins	*S. mystax*, *S. labiatus*, *S. imperator*	0.50	827714
	Sm	Midas tamarins	*S. midas*, *S. niger*	0.55	1574740
	So	Bare-faced tamarins	*S. bicolor*, *S. geoffroyi*, *S. leucopus*, *S. martinsi*, *S. oedipus*	0.44	216323
Callitrichinae: Callitrichini, Callimiconini	Cx	Atlantic marmosets	*Callithrix* spp.	0.37	2745620
	Mi	Amazonian marmosets	*Mico* spp.	0.38	1256621
	Cb	Pygmy marmosets	*Cebuella pygmaea*, *Callibella humilis*	0.12	1579650
	Le	Lion tamarins	*Leontopithecus* spp.	0.58	85208
	Cg	Goeldi's monkeys	*Callimico goeldii*	0.48	2745620
Pitheciinae	Pi	Saki monkeys	*Pithecia* spp.	2.31	3677870
	Ch	Bearded saki monkeys	*Chiropotes* spp.	2.86	3006600
	Cj	Uakaries	*Cacajao* spp.	3.05	764586

cont.

Table 6.1. cont.

Subfamily: Tribe [a]	Code	Ecospecies [b]	Taxonomic species included	Body mass (kg) [c]	Range (km^2) [d]
Homunculinae	Cm	Amazonian dusky titi monkeys	*Callicebus moloch* + *Callicebus* spp. [e]	0.96	3741840
	Cp	Atlantic dusky titi monkeys	*C. personatus* + *Callicebus* spp. [e]	1.33	896493
	Ct	Collared titi monkeys	*C. torquatus* + *Callicebus* spp. [e]	1.25	1752351
	Ao	Owl monkeys	*Aotus* spp.	0.93	7711498

[a] Taxonomy from Rosenberger (2011).

[b] Ecospecies classification updated from Peres & Janson (1999).

[c] Source: Smith & Jungers (1997).

[d] Source: Patterson et al. (2007).

[e] See Appendix 5.2 for full list of species.

For each study we recorded the primate species studied, study site location including geographic coordinates, observation methods, study duration defined in terms of the number of months and proportion of a Julian year (365 consecutive days) sampled, and the sampling effort, standardised across different sampling techniques and expressed in terms of the total number of hours (Chapter 5). In each case we recorded, wherever available, the number and identity of fruit species consumed, and the proportional composition of fruits in the overall diet. Where the total number of fruit species consumed per primate ecospecies per study was not provided in each source, we used the total sum from complete or incomplete dietary species lists, or from the isolated mention of individual plant species. We define frugivory (*sensu lato*) as including all ripe and unripe fruits, in addition to other fruit parts, including fruit pulp, seeds and seed-pod exudates. We therefore make no assessment of whether individual fruit consumption records infer effective seed dispersal or seed predation. Plant taxonomy was updated to the APG III system (APG III 2009) and synonyms in the Latin nomenclature were condensed using available sources (The Plant List 2010, IPNI 2011).

6.2.2. Measures of frugivory

We used three approaches to quantify the degree of frugivory exhibited by each primate ecospecies. Firstly, we assessed the log-linear relationships between sampling effort and the richness of plant genera in the diet of each primate ecospecies per study. For highly frugivorous ecospecies a steeper increase in the number of fruit genera consumed per unit effort would be expected than for less frugivorous ecospecies. The rate of increase with effort or the slope (Effort-based Fruit Richness Slope: EFRS) of the regression line would therefore represent one measure of the importance of fruit in the overall diet.

Secondly, we compared the richness of plant genera occurring in the fruit component of primate diets. However, the total number of fruit genera observed as present in the diet of primate ecospecies provides a misleading indication of actual dietary richness because of both varying levels in the sampling effort logged across ecospecies and the severe undersampling of dietary profiles in almost all cases (Chapter 5). Examination of non-parametric estimators of richness or indices of alpha diversity would require abundance count data for each fruit genus observed. Because most references compiled provided only a food-species list, we could only use a presence-absence matrix of confirmed plant-primate species interactions. We therefore produced sample-based rarefaction curves, to represent the cumulative number of fruit genera recorded across all studies for each primate ecospecies and to more accurately estimate the relative richness of fruit genera in the diets of all ecospecies on the basis of an equivalent sampling effort. We then re-scaled the x-axis of the sample-based rarefaction plots (where samples represented individual studies) to express effort in terms of the number of observation hours, therefore accounting for the highly variable effort per sample logged by different primatologists. Using the wide range of sampling effort allocated to different primate ecospecies, we calculated rarefied plant taxonomic richness standardised to 100, 1000 and 4000 hours of observation; only Amazonian marmosets (*Mico* spp.) and collared titi monkeys (*Callicebus torquatus* and related congeners; Table 6.1) had total efforts < 1000 h.

Thirdly, we calculated the mean proportion of frugivory (fruit pulp and other fruit parts) in the diet of each primate ecospecies. The percentage contribution of any plant parts (e.g. foliage, exudates, flowers, fruits, seeds), animal prey (vertebrates and invertebrates), and other food sources to the diet was recorded from the subset of all references reporting such information (Appendix 6.1). Due to seasonal dietary shifts, the most accurate dietary representation is provided by studies which span at least a full annual cycle. Year-round dietary data, however, were relatively scarce in the literature, particularly for certain functional groups. This required the inclusion of a few less comprehensive studies to estimate the mean degree of frugivory for each primate ecospecies, although we excluded all studies spanning less than six months of *de facto* field sampling.

6.2.3. Correlates of frugivory

We tested the relationship between total sampling effort per primate ecospecies and each of the above measures of frugivory: 1) the slope of the relationship between effort and richness of fruit genera consumed, 2) rarefied fruit genus richness, and 3) the proportion of the overall diet consisting of fruits. Finally, for each primate ecospecies we calculated the mean body mass (Smith & Jungers 1999) and geographic range size (NatureServe/IUCN range polygons: Patterson et al. 2007, IUCN 2011), and tested these predictors against the rarefied richness of fruit genera (including seeds) consumed and the degree of frugivory as a proportion of overall diet. We expect a positive relationship between food-plant (and fruit) richness and geographic range size, as a result of the continental-scale turnover in plant species composition available at different sites. We also predict a peak in frugivory as a proportion of the overall diet at the mid-range of neotropical primate body mass, as expected by Kay's Threshold of feeding/foraging investments into different classes of trophic resources. We used body mass as a metric of body size relevant to feeding ecology because it is a powerful predictor of metabolic requirements and its close relationship with digestive tract capacity (Peters 1986). All analyses were conducted in R (R Development Core Team 2010); sample-based rarefaction curves were produced using the 'vegan' package (Oksanen et al. 2011).

6.3. Results

6.3.1. Effort-based Fruit Richness Slopes

Feeding ecology studies on neotropical primates are markedly skewed towards a handful of ecospecies (Table 6.2, Figure 6.2). The most heavily studied genera are howler monkeys, spider monkeys (*Ateles* spp.), capuchins (*Cebus* spp.), and tamarins (*Saguinus* spp.; Table 6.1). Conversely, ecospecies experiencing particularly low levels of attention include the wedge-capped capuchins (*Cebus kaapori* and *C. olivaceus*), pygmy marmosets (*Cebuella pygmaea* and *Callibella humilis*), Goeldi's monkeys (*Callimico goeldii*), and collared titi monkeys.

Substantial differences are also evident between ecospecies and higher taxonomic groups in terms of the cumulative number of fruit genera consumed as a function of study effort. Notably within the Atelidae, which includes two of the best studied ecospecies, there are much steeper EFRS slopes in the regression lines for spider monkeys and woolly monkeys (*Lagothrix* spp.) than for howler monkeys and woolly-spider monkeys (*Brachyteles* spp.) (Figure 6.2a). Steep EFRS slopes are also apparent for moustached tamarins (*Saguinus mystax* and ecological analogues) and Amazonian marmosets, although the latter have been seldom studied.

Table 6.2. *Sampling effort and measures of frugivory (sensu lato) for neotropical primate ecospecies. Codes represent ecospecies (see Table 6.1).*

									Rarefied genus richness			Dietary classes	
Code	Sites	Studies	Hours	EFRS [a]	Max. spp. per study	Tot. gen. richness	Tot. fam. richness	Curve completion [b]	4000 hrs	1000 hrs	100 hrs	% fruit	N
Al	74	108	47236.4	0.17	97	294	83	65.1	68.2	19.3	2.0	35.1	41
At	29	44	18328.3	0.43	238	259	75	63.3	114.9	36.6	4.0	78.3	16
Br	7	9	3643.5	0.29	71	101	51	35.7		37.4	4.2	42.6	5
La	11	16	8714.7	0.66	183	239	78	59.7	155.7	55.6	6.4	73.4	5
Cf	17	30	21291.6	0.53	176	214	65	51.1	64.9	18.5	1.9	81.2	1
Ca	40	50	13153.6	0.38	176	260	73	54.9	126.3	39.6	4.3	48.5	7
Co	4	4	1424.5	0.33	54	112	52	20.5			14.6	54.6	1
Sa	15	19	4956.3	0.38	150	144	62	39.6	119.0	40.2	4.5	38.1	2
Sf	12	18	13585.1	0.51	251	187	66	65.3	99.4	33.6	3.8	54.1	6
Sx	8	13	12297.5	1.00	267	182	62	62.2	99.4	33.4	3.7	68.0	5
Sm	8	8	568.1	0.43	48	85	45	32.8			20.5	66.0	3
So	6	6	2033.3	0.49	23	39	24	32.2		22.4	2.7	61.5	2
Cx	14	22	6540.7	0.59	30	85	43	36.3	63.5	19.9	2.2	17.9	6
Mi	3	4	1868.4	1.30	57	52	29					18.6	1
Cb	6	6	3351.5	0.20	6	5	4	25.6		3.5	0.4	0.0	1
Le	4	8	12244.9	0.58	87	115	51	45.0	53.2	15.8	1.7	76.1	3
Cg	2	4	2505.5	0.46	55	55	31	14.7		19.9	2.6	29.0	2
Pi	12	17	6208.8	0.49	172	215	71	49.9	162.3	57.3	6.5	85.0	7
Ch	10	18	5123.9	0.54	177	240	66	60.4	219.1	93.3	11.8	84.1	7
Cj	8	9	1881.7	0.67	120	173	49	42.0		96.0	12.8	87.2	2

cont.

Table 6.2. cont.

									Rarefied genus richness			Dietary classes	
Code	Sites	Studies	Hours	EFRS [a]	Max. spp. per study	Tot. gen. richness	Tot. fam. richness	Curve completion [b]	4000 hrs	1000 hrs	100 hrs	% fruit	N
Cm	7	8	1659.3	0.13	81	94	45	23.6		59.3	6.9	53.0	2
Cp	4	6	2649.5	0.41	69	82	37	30.8		38.3	4.4	81.0	2
Ct	4	4	363.3	0.09	49	57	33					86.3	1
Ao	11	12	1661.3	0.34	63	68	33	25.7		43.6	5.2	76.5	2
Total	163	289	193291.0										

[a] Effort Fruit Richness Slope.

[b] % completion of fruit genus accumulation curve.

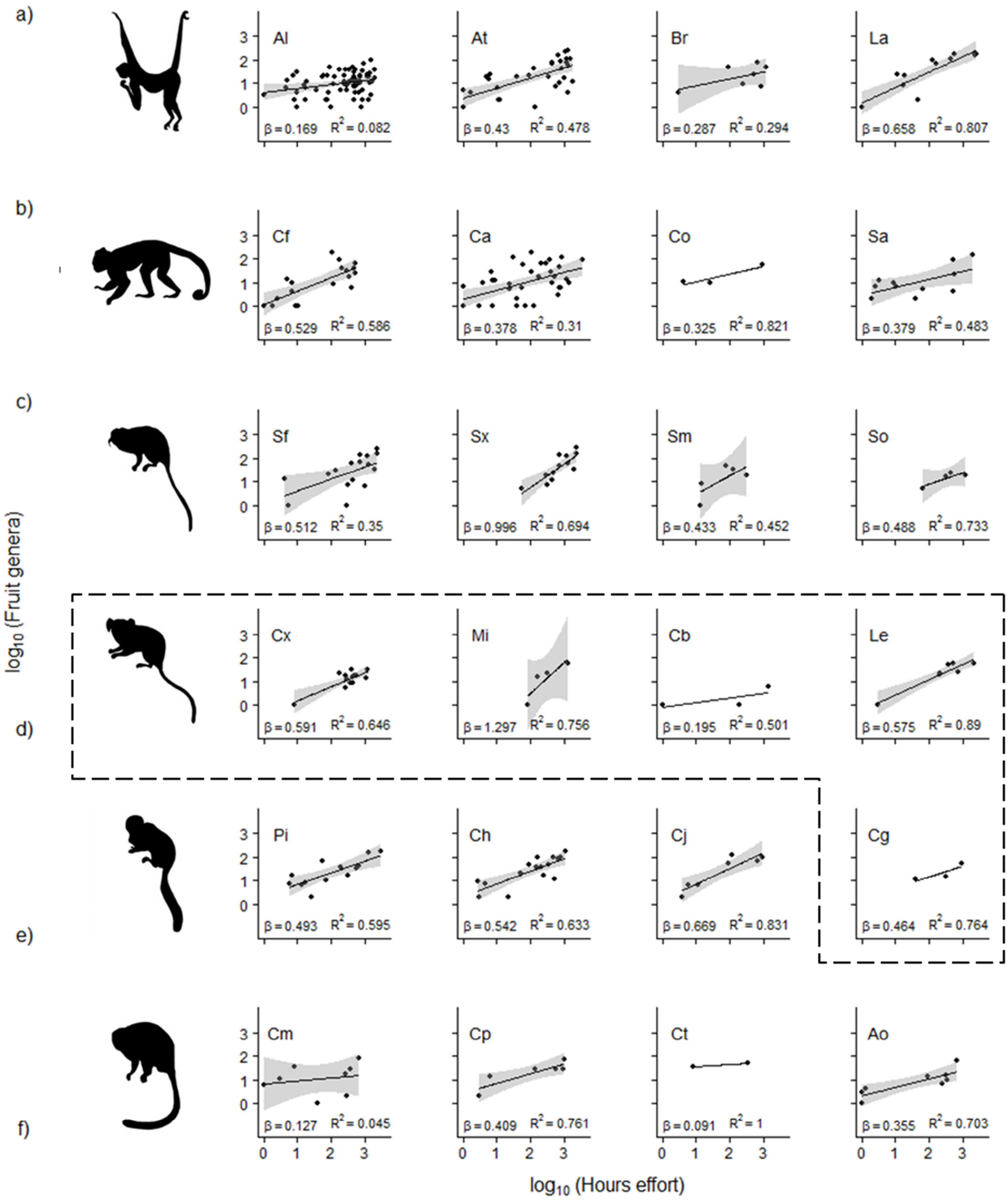


Figure 6.2. *Log-transformed relationships between sampling effort (hours) and richness of fruit and seed genera observed across dietary studies of neotropical primates. Codes represent primate ecospecies (see Table 6.1), arranged in rows according to primate subfamilies: a) Atelinae, b) Cebinae, c) Callitrichinae: tribe Saguinini, d) Callitrichinae: tribes Callimiconini and Callitrichini, e) Pitheciinae, f) Homonculinae. Lines represent linear regressions; grey shading represents 95% confidence intervals (excluded for Cb, Cg, Co, and Ct due to small samples of ≤ 3 studies); dashed box encompasses the Callimiconini (Cg) and Callitrichini tribes of the Callitrichinae.*

Ecospecies with the most shallow EFRS slopes, such as collared titi monkeys and pygmy marmosets, are often characterised by small sample sizes, but this is not the case for howler monkeys and Amazonian dusky titi monkeys (*Callicebus moloch* and analogues). Relatively shallow slopes are common across the Homunculinae, including night monkeys (*Aotus* spp.), and the Cebinae, with the exception of the intermediate slope exhibited by white-fronted capuchins (*Cebus albifrons* and *C. capucinus*) which has a value more similar to members of the Callitrichinae such as the saddle-back tamarins (*Saguinus fuscicollis* and analogues), lion tamarins (*Leontopithecus* spp.), and Atlantic marmosets (*Callithrix* spp). Finally, all Pitheciinae show relatively steep slopes, particularly in the case of the uakaries (*Cacajao* spp.) whose slope is comparable to that of woolly monkeys.

6.3.2. Fruit richness accumulation curves

The higher sampling effort devoted to the Atelinae and Cebinae subfamilies, and to howler monkeys in particular, is confirmed by examining the aggregate effort across all studies (Table 6.2, Figure 6.3). The Pitheciinae and Homunculinae are particularly undersampled but there are examples of poorly studied ecospecies in each subfamily, even including the woolly-spider monkeys and wedge-capped capuchins from the Atelinae and Cebinae, respectively.

The cumulative curves also display the richness of plant genera consumed as fruit or seeds by each ecospecies and the rate of accumulation over the course of their studies. Despite a lower sampling effort, the fruit richness curves of spider monkeys and woolly monkeys are considerably steeper than that for howler monkeys. Squirrel monkeys (*Saimiri* spp.) and brown capuchins (*Cebus apella* and analogues) exhibit steeper curves than white-fronted capuchins, while those for saddle-back tamarins and moustached tamarins are almost identical. It is difficult to interpret the least studied ecospecies but it is apparent that all pitheciines exhibit exceptionally steep accumulation curves in relation to most other ecospecies (Appendix 6.2).

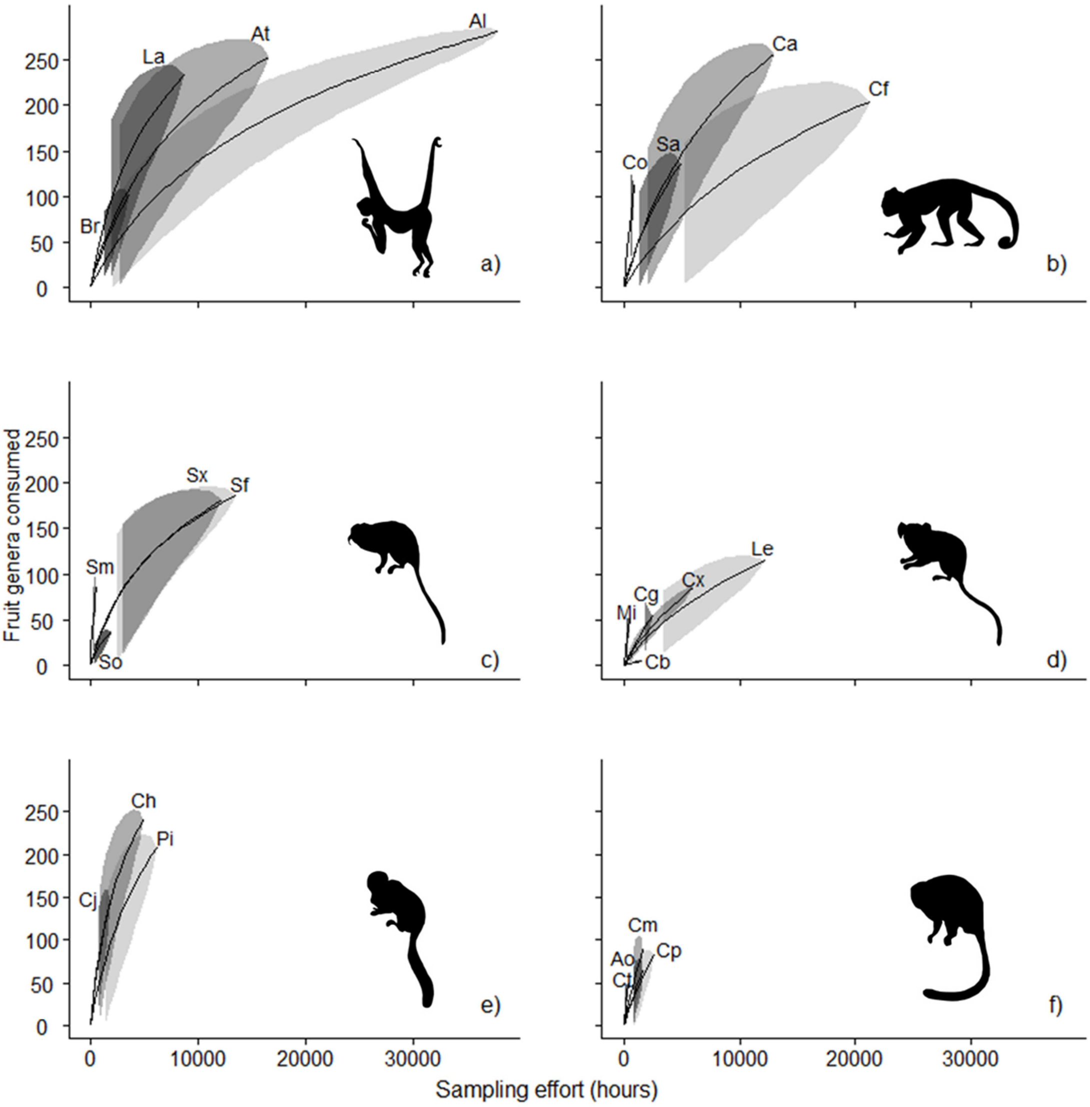


Figure 6.3. *Sample-based rarefaction curves for plant genera (fruits and seeds only) observed in dietary studies of neotropical primates, with x-axis rescaled to show cumulative observation hours across sample studies. Codes represent primate ecospecies (see Table 6.1), arranged in panels according to primate subfamilies: a) Atelinae, b) Cebinae, c) Callitrichinae: tribe Saguinini, d) Callitrichinae: tribes Callimiconini and Callitrichini, e) Pitheciinae, f) Homonculinae. Grey shading represents 95% confidence intervals.*

Direct comparisons are made possible by estimating the rarified genus-level richness of fruits and seeds consumed at a common sample effort. Using values equivalent to 4000 h of observation (Table 6.2) it is clear that pitheciines include the highest diversity of fruits and seeds in their diets, followed by woolly monkeys, brown capuchins, spider monkeys, saddle-back tamarins, and moustached tamarins. At this level of sampling, howler monkeys accounted for a plant genus richness less than half that of saki monkeys (*Pithecia* spp.) and less than a third that of bearded saki monkeys (*Chiropotes* spp.). Uakaries have received less than 4000 h study effort but appear to have a similar trajectory to the bearded saki monkeys. Midas tamarins (*Saguinus midas* and *S. niger*) and wedge-capped capuchins show some indication of steep accumulation curves using a highly rarified richness at 100 h of observation but these ecospecies have been severely undersampled.

6.3.3. Frugivory within different dietary classes

Pitheciines again rank amongst the most frugivorous when considering frugivory as a proportion of all dietary classes (Figure 6.4), albeit only when both seeds and fruit pulp are included (Appendix 6.3). Granivory also contributes to the high representation of frugivory within the diets of titi monkeys (*Callicebus* spp.), although to a lesser degree than in pitheciines. Frugivory represents a slightly lower dietary component of spider monkeys and woolly monkeys, and a considerably lower component of the other atelids, howlers and woolly-spider monkeys, which are predominantly folivorous (Figure 6.5).

