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**INFLUENCE OF FLOOD DYNAMICS ON FOREST CARBON
STOCKS, LITTERFALL SEASONALITY AND NET PRIMARY
PRODUCTIVITY IN AMAZONIAN VÁRZEA FORESTS**

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Tese de Doutorado apresentada ao
Instituto de Geociências e Ciências
Exatas do Câmpus de Rio Claro, da
Unversidade Estadual Paulista “Júlio
de Mesquita Filho”, como parte dos
requisitos para obtenção do título de
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Orientador: Prof. Dr. Thiago Sanna Freire Silva

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Resumo

Dois macro-ambientes podem ser distinguidos entre os tipos de vegetacionais da Amazônia: áreas de terra firme, predominantemente florestadas e não suscetíveis a inundações, e as áreas úmidas. A extensão total das áreas úmidas na Amazônia é de cerca de 30% da bacia amazônica, das quais mais de 25% são constituídas por planícies fluviais. Na Amazônia, a amplitude das variações sazonais do nível da água pode atingir até 16 m na Amazônia Ocidental, 10 m na Amazônia Central e 6 m na Amazônia Oriental, com extensão e duração da inundação local dependendo da interação entre precipitação, descarga fluvial e geomorfologia. Os processos ecológicos e ambientais nessas planícies são amplamente controlados pelo pulso de inundação - um conceito teórico que postula que a amplitude, duração, frequência e periodicidade (previsibilidade) dos pulsos de inundação são os principais fatores que mantêm o equilíbrio ambiental dinâmico. As planícies fluviais amazônicas desempenham um papel importante nos ciclos biogeoquímicos regionais e na manutenção da biodiversidade, além de fornecer importantes serviços ecossistêmicos para as sociedades humanas. No entanto, esses ambientes permanecem largamente negligenciados em relação às estimativas dos ciclos biogeoquímicos na escala da bacia hidrográfica. Assim, o presente estudo tem como objetivo avançar nossa compreensão de como a heterogeneidade espacial em termos de diferentes fitofisionomias florestais e padrões de inundação nas florestas de várzea controla três aspectos ecológicos principais: estoques de carbono, produção e dinâmica de serrapilheira e produtividade primária líquida. Usando imagens multitemporais de sensoriamento remoto de radar de abertura sintética (SAR) combinadas com dados de campo, derivamos mapas de fitofisionomias e de duração da inundação na área de estudo. Também desenvolvemos um método empírico de modelagem de inundação baseado em modelagem logística para nos permitir estender as capacidades atuais de prever padrões espaciais de inundação. Em seguida, exploramos como a heterogeneidade espacial gera padrões de estoques de carbono acima do solo usando métodos de inventário florestal. Monitorando um ano de queda de serrapilheira, analisamos como a produção e a dinâmica da serrapilheira variam entre comunidades florestais distintas sob diferentes regimes de inundação e também estimamos a produtividade primária líquida e discutimos como ela varia no espaço.

Palavras-chave: Várzeas Amazônicas; Sensoriamento remoto por radar; Estoques de carbono; produtividade primária líquida; serrapilheira.

Abstract

Two macro-environments can be distinguished among Amazonian vegetation types: upland areas, predominantly forested and not susceptible to flooding, and wetland areas. The full extent of wetlands in the Amazon is about c.a. 30% of the Amazon basin, where floodplains comprise more than 25% of wetland areas. In the Amazon, the amplitude of seasonal water level variations can reach up to 16 m in Western Amazon, 10 m in Central Amazon, and 6 m in Eastern Amazon, with local flood extent and duration depending on the interaction among precipitation, river discharge and geomorphology. Ecological and environmental processes in floodplains are largely controlled by the flood pulse - a theoretical concept which postulates that amplitude, duration, frequency and periodicity (predictability) of flood pulses are the major factor maintaining the dynamic environmental equilibrium in floodplains. Amazonian floodplains play an important role in the regional biogeochemical cycles and biodiversity maintenance, and provide important ecosystem services to human societies. However, these environments remain greatly overlooked regarding basin-scale estimates of biogeochemical cycles. Therefore, the present study aims to advance our understanding of how spatial heterogeneity in terms of different forest subtypes and flood patterns of várzea forests controls three key ecological aspects: carbon stocks, litterfall production and dynamics, and net primary productivity. Using multitemporal synthetic aperture radar (SAR) remote sensing imagery combined with field data, we derived vegetation structure and flood duration classes in the study area. We also developed an empirical flood modeling method based on logistic modeling to allow us to extend the current capabilities in predict spatial patterns of flooding. Then we explored how spatial heterogeneity drives patterns of aboveground carbon stocks using standard forest inventory methods. Monitoring one full year of litterfall, we asked how litter production and dynamics vary among distinct forest communities under different flood regimes and we also estimated net primary productivity and discussed how it varies in space.