Capuchins and squirrel monkeys exhibit an intermediate level of frugivory, with a correspondingly higher proportion of insectivory (Figure 6.5). Tamarins are similar in terms of percentage frugivory but with the added contribution of exudates to the diet (Figure 6.4). Exudates become the dominant dietary class in marmosets, particularly in the extreme case of pygmy marmosets which consume only a minimal amount of fruit. Lion tamarins, in contrast, exhibit a higher intake of fruits than other Callitrichinae, while Goeldi’s monkeys are unique in the substantial contribution of fungi to their diet.

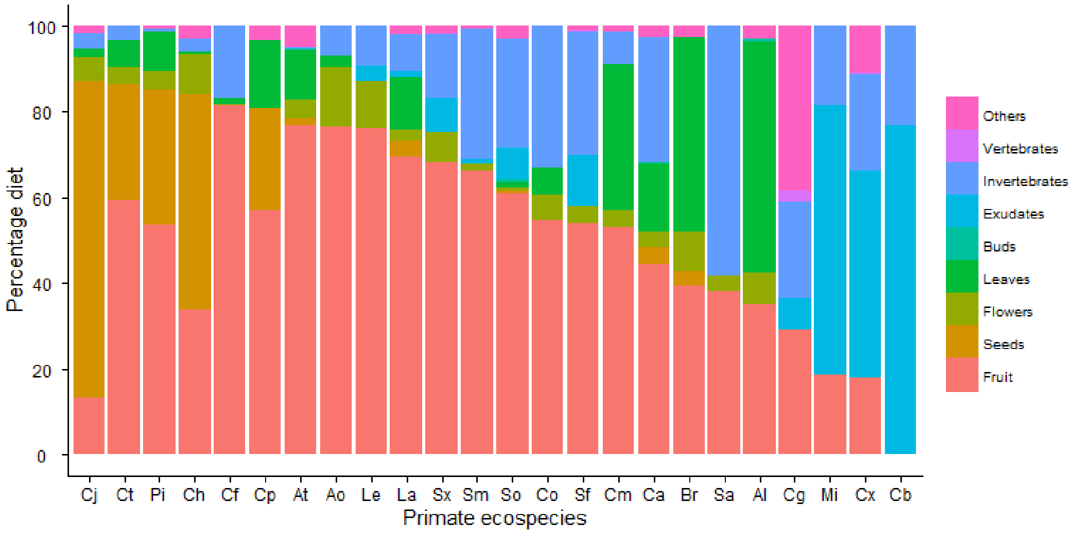


Figure 6.4. *Proportions of diet per neotropical primate ecospecies comprising different plant parts and animal prey consumed on the basis of studies longer than six months in duration. Codes represent primate ecospecies (see Table 6.1), arranged in decreasing order of percentage of frugivory sensu lato (including fruits and seeds). For full details, including sources, and further representations see Appendix 6.1 and 6.3, respectively.*

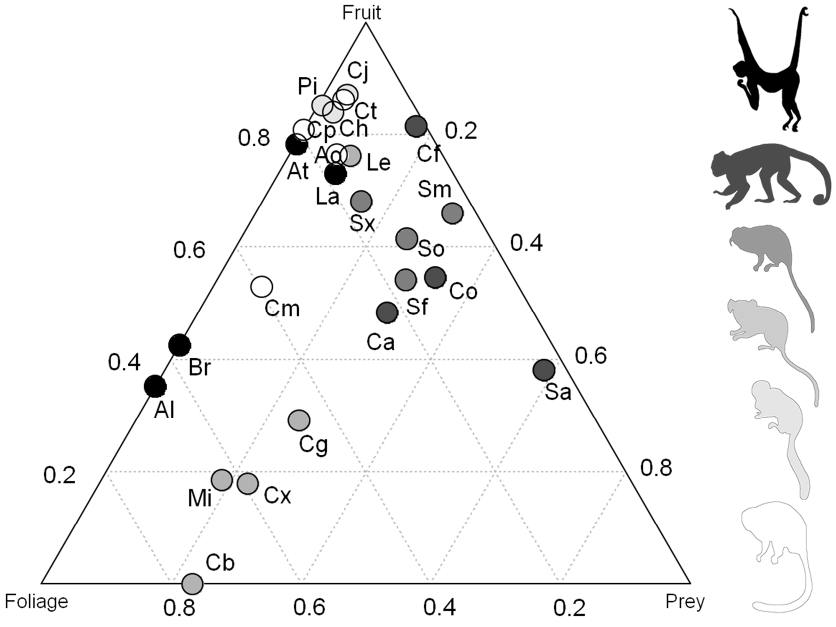


Figure 6.5. *Ternary plot describing the contribution of the three major dietary classes observed across neotropical primates from studies longer than six months in duration. Codes represent primate ecospecies; fill colours represent primate subfamilies as indicated by silhouettes (see Table 6.1).*

6.3.4. Effects of sampling effort on measures of frugivory

The completeness of each ecospecies' accumulation curve can be measured by how close it is to reaching an asymptote. As expected, this metric is positively related to overall sampling effort, in that the taxonomic richness of food species is better understood in those ecospecies studied for longer (Appendix 6.4a). Our three measures of frugivory, however, are related in contrasting manners to sampling effort, notably that the best studied ecospecies are typically those with the least diverse diets, as indicated by the rarefied genus richness (Appendix 6.4b). There is a slight positive relationship between sampling effort per ecospecies and the EFRS of studies allocated to that ecospecies (Appendix 6.4c), whereas the proportion of fruits in the diet is independent of study effort across ecospecies (Appendix 6.4d).

6.3.5. Ecological correlates of frugivory

Geographic range size was not strongly related to the richness of fruit genera consumed by primate ecospecies or to the proportion of their diets consisting of fruits (Appendix 6.5); several patterns of cumulative fruit richness were observed across all geographic range sizes, and both the highest and lowest dietary richness values were observed for ecospecies distributed across mid-sized geographic ranges. Body size, however, was positively related to rarefied fruit richness (Appendix 6.5), with a wider range of values in large-bodied species. Degree of frugivory as a proportion of the overall diet including both plant and animal matter was decisively unimodal: it was relatively low in highly faunivorous small-bodied species, reached a peak towards the upper intermediate range (2 – 3 kg) of the entire body mass spectrum with a subsequent partial decline towards the largest and most folivorous extant neotropical primates (Figure 6.6).

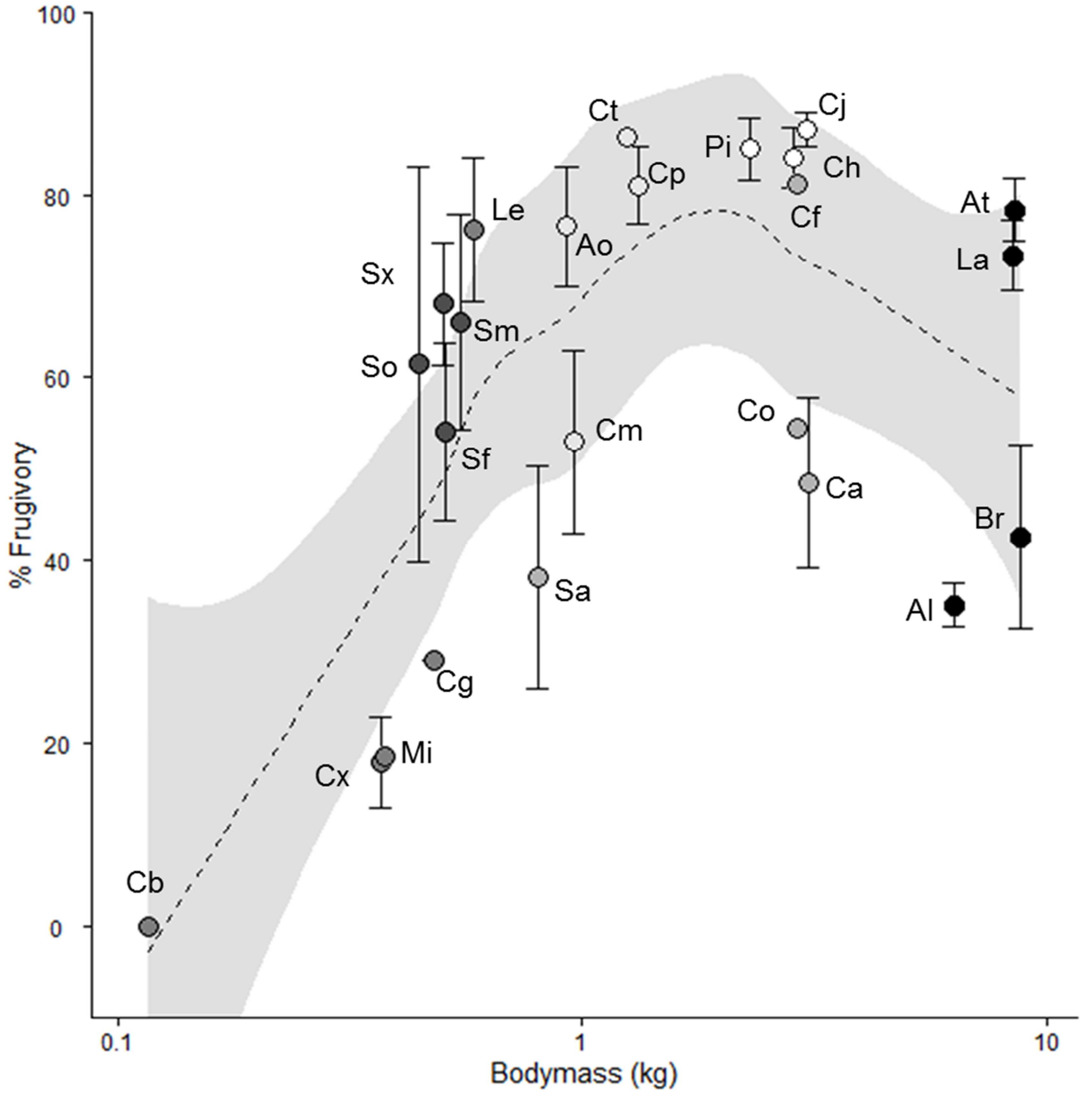


Figure 6.6. *Relationship between body size and degree of frugivory (percentage of the overall diet including fruits and/or seeds) in neotropical primates. Body mass values are derived from Smith and Jungers (1997). Codes represent primate ecospecies; fill colours represent primate subfamilies (see Table 6.1, Figure 6.5); dashed line represents smoothed mean; grey shading represents 95% confidence intervals.*

6.4. Discussion

This study provides a critical continental-scale assessment of diet, and frugivory in particular, in all neotropical primates. Few vertebrate taxa have been subjected to such dietary reviews (see Courts 1998, Virgos et al. 1999, Barrett et al. 2007, Gebert & Veryheyden-Tixier 2008, Kitamura 2011, Hibert et al. 2011), and most are restricted to a relatively narrow focus. Perhaps the most wide-ranging geographic and taxonomic coverage is provided by a global review of fig consumers (Shanahan et al. 2001), although this is limited to feeding records concerning a single pantropical plant genus. Our study represents the first large-scale quantitative review of primate dietary data worldwide, and one of the most comprehensive assessments of the feeding ecology of any terrestrial vertebrate infraorder, especially given the high diversity and disproportionately large trophic importance of platyrrhines in neotropical forests.

We uncovered the following main patterns: (1) Almost all New World primate ecospecies have been severely undersampled in terms of the species-richness of food plants exploited as fruit resources; (2) Accounting for study effort, vegetative diets vary considerably across primate ecospecies in the richness of fruit genera, which is more closely related to body size than to geographic range size; (3) Degree of frugivory as a proportion of the overall diet also varies considerably between ecospecies, and in a unimodal pattern consistent with Kay's (1984) body-size hypothesis: frugivory is most prevalent at the mid-high spectrum of body size within neotropical primates. This pattern is discussed in relation to the full range of body sizes of extinct and extant non-human primates in both the paleotropics and neotropics.

6.4.1 Severe undersampling

Despite the impressive investigation efforts of field primatologists, which have made primates the most intensively studied order of mammals, sampling effort within the neotropics is heavily skewed towards a small minority of genera both in terms of the number and spatial distribution of studies and the resulting observation time (Figure 6.2). These biases are confirmed in the total sampling effort per ecospecies accumulated across all studies (Table 6.1) and, in particular, by the cumulative curves of fruit genera recorded as consumed (Figure 6.3). Here it becomes apparent that in fact, no primate ecospecies has been successfully sampled to approach the accumulation curve asymptote. Even for howler monkeys, which easily represent the best studied platyrrhine ecospecies, we still cannot be confident that the full breadth of dietary fruit genera have been uncovered. The situation is much worse for many others, however, with clear examples from each neotropical subfamily, particularly the most poorly sampled Homunculinae (*Aotus* spp. and *Callicebus* spp.)

Furthermore, our estimates of rarefied food-species richness values, which effectively account for variable sampling effort, show that neotropical primate fieldwork has predominantly targeted those ecospecies exhibiting the least diverse in fruit diets (Appendix: Figure S3). This is important to recognise, even if understandable given the close relationship between diet and other life-history traits that influence the amenability of primate species to ecological research. Howler monkeys, for example, in addition to being ubiquitous in neotropical forests, are over-investigated relative to other ecospecies, perhaps in part because they are highly folivorous. This, in turn, is associated with a suite of traits that render any arboreal folivore more conveniently observable: notably small home ranges, high population density, a relatively lethargic lifestyle, and a high tolerance of human disturbance and edge-dominated habitats in forest fragments that are often within reach of academic institutes in large urban centres. Conversely, more frugivorous ecospecies are notoriously more challenging to study, and it is worth considering that such practical issues are likely to constrain the selection of study species and research questions, especially when much primatological fieldwork has been conducted by graduate students with particular (and highly seasonal) time limits to produce a dependable dataset (Chapter 5).

6.4.2. Variable levels of frugivory: fruit richness

The degree of frugivory across primate ecospecies is illustrated in several ways, firstly by the strength of the relationship between study effort and the number of fruit genera consumed in a study. Using genus level identification of plants helps to account for the notoriously poor botanical expertise of many field primatologists. Steep positive slopes, for example in woolly monkeys, indicate high dietary richness within an individual focal group, suggesting that the number of fruit genera observed in their diet would be further augmented by a prolonged study period. In contrast, shallow slopes such as those of howler monkeys, suggest that even short-term studies appear to capture most of the dietary richness, so that geographic variation in the composition of food sources available across studies likely plays a larger role in the overall richness of fruits consumed by less frugivorous ecospecies. This effect is likely to be substantial in ecospecies with a large geographic range, which will require a greater spread of study sites to cover the greater floristic turnover in plant communities across their ranges.

Accumulation curves provided an additional angle to assess the importance of frugivory across primate ecospecies, by amalgamating information on food-plant richness across all available studies. Shallower curves indicate that new studies will have a lower impact in terms of additional contributions towards overall fruit genus richness for that ecospecies. On the other hand, steeper curves indicate that much of the true fruit diet of that ecospecies remains undocumented and that the number of fruit genera known to be consumed can be expected to rise with future studies. Within the Atelidae, for example, despite the large number of studies and large total effort allocated to date, there are relatively few fruit genera observed in the diet of howler monkeys. Dietary curves rise much more steeply for spider monkeys and woolly monkeys, and a far greater fruit richness would therefore be predicted if they were to receive the same level of sampling effort as howler monkeys.

Rarefaction provides a more effective comparison than the extrapolation of accumulation curves, although care must be taken in interpreting the values for the most poorly sampled ecospecies, especially those observed for fewer than 1000 h (Table 6.1). The highest rarefied genus richness is displayed by the Pithecinae, which confirms their extremely steep accumulation curves despite relatively low sampling effort. Further studies, in particular targeting remote parts of Amazonia, will yield many more fruit taxa consumed by these ecospecies. However, pitheciine dietary records, in addition to ripe fruit pulp, also include unripe seeds of many tree and woody liana species, which comprise an important part of their diet.

6.4.3. Importance of frugivory as a dietary class

Although all neotropical primates are frugivorous to some degree, they adopt a wide range of dietary strategies in supplementing their fruit diets with alternative food sources. Simple models proposed previously to describe these strategies include the frugivore/folivore/insectivore trichotomy (Chivers et al. 1984), subsequently expressed as the frugivore-folivore/frugivore-insectivore dichotomy (Rosenberger 1992) to highlight the general dominance of frugivory. The proportional balance between these food classes can be shown by a ternary plot of overall dietary allocation (Figure 6.5), expressing the continuum between ripe-fruit-pulp specialists, such as spider monkeys and woolly monkeys, to the predominantly folivorous howler and woolly-spider monkeys, or the highly insectivorous squirrel monkeys. Intermediate consumers such as the opportunistically folivorous/insectivorous titi and night monkeys or the frugivorous/faunivorous capuchins are generally represented along the three dimensional gradient but any finer details are lost, particularly in relation to additional dietary sources that can comprise a substantial contribution to the total diet of a few ecospecies (Figure 6.4).

Pitheciines, for example, are more accurately described as seed specialists or granivore-frugivores than generalised frugivores (Palminteri et al. 2012), whereas dusky titi monkeys are also incipient seed eaters (Garber & Kinzey 1992, Kinzey 1992). Marmosets and pygmy marmosets are specialised exudativores, and rely on gums and resins for a large part of their diet. The most extensive study of Goeldi's monkeys to date reveals that, in excess of the contribution by exudates, the largest proportion of their diet consists of fungi (Porter 2001). Therefore, while the simplistic approach of categorising broad patterns between the major trophic guilds of frugivory, folivory and insectivory might be valuable, the reality is frequently much more complex.

6.4.4. Body mass and frugivory

The old adage of "you are what you eat" has perhaps been most dramatically demonstrated for a South-East Asian strepsirrhine, the slow loris (*Nycticebus* spp.), where consumption of toxic invertebrates has profound implications for its unique life history (Ligabue-Braun et al. 2012, Streicher et al. 2012). However, the relationship between a species' diet and many aspects of its life history is fundamental for all organisms and platyrrhine primates are no exception. Granivory in pithecids, for instance, is reflected in morphological adaptations to the biomechanics of their jaws and dentition (Kinzey 1992). Complex neural developments are also proposed within *Cebus* and *Saimiri* in relation to the cognitive requirements of an eclectic diet sourced by a highly variable spatiotemporal mosaic of fruit patches (Janson & Boinski 1992).

Body size, however, perhaps represents the key life history trait related to diet (Peters 1983, Calder 1984, Lindstedt & Boyce 1985, Fleming 1991). The relationship between diet and body size is, in turn, linked to a multitude of other ecological traits, including reproductive rate, population density, home range size, habitat composition, vertical stratification of forest use, and locomotion (Milton & May 1976, Clutton-Brock &

Harvey 1977, Terborgh 1983, Robinson & Redford 1986, Ford & Davis 1992, Rosenberger 1992). The adaptive radiation of neotropical primates has been driven by the diversification in body size with a resultant range of phyletic ‘dwarfs’ and ‘giants’ (Martin 1990, 1992). Increased body mass allows an animal to eat more in terms of both volume and diversity of food items (e.g. Campos-Arceiz et al. 2008) which has a bearing on the relationship observed between body size and fruit dietary richness. However, this evolutionary process has long been proposed to relate closely to the evolution of primate dietary strategies, with the observation of small-bodied insectivores and large-bodied folivores, with high degrees of frugivory most prevalent within the mid-range of body sizes (Kay 1984, Fleagle 1998).

The roles of body size and proportional frugivory in primates has been examined in the paleotropics, in relation to responses to habitat disturbance (Johns & Skorupa 1987) but data were primarily based on single populations. Our study compiles the relative dietary intake for all neotropical primate ecospecies (multiple populations in all but five cases) to provide an unprecedented opportunity to examine the body size-diet relationship (Figure 6.6). Frugivory is low for small body sizes, where exudativory and subsequently insectivory make large contributions to callitrichid diets. It then gradually increases with greater body size towards a peak, represented by the pitheciine granivore-frugivores, before a decline driven by the high degree of folivory in two of the large-bodied ateline ecospecies.

Interestingly, the largest prehensile-tailed neotropical primates include the highly frugivorous spider monkeys and woolly monkeys in addition to the more folivorous howler and woolly spider monkeys. Woolly-spider monkeys are generally described, in common with spider monkeys and woolly monkeys, as energy maximisers characterised by semibrachiating locomotion, large home ranges, fluid social groups and generally frugivorous diet (Peres 1994a). This contrasts with howler monkeys as energy minimisers, with their slow quadrupedal locomotion, long periods of inactivity, small home ranges, and often highly folivorous diet (Garber & Kinzey 1992, Strier 1992). The apparent disagreement regarding the ecological role of woolly-spider monkeys is perhaps explained by the proposal that leaf-eating in this ecospecies is a secondary adaptation following its recent range restriction in the Brazilian Atlantic Forest (Ford & Davis 1992). This is supported by recent studies where levels of facultative frugivory in continuous evergreen forest are higher than previously recorded in populations from heavily disturbed forest fragments in semideciduous forest (Talebi et al. 2005).

While folivory in neotropical primates is therefore more important towards the large-bodied end of the size spectrum, the predicted curve of the body size-diet relationship appears to be incomplete (Figure 6.6). The first possible explanation for this is the absence of any extant New World primate much larger than 10 kg. In mainland Africa, gorillas (*Gorilla* spp.; males 135 – 180 kg, females 68 – 113 kg) are almost exclusively folivorous (Watts 1984, Rogers et al. 2004), while baboons (*Papio* spp.; up to 40 kg) and geladas (*Theropithecus gelada*; 18.5 kg) are primarily grazers/browsers, as was almost certainly the case for the extinct giant lemurs of Madagascar (*Hadropithecus stenognathus* and *Archaeoindris fontoynonti*) (Mittermeier et al. 2010). The exception amongst the largest-bodied Old World primates is the orangutan (*Pongo* spp.; males 118 kg, females 45 kg), which is highly arboreal and frugivorous (Taylor 2006).

It had previously been assumed that there was a maximum body size within New World monkeys around the 10kg threshold, and perhaps that the phyletic gigantism radiation from a small-bodied common ancestor had not yet progressed sufficiently into large-bodied species exhibiting high levels of folivory as in the Old World (Peres 1994b). Indeed the arrival of humans in Meso and South America may have brought this progression to a sudden halt, in relation to the extinct ‘mega’ *Brachyteles* species and the currently threatened status of the most overhunted large atelines (Peres 1990). We therefore suggest that the absence of the largest-bodied forms in New World primates could explain the puzzling lack of obligate folivores, and the truncation observed in the size-diet relationship (Figure 6.6). This hypothesis could be elucidated by the subfossil discovery of *Protopithecus brasiliensis*, a giant platyrrhine estimated to have reached ~20 kg (Hartwig and Cartelle 1996, Halenar 2011), should its broad diet be investigated perhaps using stable isotope analysis.

Alternative hypotheses to explain the comparatively low representation of folivores in neotropical primates consider differences between the New and Old World tropics in the synchronicity of leafing and fruit phenology (Terborgh & van Schaik 1987) or levels of fruit protein concentrations (Ganzhorn et al. 2009). If extinct large-bodied primates from the neotropics did indeed have highly folivorous diets as predicted by the body size-diet relationship we have shown, this would open the possibility that seasonal resource availability or fruit nutritional quality were not necessarily effective constraints on the evolution of body size in platyrrhines. As a result, perhaps more attention should be directed towards the role of human pressure, particularly considering the considerable conservation threats currently facing the largest-bodied extant neotropical primates (Chapman & Peres 2001).

6.5. Conclusions

This review represents the most comprehensive assessment of neotropical primate dietary studies, and one of the most extensive compilations on the feeding ecology of any frugivorous vertebrate taxon. Coupled with a quantitative assessment of the sampling effort of the dietary studies conducted (Chapter 5), this provides an unparalleled opportunity to compare the diets of a wide-ranging and ecologically important group. The high variation observed across neotropical primate diets, both in terms of the richness of fruiting plants and in the range of dietary strategies, supports the reluctance to accept the concept of a ‘typical’ primate (Strier 1994)

Such variation in diet, and measures of frugivory in particular, has both taxonomic and ecological correlates. Many of the suite of life-history traits related to diet are potentially driven by phylogenetic constraints, in particular the influence of body size. The adaptive radiation of neotropical primates, from a common ancestor of approximately 1kg to a modern-day range spanning two orders of magnitude (~0.1 to ~10kg), offers an ideal setting to test the relationship between body size and frugivory. Our review consolidates support for the hypothesis of Kay’s Threshold, with a peak in frugivory as a proportion of total diet at intermediate sized species.

While the compiled dataset represents an impressive cumulative observation load by primatologists, and the overall trophic strategy is probably now well described for most neotropical primates, the same cannot yet be said regarding a more detailed knowledge of their dietary richness and composition. The accumulation curves of fruit genera consumed fail to approach an asymptote for all functional groups, with disconcerting ignorance on the feeding ecology of some ecospecies that remain particularly undersampled. However, an increased observation effort and spread of sample sites is likely to yield variable returns, in terms of fruit richness, for different ecospecies. Unfortunately, the frugivorous primates with the most species-rich fruit diets appear to be amongst the most poorly studied to date, with severe implications for our overall understanding of fruit-frugivore interactions and the role of primates in ecological processes such as seed dispersal or seed predation.

Finally, our continental-scale focus on such a large and important group of tropical forest consumers highlights the importance of large scale comparative analyses to quantify our current understanding of frugivores as potential seed dispersal agents. We hope this review will serve as inspiration for similar compilation efforts for paleotropical primates.

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Chapter 7

Conclusion

7.1 Introduction

As the threats to tropical forests and global biodiversity become increasingly profound, conservation biologists are becoming more aware of the need for ecosystem-scale research to complement single-species studies (Lindenmayer et al. 2007). This concept has now been developed beyond the assessment of community species richness or species diversity, to examine the richness and diversity of interactions between species. The networks of ecological interactions formed within communities point to the inexorable interdependency between individual components within the ‘web of life’ (Bascompte 2009).

The network approach to community-level studies has stimulated investigation of how network properties relate to the fragility or resilience of ecosystems (Fortuna & Bascompte 2006). In particular, plant-animal mutualistic networks are increasingly recognised as the ‘architecture of biodiversity’, and the structure of these networks may help determine their robustness (Bascompte & Jordano 2007), particularly in the face of intensified anthropogenic impacts (Morris 2010). Taking an ecosystem-wide view (Levin 1998) also enables us to consider the potentially cascading impacts of species extinctions on dependent species and ecosystem functions (e.g. Nichols et al. 2009).

Ecological networks are exceedingly complex with a myriad of direct and indirect links (Montoya et al. 2006), and Darwin aptly described the complex interactions between species as a ‘tangled bank’. This is especially true within species-rich ecosystems, and perhaps contributes much to the current paucity of ecological network studies in tropical forests worldwide. This thesis attempted to redress this imbalance, and adopted an ecosystem-orientated approach to examine the mutualistic networks of fruit-frugivore interactions in the species-rich forests of the neotropics.

7.2 Key findings

7.2.1 Seasonal floods and várzea forests

The first half of the thesis focused on the incredibly diverse forests of lowland Amazonia. Much of the beta-diversity of the Amazon is contributed to by the heterogeneity of forest types, in relation to variation in soil types and flood regimes (ter Steege et al. 2000), and the comparison of two main forest types in the Médio Juruá region of western Brazilian Amazonia were central to this part of the thesis. Seasonal flooding of the white-water Juruá river causes the annual inundation of the *várzea* forests along its banks, in contrast to upland expanses of *terra firme* forest that remain unflooded year-round. Although typically less diverse than *terra firme* forests (Prance 1979), *várzea* forests are the most species-rich floodplain forests worldwide (Wittmann et al. 2006) and the floristic turnover between the two forest types may reach 70-90% (Junk 1989, Wittmann et al. 2010).

Because of the complexity of interactions caused by the high species richness of fruiting plants and fruit consumers, the unique conditions imposed by the flood pulse (Junk et al. 1989, Parolin et al. 2004), and the shortage of previous studies on fruit-frugivore interactions in *várzea* forests (Haugaasen & Peres 2007), it became important to conduct some background studies before considering overall networks. In particular it was necessary to gain an understanding of the spatial and temporal dynamics of plant communities in the poorly known study landscape and how fruit production and vertebrate frugivore abundance and distribution might be influenced in both forest types.

Chapter 2 of this thesis (Hawes et al. 2012) started this process by examining the spatial variation in forest structure across the study landscape in both *terra firme* and *várzea* forests. This was illustrated through the estimation of aboveground forest biomass, incorporating wood density values assigned to genus-level identifications of woody stems, from an extensive sample of small plots. Employing such a widely distributed sampling effort, stratified by forest type, clearly showed that landscape-scale variation in aboveground biomass was primarily determined by forest type. Lower levels of aboveground biomass in *várzea* forest, driven in part by lower values of wood density in the predominantly fast-growing *várzea* tree flora, illustrated the overriding influence of the dramatic flood pulse on ecosystem processes in this region.

Using satellite data to define the period of inundation experienced within each *várzea* plot sampled, allowed the impact of the stress from flooding to be assessed and compared to the stress experienced in *terra firme* as a result of water deficit. Not surprisingly, the extreme stress conditions of *várzea* forests were found to be a more important influence on aboveground biomass, although interestingly aboveground biomass was highest in areas experiencing the longest flood periods. Chapter 3 confirmed the central role of the flood pulse by widening the focus from a spatial perspective to include the temporal variation in phenological patterns in the plant communities of *terra firme* and *várzea* forests. In addition to detailing the broad seasonal patterns in plant vegetative and reproductive cycles, including fruit production, this chapter found that phenological patterns appeared to be primarily triggered by floodwaters in *várzea*, as opposed to rainfall in *terra firme* forest.

7.2.2 Community-wide fruit-frugivore interactions

With consideration for how seasonal variation in fruit production would influence frugivores, the analysis of phenology patterns also included an examination of seed dispersal modes in fruiting plants, which found that while trees and woody lianas in *terra firme* forest primarily displayed zoochorous seed dispersal modes, seeds dispersed by abiotic vectors were more prevalent in *várzea* forest. This simple categorisation of the availability of fruits to frugivores was then expanded upon in Chapter 4, which built on the foundations provided by the earlier two plant-focused chapters to begin to explore the interactions between the plant and animal communities of terra firme and várzea forests. Additional fruit traits such as fruit mass, seed mass, fruit colour, and fruit dehiscency were attributed to the large variety of fruits catalogued during extensive surveys of fruit patches in each forest type. These were then assessed in an attempt to detect any evidence of trait matching between fruit resources and functional groups of frugivores.

Fruit resources in *terra firme* and *várzea* forests were clearly partitioned across the diverse coterie of frugivores but this was not clearly matched to distinct suites of fruit traits as suggested by classic notions of tightly coevolved seed dispersal syndromes (Ridley 1930, van der Pijl 1982). As might be expected, given the dominant influence of forest type on other processes within this study system, the major influence on the partitioning of fruit resources and on network structure was the difference between *terra* *firme* and *várzea* forests. This was primarily a direct or indirect result of the flood pulse. In addition to the high turnover in plant communities between the two forest types, the seasonal flood also has a dramatic influence on the animal communities. High water-levels in *várzea* forests during the aquatic phase prevent access to terrestrial frugivores, and simultaneously open up foraging opportunity for aquatic frugivores. Thus, while canopy primates and canopy birds are free to forage throughout the year, ungulates, caviomorph rodents and ground-dwelling birds and reptiles are effectively replaced for half the year by bony and cartilaginous fish, and freshwater turtles.

These substitutions within the *várzea* frugivore assemblage, however, do not necessarily confer a functional replacement, for a number of reasons. Firstly, the fruit resources available vary as starkly between the aquatic and terrestrial phases as the change in frugivore community. Secondly, the range of frugivores may have very different preferences in their selection of fruit traits within their diets. These two factors combine to create the spatiotemporal partitioning of fruit resources observed between frugivore groups, which is clearly apparent in *terra firme* forest as well as *várzea*, and is likely to reflect their widely divergent ecological roles.

7.2.3 Regional meta-analyses and primate diets

The second half of this thesis explored these ecological roles within a major group of frugivores present in the *terra firme* and *várzea* forests of the Médio Juruá. Primates were important frugivores in both forest types throughout the year, including the aquatic phase in *várzea* although they were particular dominant in the interactions with fruiting plants of *terra firme* forests. The ecological plasticity of neotropical primates in general is further demonstrated by their distribution far beyond Amazonia to span a range of forest habitats from Mesoamerica to the Atlantic Forest, and the adaptive radiation of platyrrhines throughout the American tropics has resulted in diverse range of dietary strategies. Narrowing the focus to this group of well-studied consumers allowed functional groups (or ‘ecospecies’) to be defined more precisely than for earlier community-wide analyses at a local scale.

In the same manner that the investigation of local community-wide networks (Chapter 4) required prior background research (Chapters 2-3), so the exploration of fruit-frugivore networks in neotropical primates also needed preparatory analysis, although in both these cases the ‘background’ chapters represent full and independent lines of enquiry in their own right. In this case, before considering the full network of interactions, it was essential to consider the sampling biases inherent within the continental-scale compilation of primate dietary studies. Although primates arguably represent the most charismatic and most intensively studied order of mammals, even if extinct/extant hominids are excluded, Chapter 5 identified a systematic skew in sampling effort towards large-bodied species and those with large geographic ranges. In addition, this analysis showed that studies were concentrated into specific locations, particularly in readily accessible sites with a well-developed community of either resident or foreign researchers, and that most sites were hugely undersampled in terms of the proportion of co-occurring primate taxa studied and the incompleteness of feeding ecology data. A particularly valuable contribution of this chapter was to highlight geographic and taxonomic gaps within the cumulative body of research effort spanning decades of investigation from the northern neotropical frontier in southern Mexico to the southern frontier in northern Argentina.

Using information assembled in the previous chapter, Chapter 6 was able to account for the disparities in sampling effort to quantify the levels of frugivory across primate functional groups. This resulted in the most comprehensive assessments of neotropical dietary studies, and one of the most extensive compilations on the feeding ecology of any frugivorous vertebrate taxon. One of the key findings here was that despite the impressive cumulative effort of primatologists in the neotropics over the last few decades, even the best-studied ecospecies were undersampled in terms of the richness of fruits known to occur in their diets. This chapter also quantified the variation between the diets of neotropical primates, including the levels of frugivory both in terms of richness of fruit in their diets and as a proportion of overall diet. A final key finding from this comprehensive comparative analysis of primate feeding ecology, was the clear confirmation of a unimodal relationship between frugivory as a proportion of overall diet and body size, in a manner consistent with Kay’s (1984) body-size hypothesis. While small-bodied primates were more typically faunivorous and large-bodied primates typically folivorous, frugivory was most prevalent at the mid-high spectrum of body sizes within neotropical primates.

Figure 7.1. *Fruit and seed collecting in the Médio Juruá.*

7.2.4 Contributions towards methodological advances

An additional output from this thesis is a number of contributions towards methodological advances. Use of the recently developed ALOS ScanSAR imaging is highlighted as a valuable tool to define inundation periods in floodplain forests (Lowry et al. 2009) and to map seasonal habitat availability in *várzea* forests for both terrestrial and aquatic fauna. This technique performed well in explaining the variation in aboveground biomass in *várzea* plots (Chapter 2), in contrast to the use of elevation from SRTM data which does not consider the complex interaction between topography and relative water-level of the river on floodplain inundation (Alsdorf et al. 2010).

While there are both advantages and disadvantages concerning the use of small, ‘Gentry’ style forest plots to estimate aboveground biomass (Phillips et al. 2003), the ability to widely distribute a large number of plots across a vast heterogeneous landscape, stratified by forest type (Chapter 2), is a clear benefit of this sampling protocol (Laumonier et al. 2010).

The pros and cons of the various methods for monitoring plant phenology have also been well discussed (Morellato et al. 2010), including the effectiveness of various trap designs (Stevenson & Vargas 2008). These, however, have generally been challenging to operate in seasonally flooded forests. In addition to using three complementary methods for monitoring plant phenology, this study describes the use of a novel floating trap designed to cope with the fluctuating flood levels in *várzea* forests (Chapter 3).

The completeness of fruit-frugivore networks is an important concern (Blüthgen et al. 2008). Although it is still difficult to determine the proportion of ‘missing’ and ‘forbidden’ interactions in the Médio Juruá networks, their degree of completeness was undoubtedly improved by incorporating local knowledge of fruit-frugivore interactions to supplement a large-scale sampling protocol based on direct observations (Chapter 4). To help overcome the challenges in completing fruit-frugivore networks, particularly in species-rich tropical forests, the contribution from experienced and reliable local residents could be highly advantageous.

Also in relation to the idea of completeness, fruit-frugivore networks have rarely been quantified according to the amount of sampling effort received. Furthermore, if the meta-analysis of neotropical primates is representative there can be expected to be a wide range of effort attributed among different consumers or resources in a network (Chapter 5). In addition to other traits, the degree of frugivory exhibited by each consumer is likely to influence the number of positive interactions recorded during observations. Again, differences between frugivores in other taxonomic groups may or may not reflect those within neotropical primates, where levels of frugivory varied in a non-linear relationship with body mass (Chapter 6). Without considering the distribution of sampling effort and levels of frugivory among consumers, interpretation of the structure of networks may be flawed.

7.3 Future directions

7.3.1 Seasonal floods and *várzea* forests

This thesis made a valuable contribution to the body of research comparing *várzea* and *terra firme* forests, yet *várzea* forests in particular remain one of the most understudied of tropical forest types. There remain open questions that can be investigated using data from fieldwork conducted in the Médio Juruá during the course of this thesis, including some that were not included in any of the final chapters.

During the forest structure study in the two forest types (Chapter 2), data were also collected on canopy cover and understorey density that remain unanalysed. In addition to these small plots, similar data are available for two 100-ha plots (one in *terra firme*, one in *várzea*), in which the distribution of treefall gaps were also mapped (J. Hawes, unpublished data). These combined datasets can be used to investigate potential differences in canopy structure and disturbance between flooded and unflooded forests.

The triggers of phenology patterns in flooded forests is an area that deserves much closer research attention. While Chapter 3 added support for the role of the flood pulse in driving plant phenology in *várzea* forest, it is challenging to dissociate the relative influences of other environmental variables such as rainfall. Further insight may be gained by comparing phenology patterns from multiple sites across different catchments in the Amazon basin, where rainfall and flood regimes may vary in levels of synchrony given the basin-wide variation in time lags between upstream peak precipitation and peak water-levels.

The identity of trees was also recorded within a 10 m radius of each of the traps used to measure fruit-fall in *terra firme* and *várzea* forests (J. Hawes, unpublished data). If fruits and seeds collected from these traps could all be identified, these data could potentially be used to distinguish the proportion of dispersed from undispersed seeds in each trap, and to compare between forest types.

7.3.2 Community wide interactions

While the survey of small tree plots (Chapter 2) were analysed to investigate patterns in forest structure and aboveground biomass, they could also be examined from a community composition perspective. By incorporating information on fruiting phenology and fruit traits according to the genus-level identity of sampled stems, the spatial and temporal variation in fruit production could be estimated over the scale of the two study reserves. This would be particularly interesting to assess in conjunction with patterns of vertebrate frugivore abundance, which were also assessed within the wider research effort of Projeto Médio Juruá (W. Endo & C.A. Peres, unpublished data).

Interactions between fruits and frugivores can have extended higher-order influences within the wider ecosystem, for example the close relationship between dung beetles and faecal resources produced by large mammalian frugivores (Nichols et al. 2009). Dung beetles were sampled in the same 100-ha *terra firme* plot used for fruit and frugivore surveys (E. Nichols, unpublished data), opening the possibility for a combined analysis of the spatial congruence between these three trophic levels.

7.3.3 Regional meta-analyses

The culmination of the meta-analysis of neotropical primate studies in a comprehensive network of fruit-frugivore interactions was not reached during the course of this thesis. However, the full matrices of interactions have been compiled and analysis is underway to assess the relative contributions of primate functional groups to the network accounting for both the sampling effort they have received (Chapter 5) and the degree of frugivory within their diets (Chapter 6).

Further uses for this comprehensive data set include its combination with other taxa such as bats and birds (Mello et al. 2011), and the modelling of impacts on network structure following the removal of the largest primates. This simulation of an overhunting scenario would assess the potential loss of ecosystem function through missing seed dispersal links. A reverse situation could also be envisioned to simulate selective logging with the predicted effects on network structure when harvesting timber resources that may or may not be important to generalist frugivores.

7.3.4 Antagonistic vs mutualistic interactions

Finally, an important consideration, for both the neotropical primate networks and for further analysis of the community-wide networks from the Médio Juruá, is the difference between antagonistic and mutualistic interactions (Bascompte & Jordano

2007, Estes et al. 2011). In addition to the number and identity of links between frugivores and fruit, the ecological role that is usually of interest is the consumer's contribution to the resource plant as an effective seed dispersal agent. Many frugivores (*sensu lato*, as used throughout this thesis), including primates, also operate as seed predators as opposed to effective seed dispersers. This blurred relationship is difficult to quantify since a given frugivore may be an effective disperser for one plant species but represent a predator for another. However, this issue cannot be ignored and the goal for future fruit-frugivore network analyses must include a quantified network with the strength of interactions scaled by the quality of the seed dispersal service provided, in addition to the frequency of the particular interaction.

7.4 The web of life

This thesis has been centrally concerned with a wide array of interactions. The interactions between fruiting plants and frugivorous animals are vital to the maintenance of tropical forests and global biodiversity. A species extinction event is even more significant than the loss of that single species from the ecosystem; for each species lost a host of interactions with other species may be severed. We still do not know enough about the resilience of ecosystems to cope with coextinct interactions, and the need to learn more is urgent.

Hopefully this thesis outlines the importance of truly community-wide assessments, encompassing the mutualistic interactions between the full range of fruits and frugivores. As well as studies exploring anthropogenic impacts in heavily disturbed environments, it is equally important to study the remote, inaccessible species- and interaction-rich sites frequently overlooked by researchers. The complex fully-functioning ecosystems at these sites may provide important information to help curb losses elsewhere.

In addition to these intensive single-site studies, this thesis emphasises the potential for compilations of existing research (often hidden away in unpublished sources) to be used in the construction of regional assessments of fruit-frugivore interactions. The interaction of multiple studies, compiled over space and time, can be extremely valuable in cataloguing the full collection of network links. In this manner, disparate dots can perhaps be joined in order to help reveal a fuller picture.

It is important too to recognise that people do not operate outside the networks mentioned in this thesis, and are not only responsible for the extinction of species within them. A clear example of this is provided in the communities of the Médio Juruá. Within these reserves, people interact with the forest and its other inhabitants on a daily basis. These interactions include fishing, hunting, and the extraction of many timber and nontimber forest products (Newton 2011), representing a close integration into the web of life. The Médio Juruá Extractive Reserve and the adjacent Uacari Sustainable Development Reserve are managed by local residents in recognition of the dependence of their livelihoods on both forest and aquatic resources, and their roles as guardians to ensure the long-term protection of those forest resources and ecosystem services.

Finally, I wish to acknowledge my personal interactions during the course of producing this thesis, in particular the many friendships formed during my time in the Juruá.

Figure 7.2. *Selection of fruits from the Médio Juruá.*

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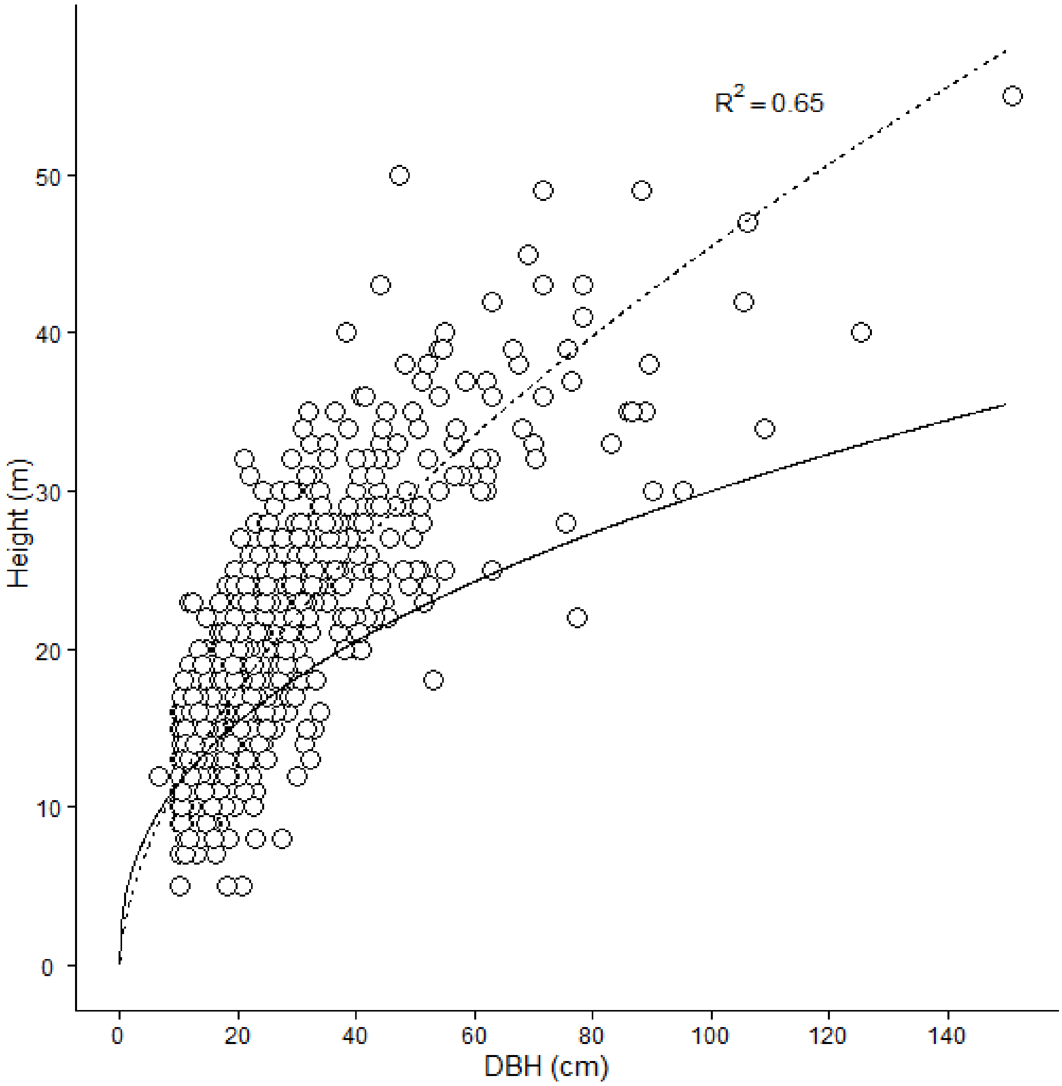
Appendices

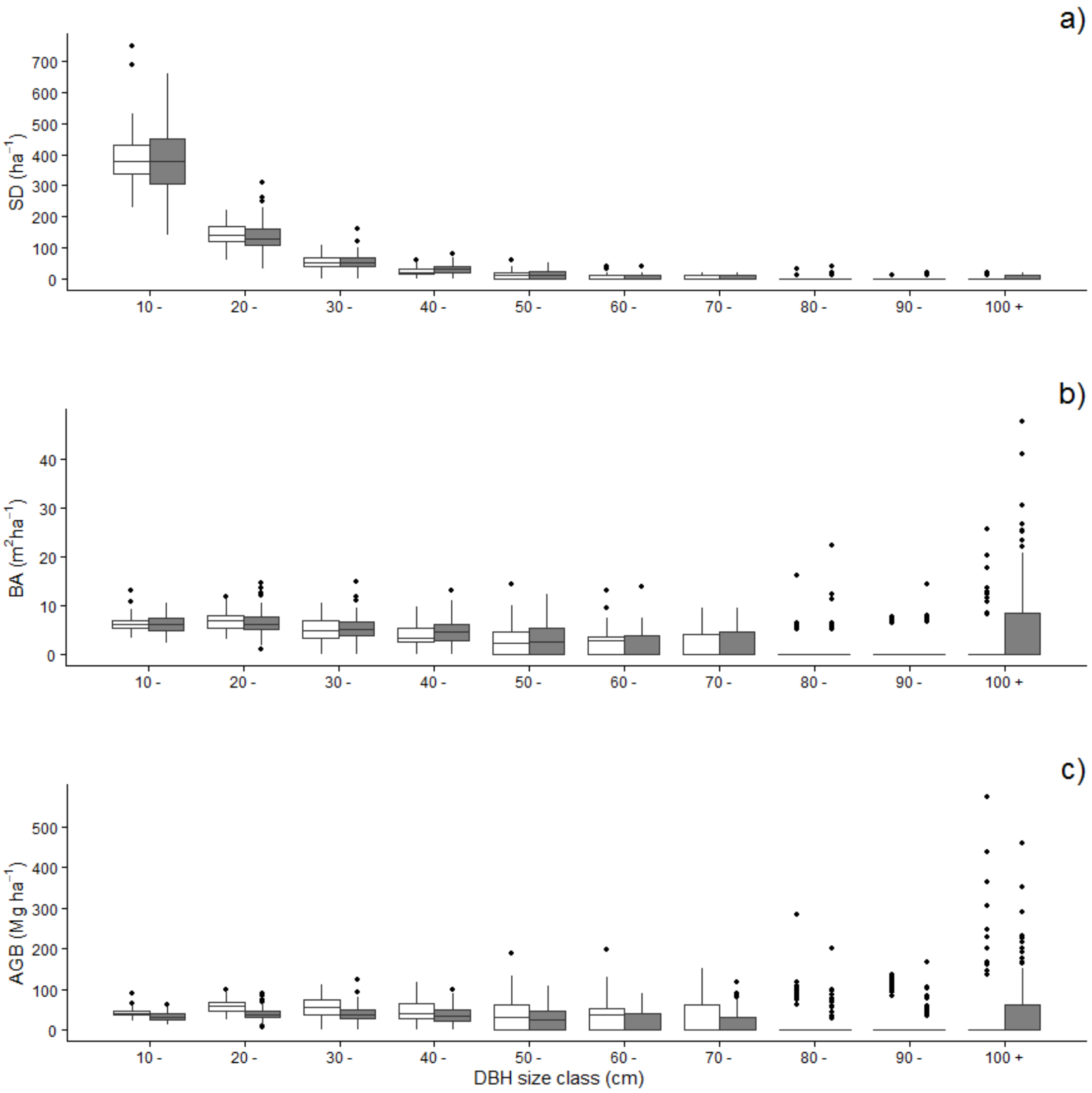
Appendices are included here in sequence, as referred to within the main text, as supplementary material relevant to each of the preceding chapters of this thesis.



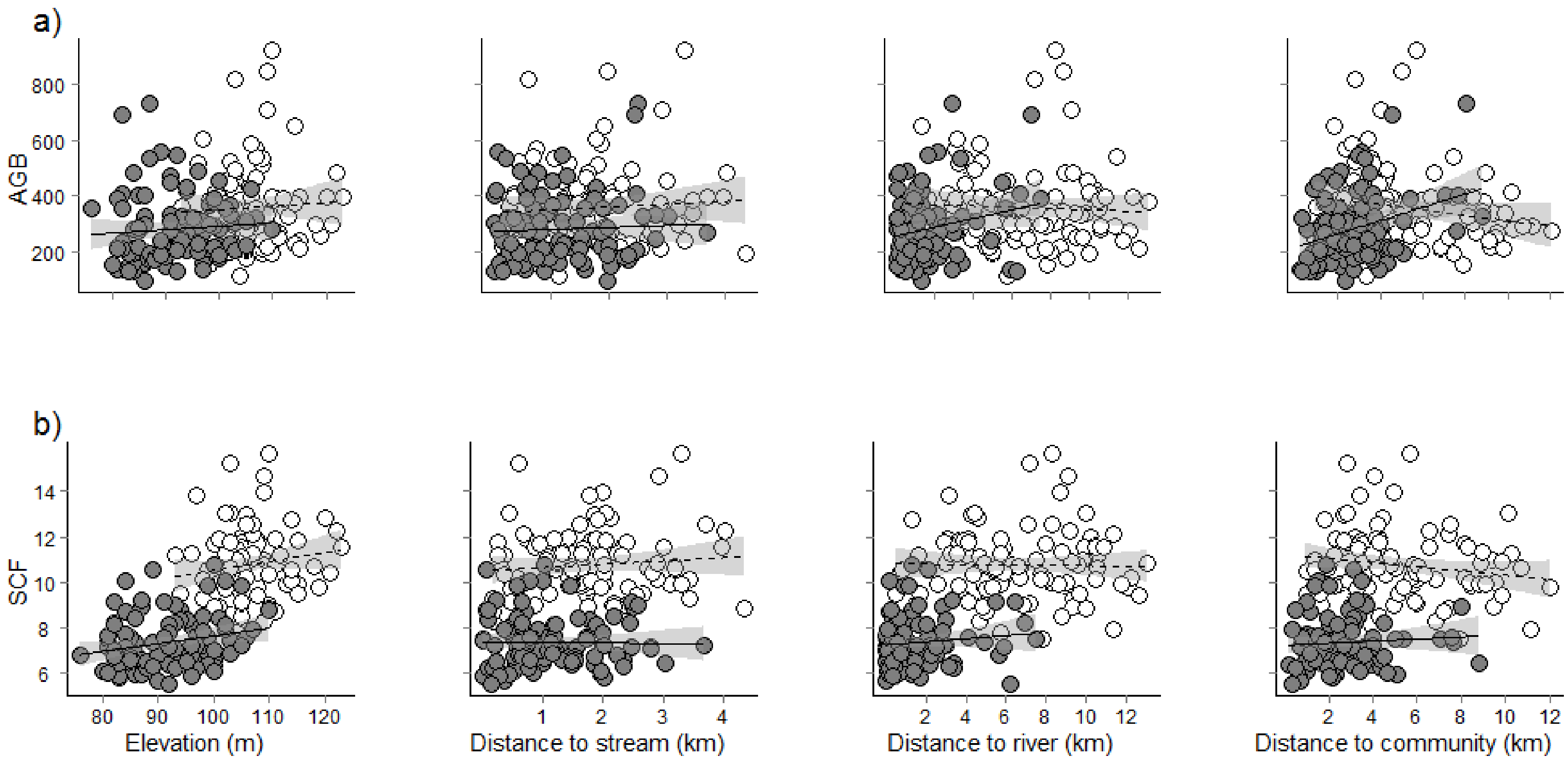
Appendix 2.1. *Relationship between tree DBH and canopy height for 996 stems measured in a remote Amazonian* terra firme *forest (dashed line) at Urucu, which is located some 200 km from our study landscape along the Rio Juruá (Peres 1994). Solid line indicates the predicted relationship for* várzea *forest assuming height = 30 m when DBH = 100 cm.*

Appendix 2.2. *Imaging dates for ALOS ScanSAR (Path 430, Frame 3750), corresponding to Juruá river stage heights measured at the Porto Gavião gauge (ANA station 12840000), and inundation period metrics based on a reconstructed 38-year stage record (1973-2010). This series of 12 ScanSAR scenes was used to classify all* várzea *forest across the study landscape by mean annual flood duration. The value for each forest plot was subsequently extracted, using the mean flood duration whenever a plot spanned more than one flood duration category (21 of the 100* várzea *plots).*

ScanSAR image date	River stage (cm)	Flooded days/yr	Flooded mo/yr	Low water recurrence interval (yrs)	High water recurrence interval (yrs)	Flood duration category (mo/yr)
09/10/2008	31	355	11.7	3.45	1	9-12
22/08/2007	123	334	11.0	1.52	1	9-12
24/08/2008	161	320	10.5	1.23	1	9-12
19/11/2006	287	285	9.4	1.03	1	9-12
07/07/2007	312	279	9.2	1.03	1	9-12
24/11/2008	541	242	8.0	1	1	6-8
04/01/2007	1074	181	6.0	1	1	6-8
07/01/2008	1318	121	4.0	1	1	3-5
22/05/2007	1360	99	3.3	1	1.03	3-5
24/05/2008	1422	26	0.9	1	1.65	1-2
08/04/2008	1457	3	0.1	1	6.33	< 1
11/04/2009	1458	3	0.1	1	7.60	< 1



Appendix 2.3. *Frequency distribution within tree DBH classes of (a) stem density (stems ha^{-1}), (b) forest basal area (m^2 ha^{-1}) and (c) aboveground biomass (Mg ha^{-1}) for* terra firme *(open boxes) and* várzea *(solid boxes) forests. Horizontal bars indicate medians, boxes indicate interquartile ranges, whiskers indicate minimum and maximum values and circles indicate outliers (observations 1.5 times higher or lower than 1st and 3rd quartile respectively).*



Appendix 2.4. *Relationships between landscape variables related to water stress (elevation and distance to nearest perennial stream) and historical logging access (distance to river and distance to community) with (a) aboveground biomass (AGB) and (b) the structural conversion factor (SCF) for 200 0.1-ha forest biomass plots in* terra firme *(open circles, dashed lines) and* várzea *(solid circles, solid lines) forests. Lines represent linear models; grey shading represents 95% confidence intervals.*

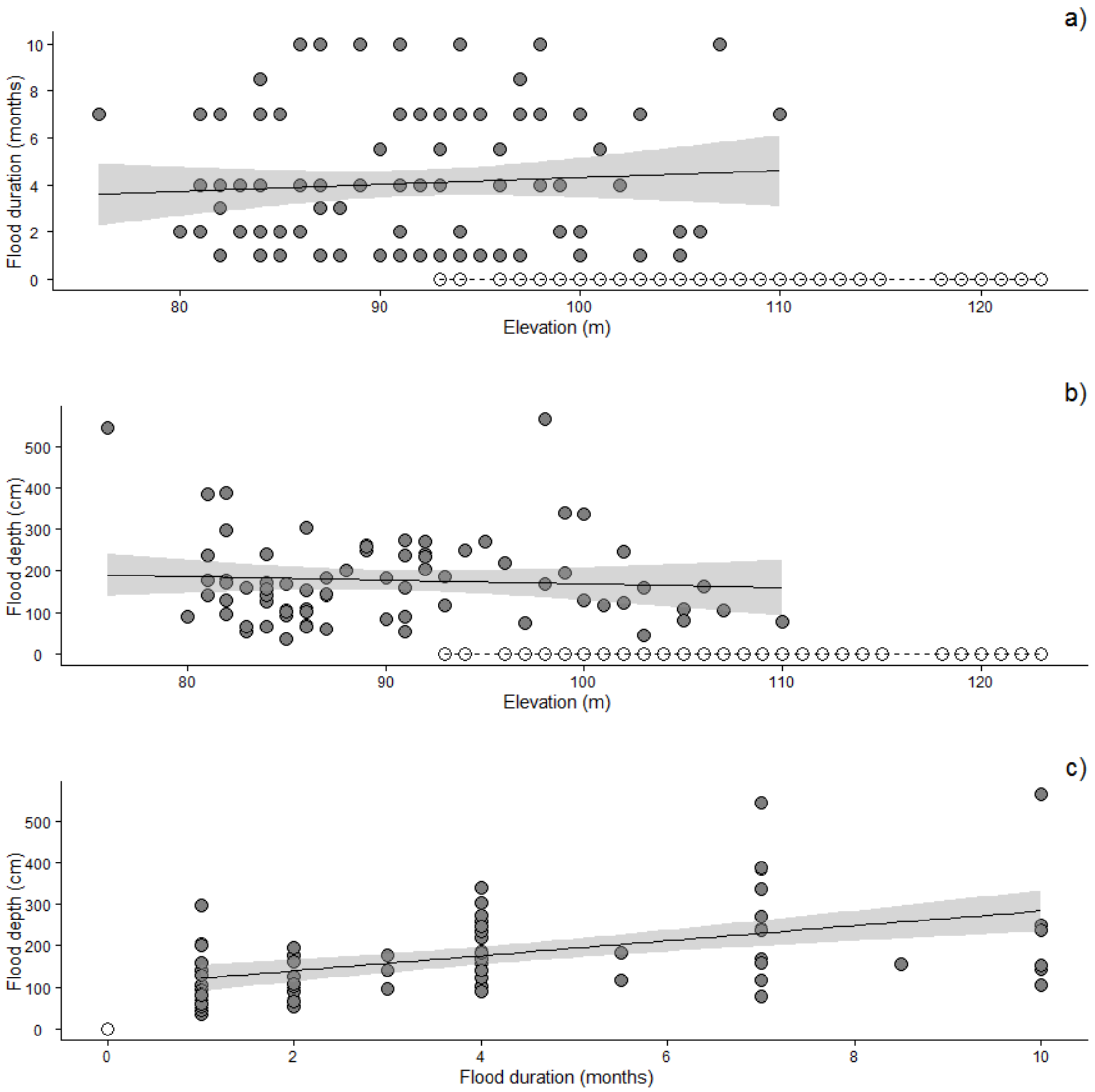
Appendix 2.5. *Spatial extent of forest types and their contributions to aboveground carbon stocks within two adjacent forest reserves from the Médio Juruá region of western Brazilian Amazonia, including flood duration categories within* várzea *forest determined by an ALOS ScanSAR remote sensing approach.*

				Reserve area (%, ha)			Carbon stock (%, Tg C)		
	No. plots	Mean WSG (g cm^{-3})	Mean AGB (Mg ha^{-1})	RESEX Médio Juruá	RDS Uacari	Total	RESEX Médio Juruá	RDS Uacari	Total
Terra firme [a]	100	0.668	358.42	81.65	80.09	80.57	85.55	84.38	84.75
Várzea [b]	100	0.581	281.92	17.40	18.08	17.87	14.45	15.62	15.25
< 1 mo/yr	24	0.569	269.92	0.81	2.26	1.81	0.64	1.79	1.43
1-2 mo/yr	16	0.567	307.68	2.78	2.15	2.35	2.01	1.56	1.70
3-5 mo/yr	29	0.589	261.85	8.03	5.84	6.52	6.30	4.60	5.13
6-8 mo/yr	23	0.591	262.18	3.80	4.37	4.19	3.38	3.91	3.75
9-12 mo/yr	8	0.605	367.81	1.97	3.46	3.00	2.12	3.74	3.24
Non-forested [c]	-	-	-	0.96	1.83	1.56	-	-	-
Total				253,227	632,949	886,176	42.8	106.1	148.9

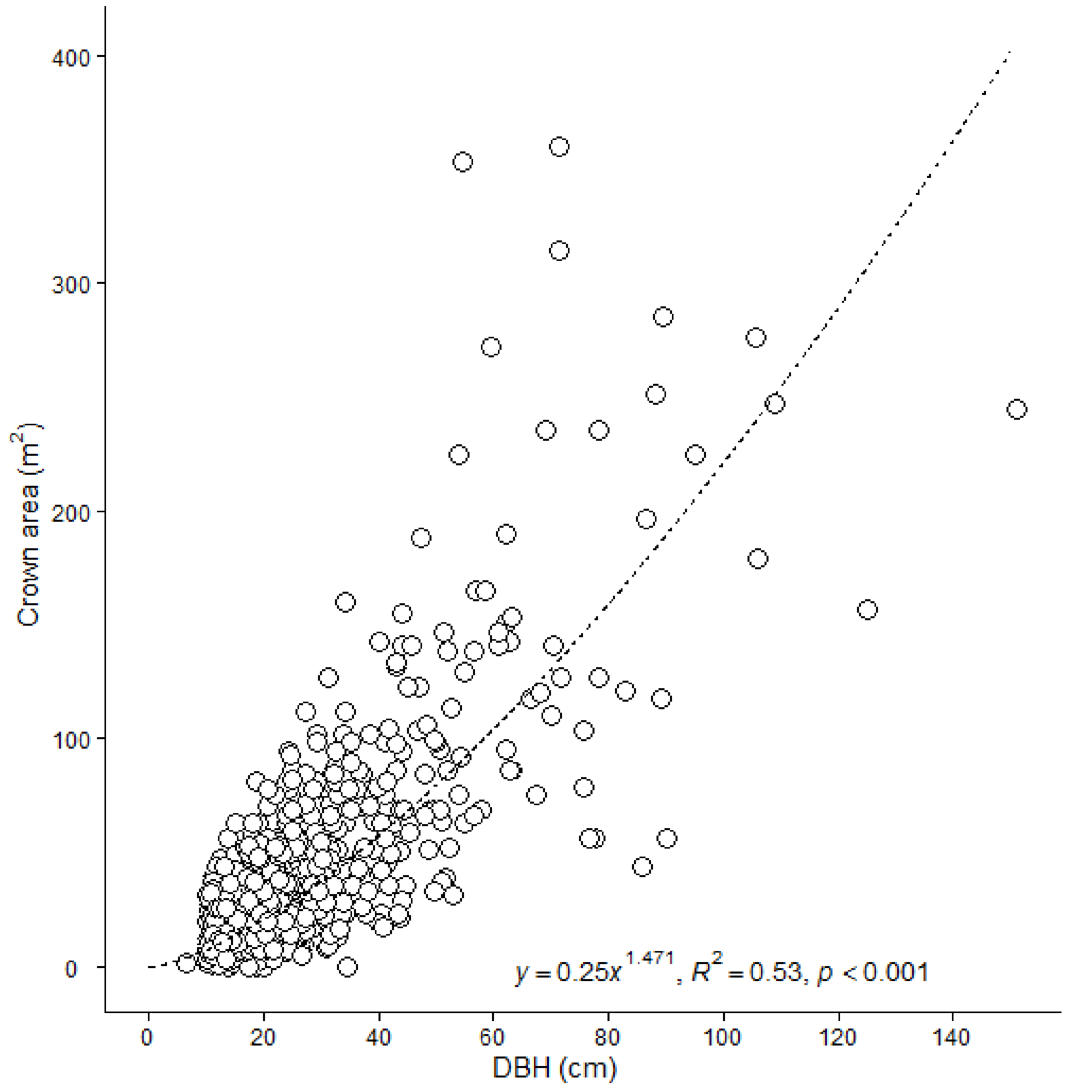
[a] Includes *paleovarzea* and upland tributaries.

[b] Includes following flood duration categories (months inundation per year).

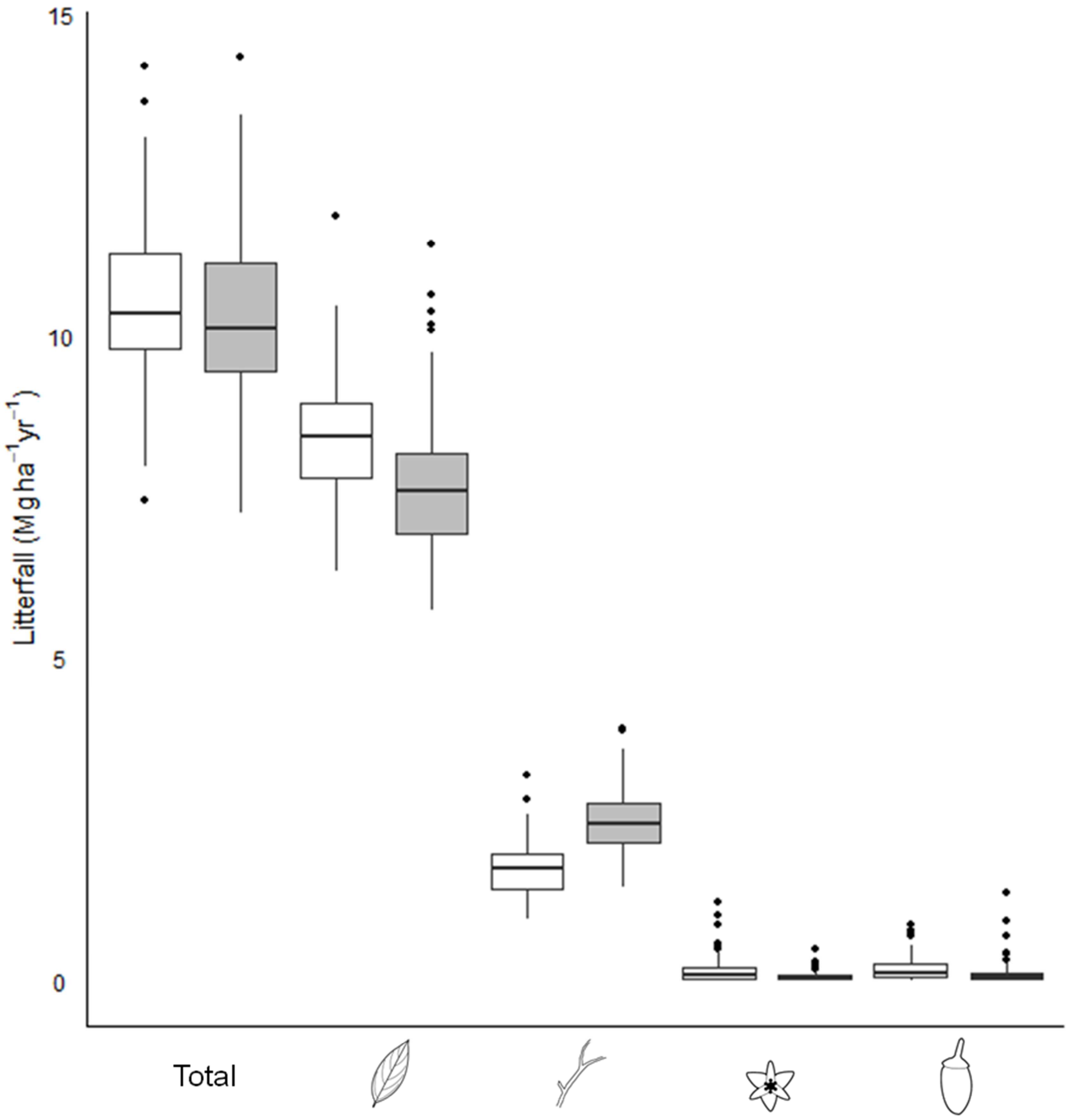
[c] Includes non-forested wetlands and permanent open water.



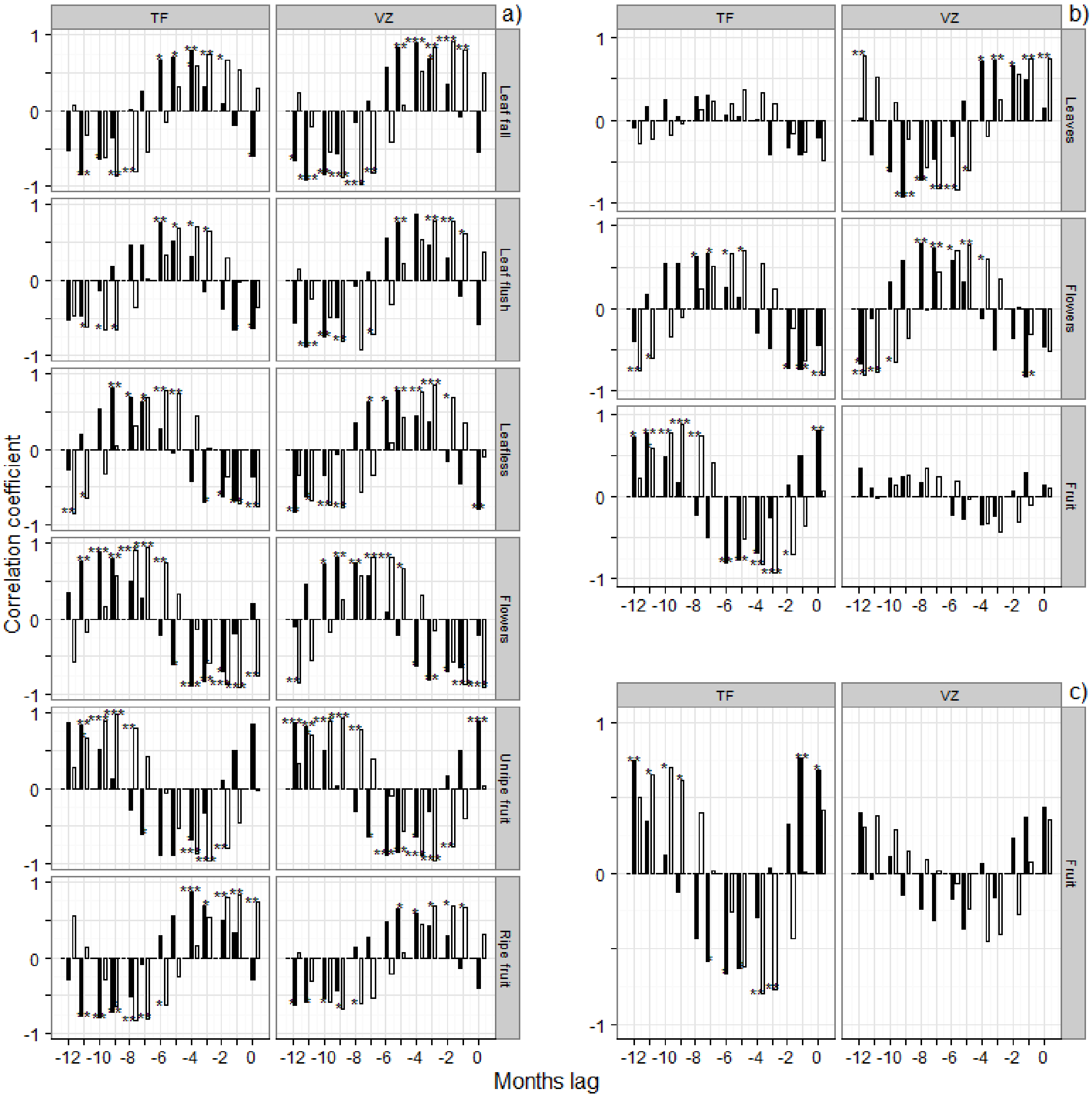
Appendix 2.6. *Relationships between SRTM-measured elevation (m), ScanSAR-measured flood duration (months) and field-measured flood depth (cm) in 73 0.1-ha forest biomass plots in* várzea *forests. Lines represent linear models; grey shading represents 95% confidence intervals.*



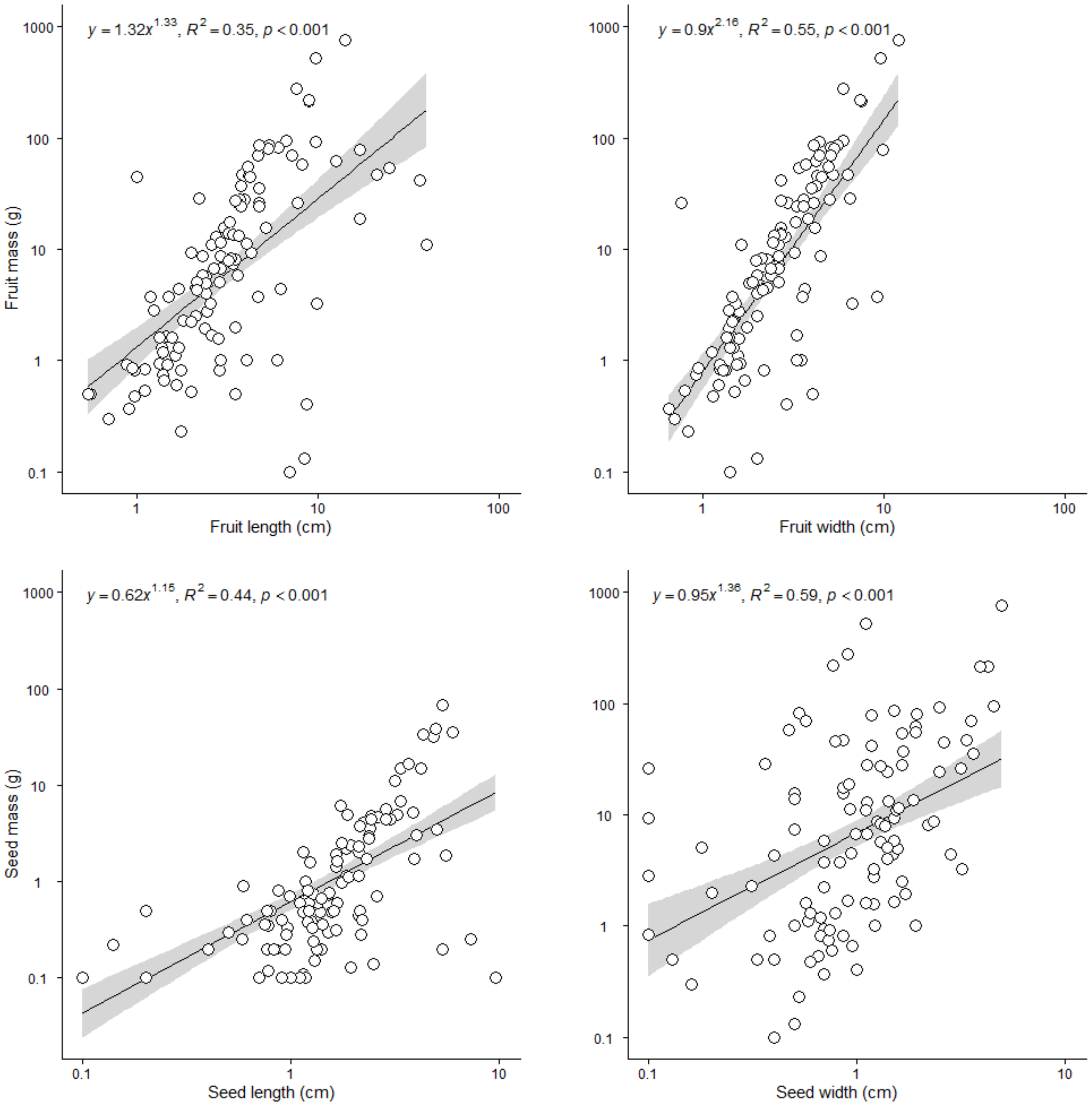
Appendix 3.1. *Relationship between tree DBH and crown area for 996 stems measured in a remote Amazonian* terra firme *forest (dashed line) at Urucu, which is located some 180 km from our study landscape along the Rio Juruá (Peres 1994). This relationship was used to predict hypothetical DBH values for lianas with measured crown areas, in order to derive a composite measure of community-wide fruit production.*



Appendix 3.2. *Annual fine litterfall (Mg ha^{-1} yr^{-1}) recorded from 24 bimonthly collections of 96 traps in both* terra firme *(open boxes) and* várzea *forest (solid boxes), showing total fine litterfall and values for individual vegetative and reproductive fractions: symbols represent (from left to right) leaves, fine woody litter (small branches, bark, trash), flowers, and fruit.*



Appendix 3.3. *Correlations coefficients (r) between plant phenophases and rainfall (solid bars) or flood water-level (open bars) within the same month and in each previous month (lag: 0 to -12) for (a) canopy observations, (b) trap collections, and (c) ground surveys of residual fruit-fall, in both* terra firme *and* várzea *forests. P-values are represented by * P < 0.05, ** P < 0.005, *** P < 0.001.*



Appendix 4.1. *Relationships between fruit and seed dimensions and fruit and seed mass in the Médio Juruá region of western Brazilian Amazonia. These were used to predict missing values for plant genera included in CART analysis (22.4% and 19.1% of cases for fruit mass and seed mass, respectively). Lines represent linear models; grey shading represents 95% confidence intervals.*

Appendix 4.2. *Frugivore species of the Medio Juruá region of Brazilian Amazonia, and their occurrence in* terra firme *and* várzea *forests. Species codes refer to numbers along the x-axis in Figure 4.3.*

	Family	Species	Brazilian name	English name	TF	VZ	Code
Mammals							
Primates							
	Atelidae	*Alouatta seniculus*	Guariba	Red Howler Monkey	+	+	11
		Ateles chamek	Macaco preto	Black Spider Monkey	+		5
		Lagothrix spp.[a]	Macaco Barrigudo	Woolly monkeys	+		1
	Cebidae	*Cebus albifrons*	Cairara	White-fronted Capuchin	+	+	2
		Cebus apella	Macaco Prego	Brown Capuchin	+	+	2
		Saguinus mystax, S. fuscicollis	Sauim/Lilico	Moustached Tamarin, Saddleback Tamarin	+		12
		Saimiri sciureus	Macaco de Cheiro	South American Squirrel Monkey	+	+	10
	Pithecidae	*Aotus nigriceps*	Macaco da Noite	Black-headed Night monkey	+	+	26
		Cacajao calvus	Uacari	Uacari	+	+	8
		Callicebus spp.[b]	Zogue-Zogue	Titi monkeys	+	+	18
		Pithecia spp.[c]	Parauacú	Saki monkeys	+		16
Ungulates							
	Cervidae	*Mazama americana, M. nemorivaga*	Veado (roxo/vermelho)	Brown Brocket, Red Brocket	+	+	17
	Tapiridae	*Tapirus terrestris*	Anta	Lowland Tapir	+		13
	Tayassuidae	*Tayassu pecari*	Queixada	White-lipped Peccary	+	+	6
		Pecari tajacu	Caititú	Collared Peccary	+	+	3
Rodents							
	Cuniculidae	*Cuniculus paca*	Paca	Spotted Paca	+		15
	Dasyproctidae	*Dasyprocta fuliginosa*	Cutia	Black Agouti	+	+	9
		Myoprocta acouchy	Cutiara	Red Acouchy	+		29
	Echymidae	*Echimys* sp., *Isothrix* sp.	Rato coró	tree rats		+	
	Sciuridae	*Sciurus* spp.	Coatipurú	squirrels	+	+	25

cont.

Appendix 4.2. cont.

	Family	Species	Brazilian name	English name	TF	VZ	Code
Carnivores							
	Mustelidae	*Eira barbara*	Irara	Tayra	+	+	37
	Procyonidae	*Nasua nasua*	Coati	Coati	+	+	33
		Potos flavus	Jupará	Kinkajou	+		38
		Bassaricyon gabbii	Janauaí	Olingo	+		
Birds							
Canopy birds							
	Cotingidae	*Cephalopterus, Cotinga, Porphyrolaema*	Anambé	cotingas	+		
	Cracidae	*Pipile cumanensis*	Cujubim	Blue-throated Piping guan	+		32
	Falconidae	*Ibycter americanus*	Cancão	Red-throated Caracara	+		
	Icteridae	*Cacicus* spp.	Japiim	caciques	+		36
		Clypicterus, Ocyalus, Psarocolius	Japó	oropendolas	+		34
	Psittacidae	*Amazona* spp.	Papagaio	amazona parrots	+	+	7
		Ara spp.	Arara	macaws	+	+	4
		Aratinga, Othopsittaca	Maracanã	aratinga parakeets and Red-bellied Macaw	+	+	23
		Brotogeris, Pyrrhura etc.	Periquito	parakeets	+	+	22
		Pionities, Pionopsitta, Pionus	Curica	parrots	+	+	27
	Ramphastidae	*Ramphastos* spp.	Tucano	toucans	+	+	14
		Pteroglossus spp.	Araçari	aracaris	+	+	28
	Trogonidae	*Trogon* spp.	Surucuá/Dorminhoco	trogons	+	+	35
Terrestrial birds							
	Columbidae	*Columba, Geotrygon, Leptotila, Patagioenas*	Juruti	pigeons/doves	+	+	
	Cracidae	*Crax globulosa*	Mutum piurí	Wattled Curassow	+	+	20
		Mitu tuberosa	Mutum	Razor-billed Curassow	+	+	20
		Ortalis guttata	Aracuã	Speckled Chachalaca	+		30
		Penelope jaquacu	Jacú	Spix's Guan	+		21
	Psophidae	*Psophia leucoptera*	Jacamim	Pale-winged Trumpeter	+		31
	Tinamidae	*Crypturellus* spp.	Nambú pequeno	small tinamous	+	+	24
		Tinamus spp.	Nambú grande	large tinamous	+	+	19

cont.

Appendix 4.2. cont.

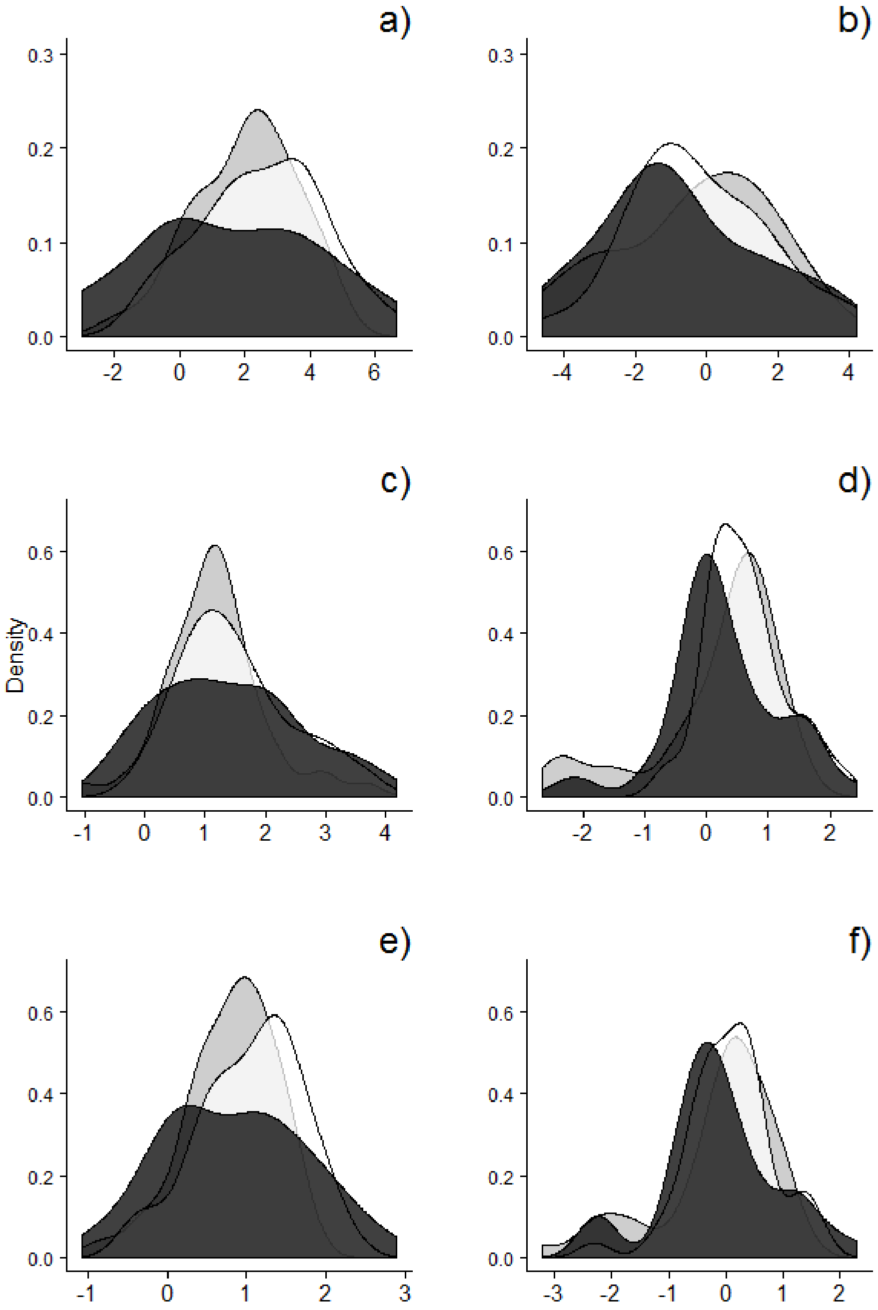
	Family	Species	Brazilian name	English name	TF	VZ	Code
Fish							
Bony fish							
	Anostomidae	*Leporinus*	Piau			+	42
		Schizodon	Aracú			+	
	Characidae	*Brycon*	Matrinxã, Mamurí			+	40
		Triportheus	Sardinha			+	44
		Colossoma spp.	Tambaquí, Pirapitinga			+	41
		Metynnis, Myleus, Myloplus, Mylossoma, Piaractus	Pacú			+	39
		Piaractus	Pirapitinga			+	43
		Pygocentrus	Piranha-cajú			+	50
		Serrasalmus	Piranha (various)			+	48
	Prochilodontidae	*Prochilodus*	Curimatã			+	53
		Semaprochilodus	Jaraquí			+	55
	Osteoglossidae	*Osteoglossum*	Aruanã			+	52
Cartilaginous fish							
	Auchenipteridae	*Trachelyopterus*	Cangati			+	54
	Doradidae	*Lithodoras, Megaladoras, Pterodoras*	Bacú			+	47
		Oxydoras	Cuiu-cuiú			+	
	Pimelodidae	*Leiarius*	Jandiá			+	46
		Phractocephalus	Pirarara			+	49
		Pimelodus	Mandi/Camisa de meia			+	51
Reptiles							
Turtles							
	Testudinidae	*Chelonoidis denticulata*	Jabuti	Yellow-footed tortoise	+	+	
		Podocnemis expansa	Tartaruga	South American river turtle		+	45
		Podocnemis sextuberculata	Iaçá	Six-tubercled river turtle		+	45
		Podocnemis unifilis	Tracajá	Yellow-spotted river turtle		+	45

[a] *L. poeppigii* (Poeppig's Woolly Monkey) and *L. cana* (Geoffroy's Woolly Monkey) on left and right bank of the Rio Juruá, respectively.

[b] *C. cupreus* (Coppery Titi Monkey) plus *C. regulus* and *C. purinus* (both = Collared Titi Monkey) on left and right bank of the Rio Juruá, respectively.

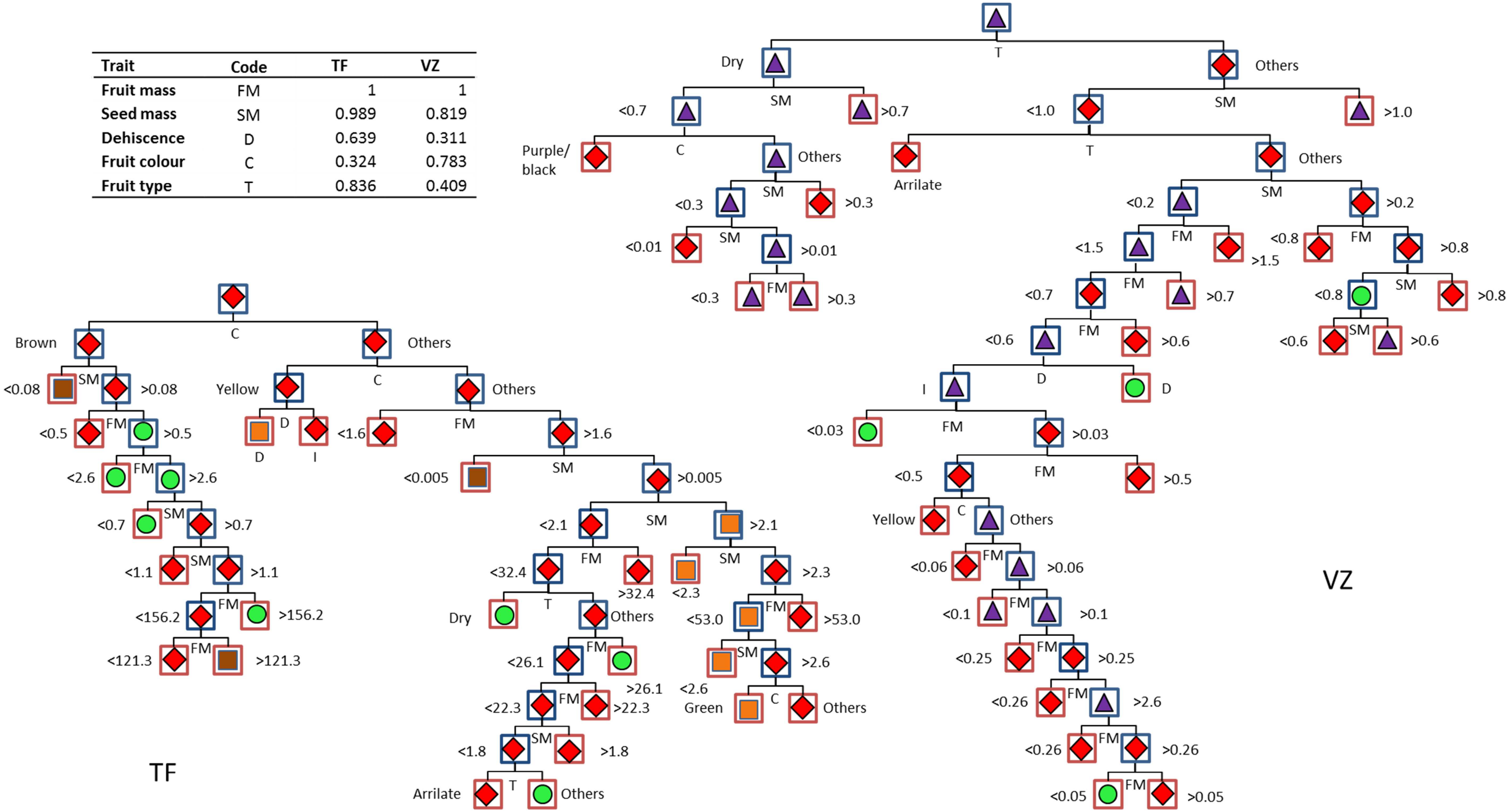
[c] *P. monachus* (Monk Saki Monkey) and *P. irrorata* (Bald-faced Saki Monkey) on left and right bank of the Rio Juruá, respectively.

Appendix 4.3. *Density distribution of log a) fruit mass (g), b) seed mass (g), c) fruit length (cm), d) seed length (cm), e) fruit width (cm), and f) seed width (cm) for plant genera occurring in* terra firme *(white curve),* várzea *(black curve) and both forest types (grey curve).*



Appendix 4.4. *Regression trees for* terra firme *and* várzea *and importance values for fruit traits. Symbols represent major classes of frugivores as in the legend for Figure 4.4.*

Trait	Code	TF	VZ
Fruit mass	FM	1	1
Seed mass	SM	0.989	0.819
Dehiscence	D	0.639	0.311
Fruit colour	C	0.324	0.783
Fruit type	T	0.836	0.409



Appendix 5.1. *Neotropical primate taxonomy (Rosenberger 2011) and corresponding functional ecospecies (updated from Peres & Janson 1999)*

Family	Subfamily	Tribe	Genus	Functional ecospecies	Code	Taxonomic species included
Atelidae	Atelinae	Alouattini	*Alouatta*	Howler monkeys	Al	*Alouatta* spp.
		Atelini	*Ateles*	Spider monkeys	At	*Ateles* spp.
			Brachyteles	Woolly spider monkeys	Br	*Brachyteles* spp.
			Lagothrix (inc. *Oreonax*)	Woolly monkeys	La	*Lagothrix* spp., *Oreonax flavicauda*
Cebidae	Cebinae	Cebini	*Cebus*	White-fronted capuchins	Cf	*C. albifrons*, *C. capucinus*
				Brown capuchins	Ca	*C. apella* + *Cebus* spp. (see Appendix 2)
				Wedge-capped capuchins	Co	*C. kaapori*, *C. olivaceus*
		Saimirini	*Saimiri*	Squirrel monkeys	Sa	*Saimiri* spp.
	Callitrichinae	Saguinini	*Saguinus*	Saddle-back tamarins	Sf	*S. fuscicollis, S. inustus, S. melanoleucus, S. nigricollis, S. tripartitus*
				Moustached tamarins	Sx	*S. mystax, S. labiatus, S. imperator*
				Midas tamarins	Sm	*S. midas, S. niger*
				Bare-faced tamarins	So	*S. bicolor, S. geoffroyi, S. leucopus, S. martinsi, S. oedipus*

cont.

Appendix 5.1. cont.

Family	Subfamily	Tribe	Genus	Functional ecospecies	Code	Taxonomic species included
Cebidae	Callitrichinae cont.	Callitrichini	*Callithrix* (inc. *Mico*)	Atlantic marmosets	Cx	*Callithrix* spp.
				Amazonian marmosets	Mi	*Mico* spp.
			Cebuella (inc. *Callibella*)	Pygmy marmosets	Cb	*Cebuella pygmaea*, *Callibella humilis*
			Leontopithecus	Lion tamarins	Le	*Leontopithecus* spp.
		Callimiconini	*Callimico*	Goeldi's monkeys	Cg	*Callimico goeldii*
Pitheciidae	Pitheciinae	Pitheciini	*Pithecia*	Saki monkeys	Pi	*Pithecia* spp.
			Chiropotes	Bearded saki monkeys	Ch	*Chiropotes* spp.
			Cacajao	Uakaries	Cj	*Cacajao* spp.
	Homunculinae	Callicebini	*Callicebus*	Amazonian dusky titi monkeys	Cm	*C. moloch* + *Callicebus* spp. (see Appendix 5.2)
				Atlantic dusky titi monkeys	Cp	*C. personatus* + *Callicebus* spp. (see Appendix 5.2)
				Collared titi monkeys	Ct	C. torquatus + *Callicebus* spp. (see Appendix 5.2)
		Aotini	Aotus	Night monkeys	Ao	Aotus spp.

Appendix 5.2. *Neotropical primate species with conservation status (IUCN 2011), body mass (kg) (Smith & Jungers 1997) and corresponding functional group (FG) or 'ecospecies' (sensu Peres & Janson 1999, see Appendix 5.1 for overview).*

Subfamily	Tribe	Genus	FG	Species	IUCN status	Body mass
Atelinae	Alouattini	*Alouatta*	Al	*Alouatta arctoidea*	LC	
				Alouatta belzebul	VU	6.40
				Alouatta caraya	LC	5.38
				Alouatta discolor	VU	
				Alouatta guariba	LC	5.54
				Alouatta juara	LC	
				Alouatta macconnelli	LC	
				Alouatta nigerrima	LC	
				Alouatta palliata	LC	6.24
				Alouatta pigra	EN	8.92
				Alouatta puruensis	LC	
				Alouatta sara	LC	
				Alouatta seniculus	LC	6.09
				Alouatta ululata	EN	
	Atelini	*Ateles*	At	*Ateles belzebuth*	EN	8.07
				Ateles chamek	EN	9.37
				Ateles fusciceps	CR	9.03
				Ateles geoffroyi	EN	7.54
				Ateles hybridus	CR	
				Ateles marginatus	EN	
				Ateles paniscus	VU	8.78
		Brachyteles	Br	*Brachyteles arachnoides*	EN	8.84
				Brachyteles hypoxanthus	CR	
		Lagothrix	La	*Lagothrix cana*	EN	8.22
				Lagothrix lagotricha	VU	7.15
				Lagothrix lugens	CR	
				Lagothrix poeppigii	VU	
		Oreonax [a]		*Oreonax flavicauda*	CR	10.00
Cebinae	Cebini	*Cebus*	Cf	*Cebus albifrons*	LC	2.74
				Cebus capucinus	LC	3.10
			Ca	*Cebus apella*	LC	3.09
				Cebus cay	LC	
				Cebus flavius	CR	
				Cebus libidinosus	LC	
				Cebus macrocephalus	LC	
				Cebus nigritus	NT	
				Cebus robustus	EN	
				Cebus xanthosternos	CR	
			Co	*Cebus kaapori*	CR	
				Cebus olivaceus	LC	2.91
	Saimirini	*Saimiri*	Sa	*Saimiri boliviensis*	LC	0.81
				Saimiri oerstedii	VU	0.79
				Saimiri sciureus	LC	0.79
				Saimiri ustus	NT	0.86
				Saimiri vanzolinii	VU	0.80

cont.

Appendix 5.2. cont.

Subfamily	Tribe	Genus	FG	Species	IUCN status	Body mass
Callitrichinae	Saguinini	*Saguinus*	Sf	*Saguinus fuscicollis*	LC	0.35
				Saguinus inustus	LC	0.69
				Saguinus melanoleucus	LC	
				Saguinus nigricollis	LC	0.48
				Saguinus tripartitus	NT	
			Sx	*Saguinus imperator*	LC	0.47
				Saguinus labiatus	LC	0.51
				Saguinus mystax	LC	0.52
			Sm	*Saguinus midas*	LC	0.55
				Saguinus niger	VU	
			So	*Saguinus bicolor*	EN	0.43
				Saguinus geoffroyi	LC	
				Saguinus leucopus	EN	0.49
				Saguinus martinsi	LC	
				Saguinus oedipus	CR	0.41
	Callitrichini	*Callithrix*	Cx	*Callithrix aurita*	VU	0.43
				Callithrix flaviceps	EN	0.41
				Callithrix geoffroyi	LC	0.36
				Callithrix jacchus	LC	0.35
				Callithrix kuhlii	NT	0.38
				Callithrix penicillata	LC	0.33
		Mico [b]	Mi	*Mico acariensis*	DD	
				Mico argentatus	LC	0.35
				Mico chrysoleucus	DD	
				Mico emiliae	DD	0.32
				Mico humeralifer	DD	0.42
				Mico intermedius	LC	
				Mico leucippe	VU	
				Mico manicorensis	LC	
				Mico marcai	DD	
				Mico mauesi	LC	0.37
				Mico melanurus	LC	
				Mico nigriceps	DD	0.38
				Mico rondoni	VU	
				Mico saterei	LC	
		Callibella [c]	Cb	*Callibella humilis*	VU	
		Cebuella		*Cebuella pygmaea*	LC	0.12
		Leontopithecus	Le	*Leontopithecus caissara*	CR	0.57
				Leontopithecus chrysomelas	EN	0.58
				Leontopithecus chrysopygus	EN	0.58
				Leontopithecus rosalia	EN	0.61
	Callimiconin	*Callimico*	Cg	*Callimico goeldii*	VU	0.48
Pitheciinae	Pithecini	*Pithecia*	Pi	*Pithecia aequatorialis*	LC	2.25
				Pithecia albicans	VU	3.00
				Pithecia irrorata	LC	2.16
				Pithecia monachus	LC	2.36
				Pithecia pithecia	LC	1.76
		Chiropotes	Ch	*Chiropotes albinasus*	EN	2.82
				Chiropotes chiropotes	LC	2.74
				Chiropotes satanas	CR	3.03
				Chiropotes utahickae	EN	

cont.

Appendix 5.2. cont.

Subfamily	Tribe	Genus	FG	Species	IUCN status	Body mass
		Cacajao	Cj	*Cacajao ayresi*	VU	
				Cacajao calvus	VU	3.17
				Cacajao hosomi	VU	
				Cacajao melanocephalus	LC	2.94
Homunculinae	Callicebini	*Callicebus*	Cm	*Callicebus aureipalatii*	LC	
				Callicebus baptista	LC	
				Callicebus bernhardi	LC	
				Callicebus brunneus	LC	0.83
				Callicebus caligatus	LC	0.88
				Callicebus cinerascens	LC	
				Callicebus cupreus	LC	1.07
				Callicebus discolor	LC	
				Callicebus donacophilus	LC	0.95
				Callicebus dubius	LC	
				Callicebus hoffmannsi	LC	1.06
				Callicebus modestus	EN	
				Callicebus moloch	LC	0.99
				Callicebus oenanthe	CR	
				Callicebus olallae	EN	
				Callicebus ornatus	VU	
				Callicebus pallescens	LC	
				Callicebus stephennashi	DD	
			Cp	*Callicebus barbarabrownae*	CR	
				Callicebus coimbrai	EN	
				Callicebus melanochir	VU	
				Callicebus nigrifrons	NT	
				Callicebus personatus	VU	1.33
			Ct	*Callicebus lucifer*	LC	
				Callicebus lugens	LC	
				Callicebus medemi	VU	
				Callicebus purinus	LC	
				Callicebus regulus	LC	
				Callicebus torquatus	LC	1.25
	Aotini	*Aotus*	Ao	*Aotus azarae*	LC	1.21
				Aotus brumbacki	VU	
				Aotus griseimembra	VU	
				Aotus jorgehernandezi	DD	
				Aotus lemurinus	VU	0.90
				Aotus miconax	VU	
				Aotus nancymaae	LC	0.79
				Aotus nigriceps	LC	0.96
				Aotus trivirgatus	LC	0.77
				Aotus vociferans	LC	0.70
				Aotus zonalis	DD	

[a] Included in *Lagothrix* by Rosenberger (2011)
[b] Included in *Callithrix* by Rosenberger (2011)
[c] Included in *Cebuella* by Rosenberger (2011)

Appendix 6.1. *Diet composition of neotropical primate with mean values in bold per ecospecies.*

	Proportions of dietary classes [a]																		
Ecospecies: Species	Fr	Sd	Fr+Sd	Fl	Lv	Bd	Lv+Bd	Ex	Invert.	Vert.	Prey	Other	Prop. year	Mths	Hrs	Cal. [b]	Met. [c]	Cou. [d]	Reference
Al - Howler monkeys	**34.9**	**0.2**	**35.1**	**7.2**	**53.8**	**0.8**	**54.7**	**0.0**	**0.0**	**0.0**	**0.0**	**2.9**							
Alouatta caraya	19.0	0.0	19.0	12.0	64.0	4.0	68.0	0.0	0.0	0.0	0.0	1.0	0.92	17	1680	R	GF	AR	Bravo & Sallenave 2003
Alouatta caraya	19.0	0.0	19.0	6.0	64.0	0.0	64.0	0.0	0.0	0.0	0.0	10.0	1.00	12	1437	T	GF	AR	Agostini et al. 2010
Alouatta guariba	24.0	0.0	24.0	6.0	62.0	0.0	62.0	0.0	0.0	0.0	0.0	7.0	1.00	12	1437	T	GF	AR	Agostini et al. 2010
Alouatta pigra	40.8	0.0	40.8	10.6	45.1	0.0	45.1	0.0	0.0	0.0	0.0	3.4	1.00	14	1160	T	GF	BZ	Silver et al. 1998
Alouatta belzebul	43.4	0.0	43.4	11.3	45.0	0.0	45.0	0.0	0.0	0.0	0.0	0.4	0.83	10	1203	T	GF	BR	Pinto et al. 2003
Alouatta guariba	41.0	0.0	41.0	1.7	57.3	0.0	57.3	0.0	0.0	0.0	0.0	0.0	1.00	12	77	T	GF	BR	Miranda & Passos 2004
Alouatta guariba	15.6	0.0	15.6	8.4	70.6	5.4	76.0	0.0	0.0	0.0	0.0	0.0	0.75	11	493		GF	BR	Mendes 1989
Alouatta guariba	16.2	0.0	16.2	9.9	55.2	4.6	59.8	0.0	0.0	0.0	0.0	13.8	1.00	12	580	R	GF	BR	Marques 2001
Alouatta seniculus	47.3	0.0	47.3	1.5	45.5	0.0	45.5	0.0	0.0	0.0	0.0	5.7	0.83	10	492		GF	BR	Queiroz 1995
Alouatta caraya	28.9	0.0	28.9	2.7	60.9	0.0	60.9	0.0	0.0	0.0	0.0	7.5	1.00	12	745	R	GF	BR	Bicca-Marques & Callegaro-Marques 1994
Alouatta guariba	8.0	3.7	11.7	7.5	80.7	0.0	80.7	0.0	0.0	0.0	0.0	0.0	1.00	12	555	R	GF	BR	Martins 2008
Alouatta belzebul	36.5	0.0	36.5	4.9	58.6	0.0	58.6	0.0	0.0	0.0	0.0	0.0	1.00	12	2002		GF	BR	Souza et al. 2002
Alouatta guariba	47.9	0.0	47.9	1.4	50.6	0.0	50.6	0.0	0.0	0.0	0.0	0.0	1.00	12	122	R	GF	BR	Aguiar et al. 2003
Alouatta belzebul	55.6	0.0	55.6	5.7	24.8	0.0	24.8	0.0	0.0	0.0	0.0	13.9	0.83	10	540	R	GF	BR	Pinto & Setz 2004
Alouatta guariba	46.9	0.0	46.9	11.9	34.1	6.3	40.4	0.0	0.0	0.0	0.0	0.9	1.00	12	484	R	GF	BR	Marques 2001
Alouatta guariba	5.0	0.0	5.0	12.0	73.0	0.0	73.0	0.0	0.0	0.0	0.0	10.0	1.00	12	719	R	GF	BR	Chiarello 1994
Alouatta guariba	15.0	0.0	15.0	10.0	75.0	0.0	75.0	0.0	0.0	0.0	0.0	0.0	1.00	42	61	B	T	BR	Galetti et al. 1994
Alouatta belzebul	70.0	0.0	70.0	20.5	9.5	0.0	9.5	0.0	0.0	0.0	0.0	0.0	1.00	13	262		GF	BR	Bonvicino 1989
Alouatta belzebul	37.2	0.0	37.2	10.6	51.6	0.0	51.6	0.0	0.0	0.0	0.0	0.7	0.50	6	749	R	GF	BR	Camargo 2005

cont.

Appendix 6.1. cont.

	Proportions of dietary classes [a]																		
Ecospecies: Species	Fr	Sd	Fr+Sd	Fl	Lv	Bd	Lv+Bd	Ex	Invert.	Vert.	Prey	Other	Prop. year	Mths	Hrs	Cal. [b]	Met. [c]	Cou. [d]	Reference
Alouatta seniculus	52.3	1.0	53.3	1.1	35.3	0.0	35.3	0.0	0.0	0.0	0.0	10.3	0.83	10	497	T	GF	CO	Palacios & Rodrigues 2001
Alouatta seniculus	42.3	0.0	42.3	5.4	52.1	0.0	52.1	0.0	0.0	0.0	0.0	0.0	0.83	10	340	T	GF	CO	Gaulin & Gaulin 1982
Alouatta seniculus	39.0	4.0	43.0	4.0	51.0	0.0	51.0	0.0	0.0	0.0	0.0	2.0	1.00	13	900	R	GF	CO	Stevenson et al. 2000
Alouatta seniculus	45.1	0.0	45.1	5.7	49.2	0.0	49.2	0.0	0.0	0.0	0.0	0.0	0.50	6	388	R	GF	CO	Giraldo et al. 2007
Alouatta palliata	17.7	0.0	17.7	18.5	63.7	0.0	63.7	0.0	0.0	0.0	0.0	0.0	1.00	14	2071	T	GF	CR	Rockwood & Glander 1979
Alouatta palliata	23.0	0.0	23.0	8.5	62.0	6.5	68.5	0.0	0.0	0.0	0.0	0.0	1.00	15	348	R	GF	CR	Stoner 1996
Alouatta palliata	28.5	0.0	28.5	22.5	45.1	3.9	49.0	0.0	0.0	0.0	0.0	0.0	0.67	24	394	T	GF	CR	Chapman 1987
Alouatta seniculus	45.8	0.0	45.8	0.4	53.4	0.0	53.4	0.0	0.1	0.0	0.1	0.4	1.00	21	180		None	FG	Guillotin et al. 1994
Alouatta seniculus	25.3	0.0	25.3	12.4	57.0	0.0	57.0	0.0	0.0	0.0	0.0	4.9	1.00	19	1540	R	GF	FG	Julliot 1996
Alouatta seniculus	42.0	0.0	42.0	0.7	56.9	0.0	56.9	0.0	0.0	0.0	0.0	0.5	0.50	6	432	R	GF	FG	Simmen & Sabatier 1996
Alouatta palliata	35.0	0.0	35.0	5.0	60.0	0.0	60.0	0.0	0.0	0.0	0.0	0.0	0.75	9	509	T	GF	MX	Muñoz et al. 2006
Alouatta pigra	17.4	0.0	17.4	5.3	76.4	0.0	76.4	0.0	0.0	0.0	0.0	0.9	1.00	12	499	T	GF	MX	Pozo-Montuy & Serio-Silva 2006
Alouatta palliata	15.0	0.0	15.0	13.0	72.0	0.0	72.0	0.0	0.0	0.0	0.0	0.0	0.67	8	302	T	GF	MX	Valle et al. 2001
Alouatta palliata	43.3	0.0	43.3	2.5	47.4	0.0	47.4	0.0	0.0	0.0	0.0	6.8	0.92	11	900	T	GF	MX	Asensio et al. 2007
Alouatta palliata	39.3	0.0	39.3	0.9	54.3	0.0	54.3	0.0	0.0	0.0	0.0	4.3	1.00	12	2357	T	GF	MX	Estrada et al. 1999; Solano et al. 1999
Alouatta palliata	44.3	0.0	44.3	1.6	53.3	0.0	53.3	0.0	0.0	0.0	0.0	0.9	1.00	12	960	T	GF	MX	Dunn et al. 2009
Alouatta palliata	24.5	0.0	24.5	0.3	72.5	0.0	72.5	0.0	0.0	0.0	0.0	3.5	0.58	14	1680	T	GF	MX	Gonzalez-Picaso et al. 2001
Alouatta palliata	34.8	0.0	34.8	7.9	55.7	0.0	55.7	0.0	0.0	0.0	0.0	1.6	1.00	14	1300	B	GF	NI	Williams-Guillén 2003
Alouatta palliata	33.3	0.0	33.3	8.5	47.2	2.9	50.1	0.0	0.0	0.0	0.0	8.1	1.00	13	1286	B	GF	NI	Raguet-Schofield 2010
Alouatta palliata	42.1	0.0	42.1	9.6	48.2	0.0	48.2	0.0	0.0	0.0	0.0	0.0	0.75	9	540	?	GF	PA	Milton 1979 (cites Milton 1977)
Alouatta seniculus	56.0	0.0	56.0	4.5	39.0	0.0	39.0	0.0	0.0	0.0	0.0	0.5	1.00	36	247	R	GF	PE	Soini 1986
Alouatta seniculus	69.0	0.0	69.0	2.4	28.6	0.0	28.6	0.0	0.0	0.0	0.0	0.0	1.00	12	16		T	SR	Mittermeier & van Roosmalen 1981

cont.

Appendix 6.1. cont.

	Proportions of dietary classes [a]												Prop.						
Ecospecies: Species	Fr	Sd	Fr+Sd	Fl	Lv	Bd	Lv+Bd	Ex	Invert.	Vert.	Prey	Other	year	Mths	Hrs	Cal. [b]	Met. [c]	Cou. [d]	Reference
At - Spider monkeys	**76.8**	**1.5**	**78.3**	**4.4**	**11.7**	**0.3**	**12.0**	**0.0**	**0.3**	**0.0**	**0.3**	**5.1**							
Ateles chamek	96.1	0.0	96.1	0.0	3.9	0.0	3.9	0.0	0.0	0.0	0.0	0.0	1.00	15	90	R	GF	BO	Quevedo et al. 2008
Ateles chamek	82.0	0.0	82.0	4.7	13.0	0.0	13.0	0.0	0.1	0.0	0.1	0.2	0.67	8	863	T	GF	BO	Felton et al. 2008
Ateles chamek	85.8	0.0	85.8	2.9	10.7	0.0	10.7	0.0	0.0	0.0	0.0	0.6	1.00	12	1199	T	GF	BO	Wallace et al. 2005
Ateles belzebuth	91.7	0.0	91.7	0.0	8.3	0.0	8.3	0.0	0.0	0.0	0.0	0.0	1.00	14	1356	R	GF	BR	Nunes 1998
Ateles belzebuth	72.0	2.0	74.0	5.0	12.0	0.0	12.0	0.0	0.0	0.0	0.0	9.0	1.00	24	1567	R	GF	CO	Stevenson et al. 2000
Ateles hybridus	45.0	1.0	46.0	2.0	24.0	0.0	24.0	0.0	0.0	0.0	0.0	28.0	0.75	9	40	R	GF	CO	Saavedra 2009
Ateles geoffroyi	60.0	0.0	60.0	26.0	14.0	0.0	14.0	0.0	0.0	0.0	0.0	0.0	1.00	12	460	T	GF	CR	Riba-Hernández & Stoner 2005
Ateles geoffroyi	77.8	0.0	77.8	9.8	8.5	2.6	11.1	0.0	1.3	0.0	1.3	0.0	0.67	24	335	T	GF	CR	Chapman 1987
Ateles belzebuth	87.0	0.0	87.0	1.0	9.0	0.0	9.0	0.0	0.7	0.0	0.7	2.3	1.00	18	457	R	GF	EC	Dew 2005
Ateles belzebuth	78.8	0.0	78.8	1.3	7.7	0.0	7.7	0.0	0.0	0.0	0.0	12.2	0.58	9	1268	T	GF	EC	Russo et al. 2005; Suarez 2006
Ateles paniscus	90.2	0.0	90.2	0.0	9.6	0.0	9.6	0.0	0.1	0.1	0.2	0.0	1.00	21	132		None	FG	Guillotin et al. 1994
Ateles paniscus	85.4	1.8	87.2	2.5	9.5	0.0	9.5	0.0	0.0	0.0	0.0	0.8	0.50	6	432	R	GF	FG	Simmen & Sabatier 1996
Ateles geoffroyi	56.5	19.5	76.0	6.4	14.1	1.4	15.5	0.0	2.0	0.0	2.0	0.0	0.75	10	581		GF	GT	Cant 1990
Ateles geoffroyi	55.6	0.0	55.6	1.2	18.5	0.0	18.5	0.0	0.0	0.0	0.0	24.7	0.75	15	1000	T	GF	MX	Chaves et al. 2011
Ateles geoffroyi	82.2	0.0	82.2	1.0	17.2	0.0	17.2	0.0	0.0	0.0	0.0	0.9	1.00	13	1200	?	GF	PA	Russo et al. 2005 (Campbell 2000)
Ateles paniscus	82.9	Fruit[e]	82.9	6.4	7.9	0.0	7.9	0.0	0.2	0.0	0.2	2.5	1.00	26	1107		GF	SR	van Roosmalen 1985
Br - Woolly spider monkeys	**39.3**	**3.3**	**42.6**	**9.3**	**45.5**	**0.0**	**45.5**	**0.0**	**0.0**	**0.0**	**0.0**	**2.5**							
Brachyteles hypoxanthus	32.0	0.0	32.0	11.0	51.0	0.0	51.0	0.0	0.0	0.0	0.0	6.0	1.00	14	1200		GF	BR	Strier 1991
Brachyteles arachnoides	12.1	16.5	28.6	16.1	55.3	0.0	55.3	0.0	0.0	0.0	0.0	0.0	1.00	12	534	R	GF	BR	Martins 2008
Brachyteles arachnoides	20.0	0.0	20.0	13.4	66.6	0.0	66.6	0.0	0.0	0.0	0.0	0.0	0.83	10	900	T	GF	BR	Milton 1984

cont.

Appendix 6.1. cont.

	Proportions of dietary classes [a]												Prop.						
Ecospecies: Species	Fr	Sd	Fr+Sd	Fl	Lv	Bd	Lv+Bd	Ex	Invert.	Vert.	Prey	Other	year	Mths	Hrs	Cal. [b]	Met. [c]	Cou. [d]	Reference
Brachyteles arachnoides	73.2	0.0	73.2	1.7	21.6	0.0	21.6	0.0	0.0	0.0	0.0	3.1	1.00	12	672	R	GF	BR	Talebi et al. 2005
Brachyteles arachnoides	59.1	0.0	59.1	4.1	33.2	0.0	33.2	0.0	0.0	0.0	0.0	3.6	1.00	?	?	R	GF	BR	Carvalho Jr et al. 2004
La - Woolly monkeys	**69.8**	**3.5**	**73.4**	**2.5**	**12.2**	**0.0**	**12.2**	**1.5**	**8.6**	**0.0**	**8.6**	**2.0**							
Lagothrix cana	66.6	7.9	74.5	3.1	16.2	0.0	16.2	6.2	0.0	0.0	0.0	0.0	0.92	11	594	R	GF	BR	Peres 1994a
Lagothrix lagotricha	78.9	4.3	83.2	0.1	11.4	0.0	11.4	0.0	4.9	0.0	4.9	0.4	1.00	33	2400	R	GF	CO	Defler & Defler 1996
Lagothrix lugens	55.0	5.0	60.0	1.0	16.0	0.0	16.0	0.0	23.0	0.0	23.0	1.0	1.00	55	2488	R	GF	CO	Stevenson et al. 2000
Lagothrix poeppigii	73.0	0.0	73.0	5.0	10.0	0.0	10.0	0.0	6.0	0.0	6.0	6.0	1.00	18	429	R	GF	EC	Dew 2005
Lagothrix poeppigii	75.5	0.5	76.1	3.5	7.4	0.0	7.4	1.1	9.2	0.1	9.3	2.6	1.00	12	2420	R	GF	EC	Di Fiore 2004
Cf - White-fronted capuchins	**81.2**	**0.0**	**81.2**	**0.2**	**1.2**	**0.1**	**1.3**	**0.0**	**16.9**	**0.0**	**16.9**	**0.0**							
Cebus capucinus	81.2	0.0	81.2	0.2	1.2	0.1	1.3	0.0	16.9	0.0	16.9	0.0	0.67	24	534	T	GF	CR	Chapman 1987
Ca - Brown capuchins	**44.5**	**3.9**	**48.5**	**3.6**	**16.2**	**0.1**	**16.2**	**0.0**	**29.3**	**0.0**	**22.5**	**2.8**							
Cebus nigritus	2.9	0.0	2.9	0.0	72.3	0.0	72.3	0.0	24.9	0.0	24.9	0.0	1.00	12	38	R	GF	AR	Brown & Zunino 1990
Cebus nigritus	37.2	0.0	37.2	3.9	18.6	0.0	18.6	0.0	40.3	0.0	40.3	0.0	1.00	12	73	R	GF	AR	Brown & Zunino 1990
Cebus nigritus	67.4	3.6	71.0	3.2	0.8	0.4	1.2	0.0	22.7	Invt [f]	22.7	1.9	1.00	12	180	R	GF	BR	Ludwig et al. 2005
Cebus nigritus	53.9	16.0	69.9	11.1	6.3	0.0	6.3	0.0	0.0	0.0	0.0	15.4	1.00	44	62	B	T	BR	Galetti & Pedroni 1994
Cebus apella	33.0	8.0	41.0	4.0	10.0	0.0	10.0	0.0	43.0	0.0	43.0	2.0	1.00	13	672	R	GF	CO	Stevenson et al. 2000
Cebus apella	68.3	Fruit[e]	68.3	0.0	4.7	0.0	4.7	0.0	26.7	0.2	26.9	0.1	1.00	21	291		SC	FG	Guillotin et al. 1994
Cebus apella	49.1	Fruit[e]	49.1	3.0	0.6	0.0	0.6	0.0	47.3	0.0	0.0	0.0	0.92	11	856		T	SR	Mittermeier & van Roosmalen 1981
Co - Wedge-capped capuchins	**54.6**	**0.0**	**54.6**	**6.1**	**6.1**	**0.0**	**6.1**	**0.0**	**33.3**	**0.0**	**0.0**	**0.0**							
Cebus olivaceus	54.6	0.0	54.6	6.1	6.1	0.0	6.1	0.0	33.3	0.0	0.0	0.0	1.00	12	4		T	SR	Mittermeier & van Roosmalen 1981

cont.

Appendix 6.1. cont.

	Proportions of dietary classes [a]												Prop.						
Ecospecies: Species	Fr	Sd	Fr+Sd	Fl	Lv	Bd	Lv+Bd	Ex	Invert.	Vert.	Prey	Other	year	Mths	Hrs	Cal. [b]	Met. [c]	Cou. [d]	Reference
Sa - Squirrel monkeys	**38.1**	**0.0**	**38.1**	**3.4**	**0.0**	**0.0**	**0.0**	**0.0**	**58.5**	**0.0**	**58.5**	**0.0**							
Saimiri sciureus	25.9	0.0	25.9	2.1	0.0	0.0	0.0	0.0	72.0	0.0	72.0	0.0	1.00	12	10		T	SR	Mittermeier & van Roosmalen 1981
Saimiri sciureus	50.3	0.0	50.3	4.8	0.0	0.0	0.0	0.0	44.9	0.0	44.9	0.0	0.5	6	588		GF	BR	Lima & Ferrari 2003
Sf - Saddle-back tamarins	**54.1**	**0.0**	**54.1**	**3.8**	**0.0**	**0.0**	**0.0**	**12.0**	**28.8**	**0.3**	**29.1**	**1.1**							
Saguinus fuscicollis	49.0	0.0	49.0	7.0	0.0	0.0	0.0	12.0	26.0	0.0	26.0	6.0	1.00	12	757	R	GF	BO	Porter 2001
Saguinus fuscicollis	73.5	0.0	73.5	5.9	0.0	0.0	0.0	14.4	5.7	Invt [f]	5.7	0.4	1.00	14	731	T	GF	BR	Peres 1991
Saguinus fuscicollis	18.5	0.0	18.5	0.3	0.0	0.0	0.0	4.8	76.5	0.0	76.5	0.0	0.75	16	416	R	GF	PE	Soini 1981
Saguinus fuscicollis	39.0	0.0	39.0	5.0	0.0	0.0	0.0	8.0	47.7	0.0	47.7	0.0	1.00	12	430	T	GF	PE	Garber 1993a
Saguinus fuscicollis	59.8	0.0	59.8	4.4	0.0	0.0	0.0	30.3	5.8	0.0	5.8	0.0	1.00	29	2360	R?	GF	PE	Knogge & Heymann 2003
Saguinus fuscicollis	84.7	0.0	84.7	0.0	0.0	0.0	0.0	2.3	11.1	1.6	12.7	0.0	0.50	6	1367		GF	PE	Fang 1987
Sx - Moustached tamarins	**68.0**	**0.0**	**68.0**	**7.0**	**0.0**	**0.0**	**0.0**	**8.1**	**14.9**	**0.3**	**15.2**	**1.7**							
Saguinus labiatus	58.0	0.0	58.0	15.0	0.0	0.0	0.0	8.0	11.0	0.0	11.0	8.0	0.83	10	757	R	GF	BO	Porter 2001
Saguinus mystax	70.6	0.0	70.6	6.2	0.0	0.0	0.0	10.4	12.4	Invt [f]	12.4	0.3	1.00	14	731	T	GF	BR	Peres 1991
Saguinus mystax	51.6	0.0	51.6	5.6	0.0	0.0	0.0	2.2	40.4	0.0	40.4	0.0	1.00	12	430	T	GF	PE	Garber 1993a
Saguinus mystax	69.6	0.0	69.6	8.0	0.0	0.0	0.0	19.8	2.7	0.0	2.7	0.0	1.00	29	2360	R?	GF	PE	Knogge & Heymann 2003
Saguinus mystax	90.3	0.0	90.3	0.0	0.0	0.0	0.0	0.2	8.0	1.3	9.3	0.0	0.50	6	1290		GF	PE	Fang 1987
Sm - Midas tamarins	**66.0**	**0.0**	**66.0**	**1.8**	**0.0**	**0.0**	**0.0**	**1.0**	**30.3**	**0.0**	**30.3**	**0.8**							
Saguinus niger	87.5	0.0	87.5	0.0	0.0	0.0	0.0	3.1	9.4	0.0	9.4	0.0	0.50	6	330	R	GF	BR	Oliveira & Ferrari 2000
Saguinus midas	47.1	0.0	47.1	0.0	0.0	0.0	0.0	0.0	50.2	0.0	50.2	2.3	-	-	129	W	SC	FG	Pack et al. 1999
Saguinus midas	63.5	Fruit[e]	63.5	5.3	0.0	0.0	0.0	0.0	31.3	0.0	0.0	0.0	1.00	12	15		T	SR	Mittermeier & van Roosmalen 1981

cont.

Appendix 6.1. cont.

	Proportions of dietary classes [a]												Prop.						
Ecospecies: Species	Fr	Sd	Fr+Sd	Fl	Lv	Bd	Lv+Bd	Ex	Invert.	Vert.	Prey	Other	year	Mths	Hrs	Cal. [b]	Met. [c]	Cou. [d]	Reference
So - Bare-faced tamarins	**60.7**	**0.8**	**61.5**	**0.8**	**1.2**	**0.9**	**2.0**	**7.2**	**25.5**	**0.0**	**25.5**	**3.0**							
Saguinus leucopus	83.0	Fruit[e]	83.0	1.5	0.0	0.0	0.0	0.0	11.5	0.0	11.5	4.0	0.50	6	331	R	GF	CO	Poveda & Sánchez-Palomino 2004
Saguinus geoffroyi	38.4	1.5	39.9	0.1	2.3	1.7	4.0	14.4	39.4	0.0	39.4	2.0	0.67	8	1200	T	GF	PA	Garber 1984
Cx - Atlantic marmosets	**17.9**	**0.0**	**17.9**	**0.0**	**0.0**	**0.0**	**0.0**	**48.4**	**22.4**	**0.4**	**22.8**	**11.0**							
Callithrix geoffroyi	15.0	0.0	15.0	0.0	0.0	0.0	0.0	68.6	14.6	0.8	15.4	1.0	1.00	12	464	R	GF	BR	Passamani & Rylands 2000
Callithrix flaviceps	3.3	0.0	3.3	0.0	0.0	0.0	0.0	6.1	25.8	Invt [f]	25.8	64.8	1.00	12	1092	R	GF	BR	Hilario & Ferrari 2010
Callithrix flaviceps	14.4	0.0	14.4	0.0	0.0	0.0	0.0	65.7	18.3	1.6	19.9	0.0	1.00	13	1250	R	GF	BR	Ferrari et al. 1996
Callithrix aurita	11.0	0.0	11.0	0.0	0.0	0.0	0.0	50.5	38.5	0.0	38.5	0.0	1.00	12	305	R	GF	BR	Martins & Setz 2000
Callithrix aurita	37.6	0.0	37.6	0.0	0.0	0.0	0.0	43.9	18.6	0.0	18.6	0.0	1.00	17	410	R	GF	BR	Ferrari et al. 1996
Callithrix jacchus	25.9	0.0	25.9	0.0	0.0	0.0	0.0	55.6	18.5	0.0	18.5	0.0	0.75	11	375		GF	BR	Alonso & Langguth 1989
Mi - Amazonian marmosets	**18.6**	**0.0**	**18.6**	**0.0**	**0.0**	**0.0**	**0.0**	**63.3**	**18.6**	**0.0**	**18.6**	**0.0**							
Mico argentatus	18.6	0.0	18.6	0.0	0.0	0.0	0.0	63.3	18.6	0.0	18.6	0.0	0.50	6	321		GF	BR	Tavares & Ferrari 2002
Cb - Pygmy marmosets	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**76.7**	**23.3**	**0.0**	**23.3**	**0.0**							
Cebuella pygmaea	0.0	0.0	0.0	0.0	0.0	0.0	0.0	76.7	23.3	0.0	23.3	0.0	0.58	14	1742	R	GF	EC	Yepes et al. 2005
Le - Lion tamarins	**76.1**	**0.0**	**76.1**	**10.8**	**0.0**	**0.0**	**0.0**	**3.5**	**9.5**	**0.0**	**9.5**	**0.0**							
Leontopithecus chrysopygus	78.5	0.0	78.5	0.0	0.0	0.0	0.0	7.8	13.5	Invt [f]	13.5	0.0	1.00	12	540		GF	BR	Valladares-Padua 1993
Leontopithecus rosalia	61.6	0.0	61.6	21.9	0.0	0.0	0.0	1.4	14.9	Invt [f]	14.9	0.0	0.58	15	2164	R	GF	BR	Dietz et al. 1997
Leontopithecus rosalia	88.3	0.0	88.3	10.4	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	1.00	13	373	T	GF	BR	Miller & Dietz 2006

cont.

Appendix 6.1. cont.

	Proportions of dietary classes [a]												Prop.						
Ecospecies: Species	Fr	Sd	Fr+Sd	Fl	Lv	Bd	Lv+Bd	Ex	Invert.	Vert.	Prey	Other	year	Mths	Hrs	Cal. [b]	Met. [c]	Cou. [d]	Reference
Cg - Goeldi's monkeys	**29.0**	**0.0**	**29.0**	**0.0**	**0.0**	**0.0**	**0.0**	**7.3**	**22.5**	**2.5**	**25.0**	**38.3**							
Callimico goeldii	29.0	0.0	29.0	0.0	0.0	0.0	0.0	1.0	31.0	3.0	34.0	36.0	1.00	12	957	R	GF	BO	Porter 2001
Callimico goeldii	29.0	0.0	29.0	0.0	0.0	0.0	0.0	13.5	14.0	2.0	16.0	40.5	1.00	12	1198	R	GF	BO	Porter et al. 2009
Pi - Saki monkeys	**53.5**	**31.5**	**85.0**	**4.2**	**9.1**	**0.0**	**9.1**	**0.1**	**0.8**	**0.0**	**0.8**	**0.6**							
Pithecia pithecia	60.9	20.4	81.3	7.8	10.8	0.0	10.8	0.0	0.0	0.0	0.0	0.0	0.92	28	1268	R	GF	BR	Setz 1993
Pithecia albicans	50.0	18.5	68.5	0.0	29.6	0.0	29.6	0.0	0.0	0.0	0.0	1.9	1.00	12	72	R	GF	BR	Johns 1986
Pithecia albicans	34.0	46.2	80.2	8.0	9.5	0.0	9.5	0.8	0.4	0.0	0.4	1.1	1.00	20	56	R	GF	BR	Peres 1993a
Pithecia irrorata	20.0	75.0	95.0	3.0	1.0	0.0	1.0	0.0	0.0	0.0	0.0	1.0	1.00	31	3000	R	GF	PE	Palminteri 2010
Pithecia pithecia	93.3	Fruit[e]	93.3	6.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.00	12	6		T	SR	Mittermeier & van Roosmalen 1981
Pithecia pithecia	88.3	Fruit[e]	88.3	1.8	5.7	0.0	5.7	0.0	3.0	0.0	3.0	0.0	1.00	17	578	R	GF	VE	Norconk & Conklin-Brittain 2004
Pithecia pithecia	27.8	60.6	88.4	2.2	7.1	0.0	7.1	0.0	2.3	0.0	2.3	0.0	1.00	16	650	T	GF	VE	Kinzey & Norconk 1993
Ch - Bearded saki monkeys	**33.8**	**50.4**	**84.1**	**9.5**	**0.6**	**0.0**	**0.7**	**0.0**	**2.9**	**0.0**	**2.9**	**3.0**							
Chiropotes albinasus	54.0	36.0	89.9	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.6	1.00	12	154	R	GF	BR	Ayres 1989
Chiropotes satanas	35.9	36.5	72.4	26.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.50	6	336	R	GF	BR	Silva 2003
Chiropotes satanas	19.0	57.1	76.1	15.0	3.3	0.0	3.3	0.0	4.1	0.0	4.1	1.5	0.83	12	1153	R	GF	BR	Veiga 2006
Chiropotes utahickae	43.0	37.0	80.0	16.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0	0.50	6	480	R	GF	BR	Vieira 2005
Chiropotes chiropotes	30.0	66.2	96.2	3.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	1.00	18	164		GF	SR	van Roosmalen et al. 1988
Chiropotes chiropotes	19.0	63.5	82.5	1.2	0.2	0.0	0.2	0.0	12.4	0.0	12.4	3.6	1.00	17	512	R	GF	VE	Norconk 1996
Chiropotes chiropotes	35.4	56.3	91.7	1.2	1.0	0.1	1.1	0.0	3.9	0.0	3.9	2.1	1.00	15	793		GF	VE	Peetz 2001

cont.

Appendix 6.1. cont.

	Proportions of dietary classes [a]												Prop.						
Ecospecies: Species	Fr	Sd	Fr+Sd	Fl	Lv	Bd	Lv+Bd	Ex	Invert.	Vert.	Prey	Other	year	Mths	Hrs	Cal. [b]	Met. [c]	Cou. [d]	Reference
Cj - Uakaries	**13.2**	**74.0**	**87.2**	**5.6**	**2.0**	**0.0**	**2.0**	**0.0**	**3.6**	**0.0**	**3.6**	**1.7**							
Cacajao calvus	18.4	66.9	85.3	6.2	0.0	0.0	0.0	0.0	5.2	0.0	5.2	3.3	1.00	12	700	R	GF	BR	Ayres 1989
Cacajao melanocephalus	8.0	81.0	89.0	5.0	4.0	0.0	4.0	0.0	2.0	0.0	2.0	0.0	0.92	16	120	R	GF	BR	Boubli 1999
Cm - Amazonian dusky titi monkeys	**53.0**	**0.0**	**53.0**	**4.0**	**34.0**	**0.0**	**34.0**	**0.0**	**7.5**	**0.0**	**7.5**	**1.5**							
Callicebus discolor	63.0	0.0	63.0	6.0	28.0	0.0	28.0	0.0	0.0	0.0	0.0	3.0	0.67	8	260	R	GF	EC	Carrillo-Bilbao et al. 2005
Callicebus moloch	43.0	0.0	43.0	2.0	40.0	0.0	40.0	0.0	15.0	0.0	15.0	0.0	0.92	11	660		GF	PE	Wright 1985
Cp - Atlantic dusky titi monkeys	**56.8**	**24.2**	**81.0**	**0.0**	**15.7**	**0.0**	**15.7**	**0.0**	**0.0**	**0.0**	**0.0**	**3.5**							
Callicebus melanochir	58.8	26.4	85.2	0.0	14.1	0.0	14.1	0.0	0.0	0.0	0.0	0.7	0.92	12	564	R	GF	BR	Heiduck 1997
Callicebus melanochir	54.8	21.9	76.7	0.0	17.2	0.0	17.2	0.0	0.0	0.0	0.0	6.2	0.92	11	1030		GF	BR	Müller 1996
Ct - Collared titi monkeys	**59.4**	**26.9**	**86.3**	**3.9**	**6.4**	**0.0**	**6.4**	**0.0**	**3.4**	**0.0**	**3.4**	**0.0**							
Callicebus torquatus	59.4	26.9	86.3	3.9	6.4	0.0	6.4	0.0	3.4	0.0	3.4	0.0	0.50	6	340	R	GF	CO	Palacios et al. 1997
Ao - Night monkeys	**76.5**	**0.0**	**76.5**	**14.0**	**2.3**	**0.0**	**2.3**	**0.0**	**7.2**	**0.0**	**7.2**	**0.0**							
Aotus nigriceps	70.0	0.0	70.0	11.0	4.7	0.0	4.7	0.0	14.3	0.0	14.3	0.0	0.92	11	660		GF	PE	Wright 1985
Aotus vociferans	83.0	0.0	83.0	17.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.75	9	320	R	GF	PE	Puertas et al. 1992

[a] Dietary class codes: Fr = fruit, Sd = seeds, Fr+Sd = fruits and seeds combined, Fl = flowers, Lv = leaves, Bd = buds, Lv+Bd = leaves and buds combined, Ex = exudates, Invert. = invertebrate prey, Vert. = vertebrate prey, Prey = all prey combined

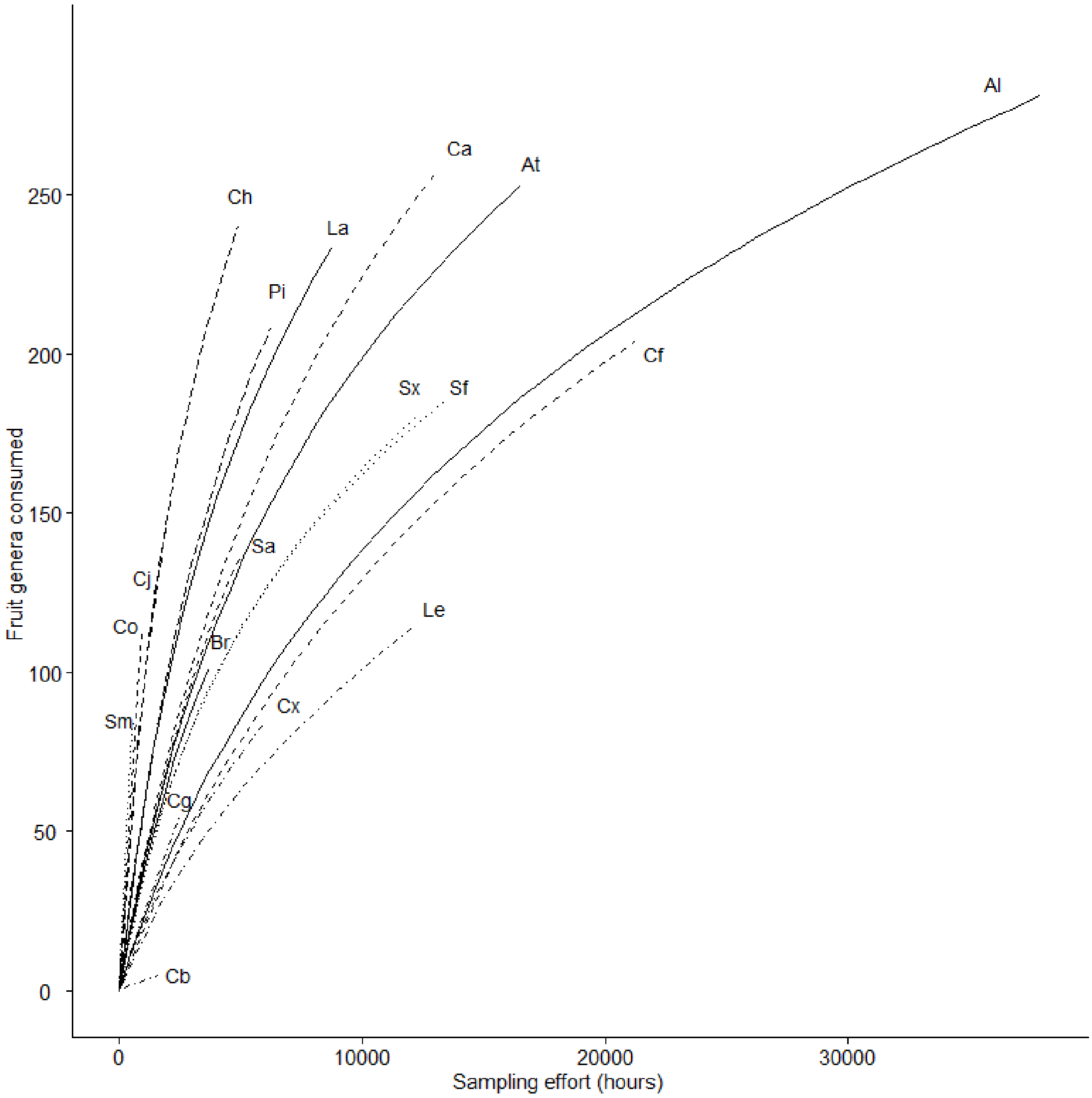
[b] Calculation of percentages: B = feeding bouts, R = feeding records, T = feeding time, W = weight of stomach contents

[c] Method of observations: GF = group follows, SC = stomach contents , T = transects

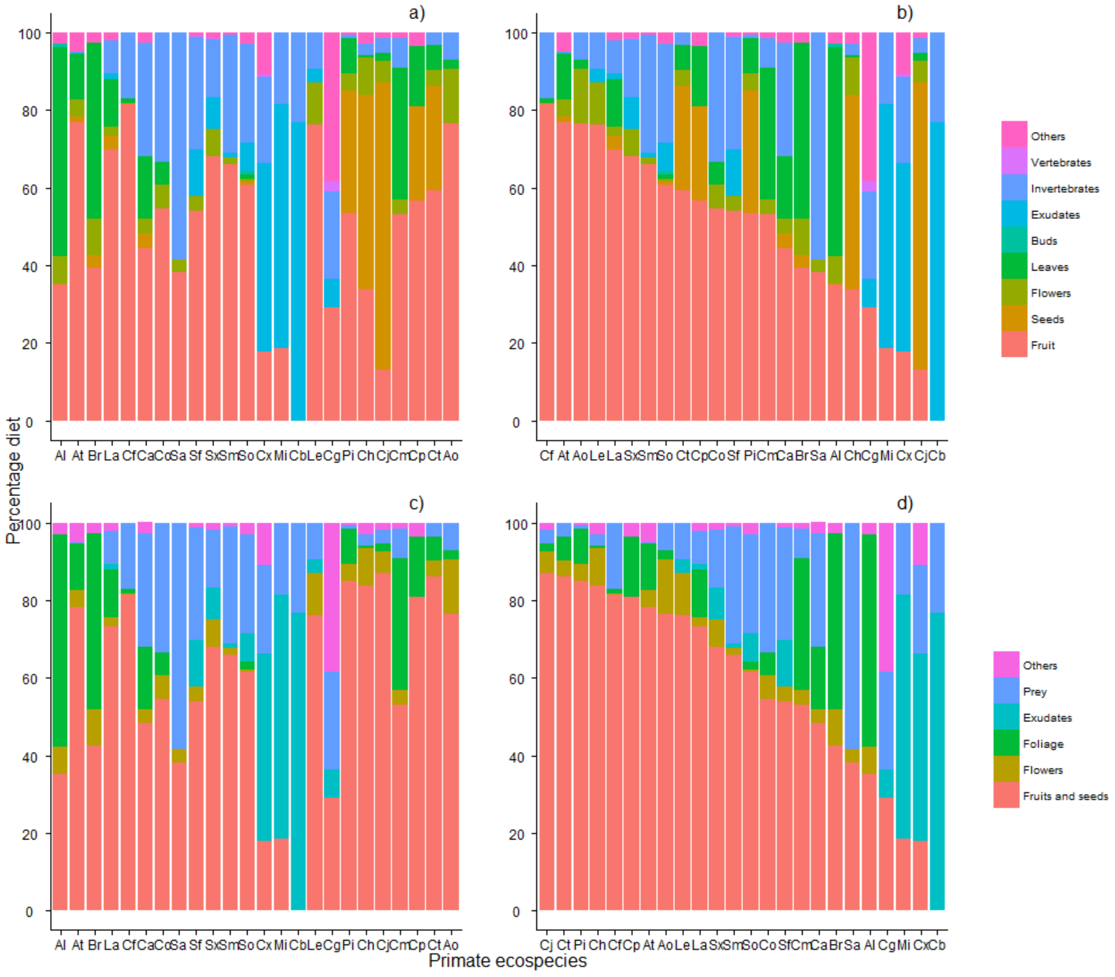
[d] Country codes: AR = Argentina, BO = Bolivia, BR = Brazil, BZ = Belize, CO = Colombia, CR = Costa Rica, EC = Ecuador, FG = French Guiana, GT = Guatemala, MX = Mexico, NI = Nicaragua, PA = Panama, PE = Peru, SR = Suriname, VE = Venezuela

[e] Seeds included with fruit

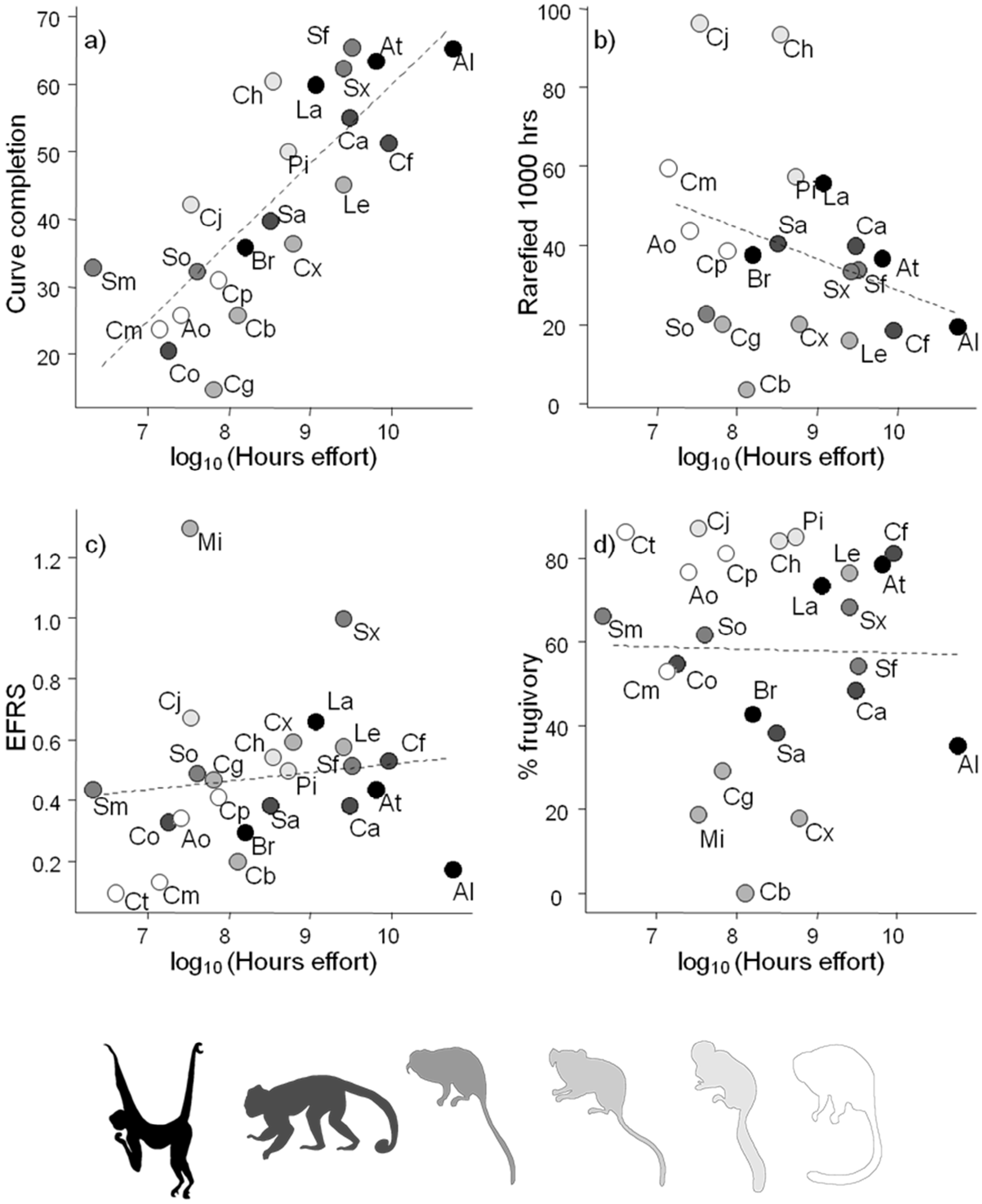
[f] Vertebrate prey included with invertebrates.



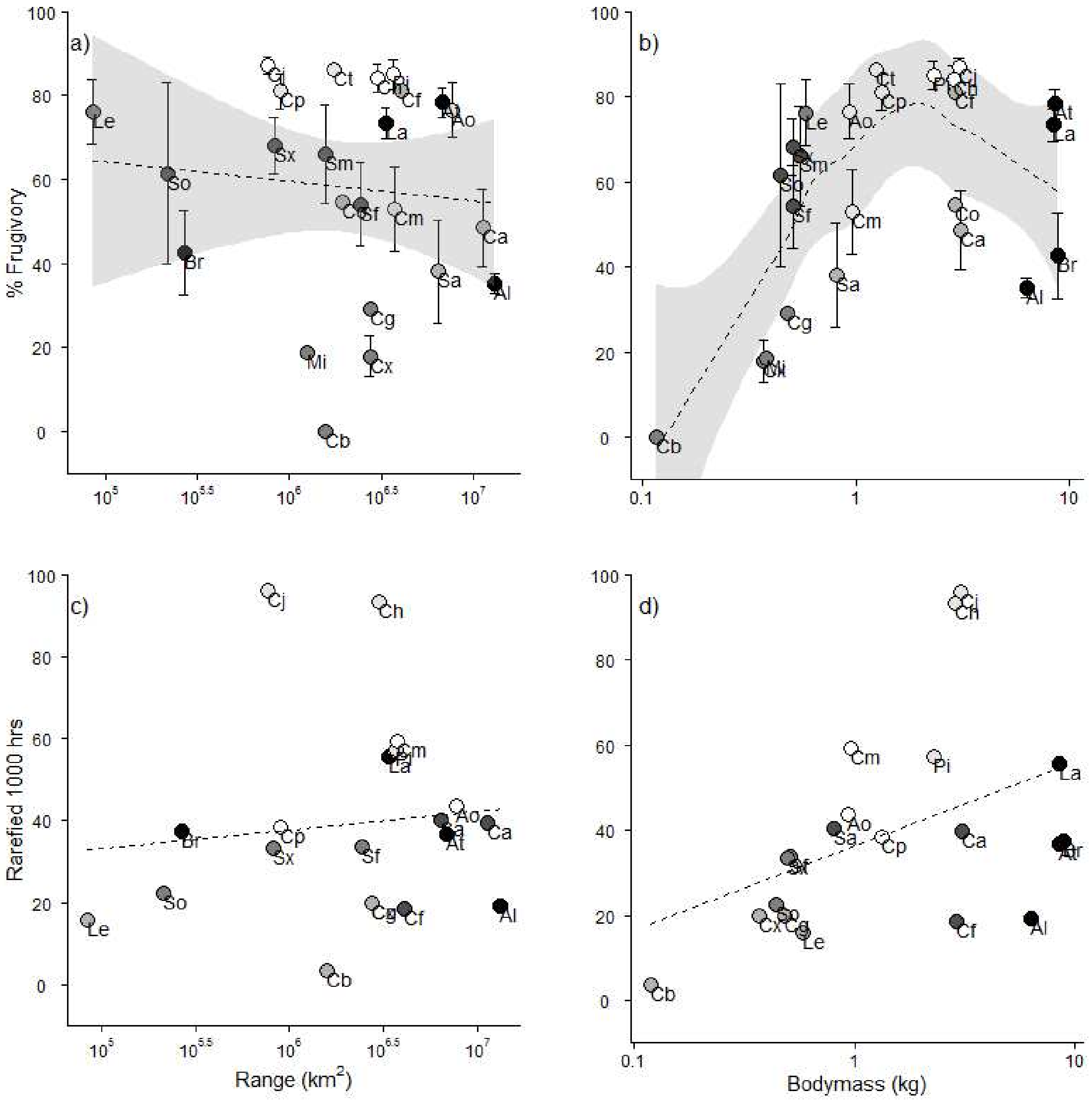
Appendix 6.2. *Sample-based rarefaction curves for plant genera (fruits and seeds only) observed in diet studies of neotropical primates, with x-axis rescaled to show cumulative observation hours across sample studies. Codes represent primate ecospecies (see Table 6.1), excluding So, Mi, Cm, Cp, Ct and Ao due to small sample size; line types represent primate subfamilies.*



Appendix 6.3. *Proportions of diet comprising different plant parts and animal prey per neotropical primate ecospecies from studies of six or more months duration, shown in full detail (a and b) and in summary categories (c and d). Codes represent primate ecospecies, arranged in taxonomic order (a and c; see Table 6.1), and in decreasing order of percentage frugivory (b: fruits only, d: including fruits and seeds).*



Appendix 6.4. *Relationships between sampling effort and measures of frugivory from diet studies of neotropical primates. Dashed lines represent linear regressions; codes represent primate ecospecies; fill colours represent primate subfamilies as indicated by silhouettes (see Table 6.1).*



Appendix 6.5. *Relationships between geographic range, bodymass and measures of frugivory in neotropical primates. Frugivory presented as (a and b) percentage of diet comprising fruits and seeds, and (c and d) rarefied richness of plant genera consumed (fruits and seeds only). Geographic ranges calculated from NatureServe/IUCN polygons (Patterson et al. 2007); bodymasses calculated from Smith and Jungers (1997). Codes represent primate ecospecies; fill colours represent primate subfamilies (see Table 6.1, Figure 6.5).*

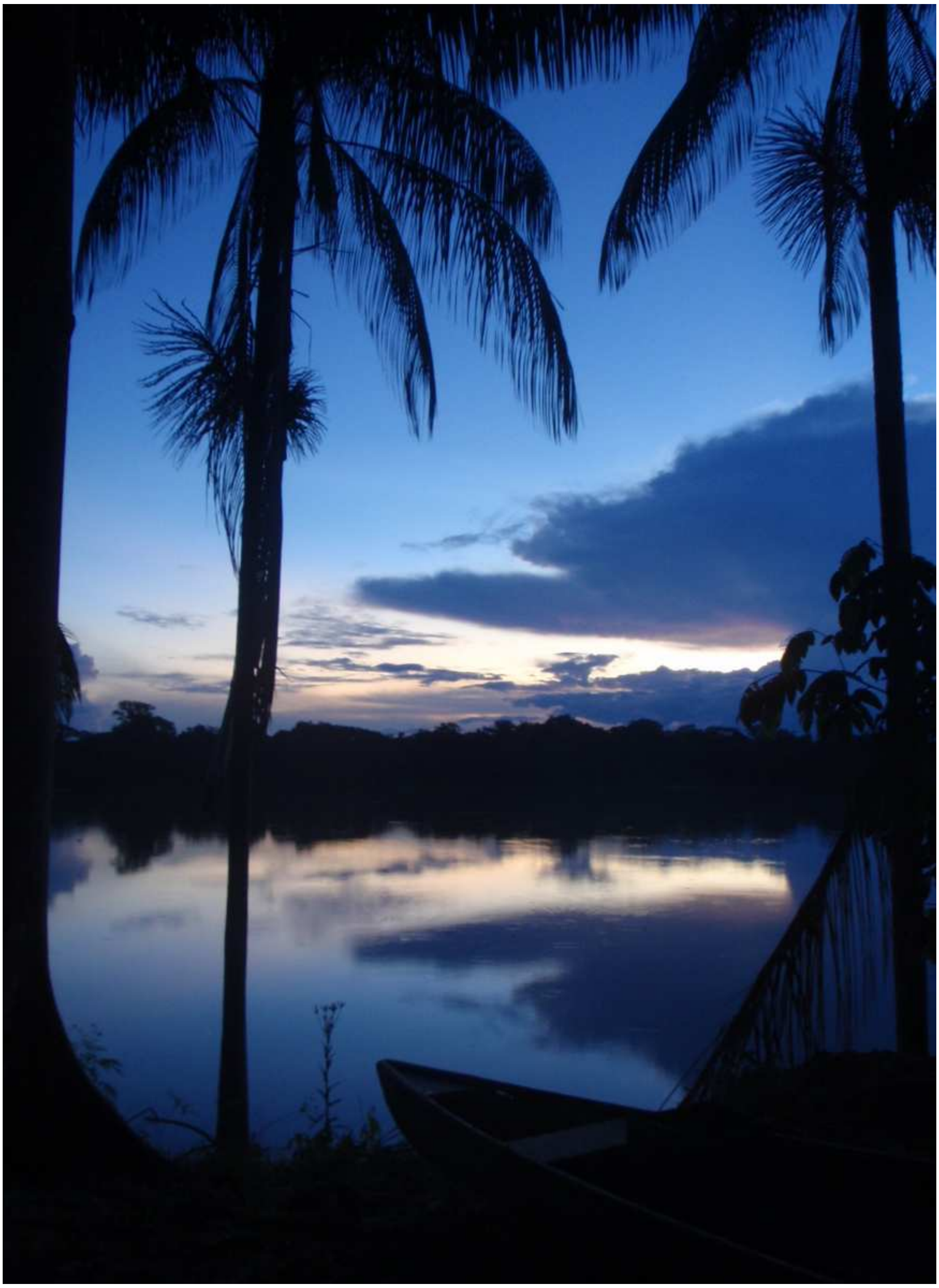


Photo: *Rio Juruá at dusk.*