Keywords: Amazonian várzeas; Radar remote sensing; Carbon stocks; Net primary productivity; litterfall.

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Chapter 1

INTRODUCTION

Throughout the relatively long Amazonian natural history, the changing climatic, biotic, and landscape configurations (Hoorn and Wesselingh 2011; Mertes and Dunne 2007) have established complex environmental mosaics. As result, the uneven spatial distribution of current geologic, climatic, edaphic and ecological conditions (Anderson 2012; Mertes and Dunne 2007; Saatchi et al. 2007; Silva et al. 2013a) create an heterogeneous mosaic of plant communities.

Two macro-environments can be distinguished among Amazonian vegetation types: upland areas, predominantly forested and not susceptible to flooding, and wetland areas. Amazonian wetlands play an important role in the regional biogeochemical cycles and biodiversity maintenance, and provide important ecosystem services to human societies (Luize et al. 2018; Melack and Forsberg 2001; Mitsch and Gosselink 2000; Pangala et al. 2017; Wittmann et al. 2012).

However, Amazonian wetlands remain greatly overlooked regarding basin-scale estimates of biogeochemical cycles. For instance, it has been estimated that the flooded forests of the Amazon basin can contribute to carbon accumulations of about $0.04 \pm 0.01 \text{ Pg}^1 \text{ C year}^{-1}$ in living aboveground biomass (Aragão et al. 2014). Nonetheless this value is still considered highly uncertain (Aragão et al. 2014) and depends on better estimates based on wetland habitat and vegetation maps such as those conducted by Silva et al. 2010 and Ferreira-Ferreira et al. 2015. Such estimates do not consider, for instance, the ecogeographical differences between várzea and igapó forests, determined by the different nutritional status of these floodplains, nor the average time that each forested region remains flooded annually.

Junk et al. 2011 developed a comprehensive classification of Amazonian wetlands, using climatic, hydrological, botanical, and limnological parameters. The authors estimate that, including riparian forests along lower-order rivers (1 to 5 in river order) and floodable interfluves (white-sand vegetation known as *campinas* and *campinaranas*), the full extent of wetlands in the Amazon is about c.a. 30% of the Amazon basin, where floodplains comprise more than 25% of wetland areas (Table 1.1).

The oligotrophic river floodplains of black- and clear-water rivers are called *igapó*, being poor in nutrients, while eutrophic white-water river floodplains are rich in nutrients and locally and scientifically known as *várzea* (Junk et al. 2012;

¹1 Petagram (Pg) = 1 Gigatonne (Gt) = 10^3 Teragram (Tg) = 10^6 Megagram (Mg) = 10^6 grams (g).

Table 1.1: Classification and coverage of Amazonian wetland environments according to Junk et al. 2011.

Wetland Environments	Area (km ²)	% of Basin	% of wetlands	% of wetlands (excluded *)
Várzea Floodplains [†]	275,000	3.93	13.62	27.00
Blackwater Floodplains [‡]	118,000	1.69	5.85	11.59
Clearwater Floodplains	126,100	1.80	6.25	12.38
Interfluvial Wetlands	488,374	6.98	24.20	47.96
Mangroves [§]	10,900	0.16	0.54	1.07
Riparian Wetlands of Low-Order Rivers [*]	1,000,000	14.29	49.54	
Total	2,018,374	28.83		
Basin area (approx)	7,000,000			

[†] excluding paleo-várzea environments $\approx 125,000 \text{ km}^2$.

[‡] only Negro River catchment considered.

[§] Brazilian Mangroves = $10,000 \text{ km}^2 + 900 \text{ km}^2$ in Guiana

Sioli 1954).

Sioli 1954 developed the first scientific classification of Amazonian rivers to explain their limnological characteristics and relate them to the geological and geomorphological properties of their respective catchments. According to Sioli's classification, the black-water rivers (e.g. Negro, Jutai, and Tefé rivers) drain the Precambrian Guyana Shield, bordering the northern Amazon basin. Their waters have transparencies of 60-120cm (Secchi disk depth) with low amounts of suspended matter and moderate acidity ($\text{pH} < 5$), and both the water and the substrate are relatively nutrient-poor, with large amounts of humic acids that result in reddish-brown water colors. Clear-water rivers (e.g. Branco, Tapajós, and Xingu rivers) mostly drain the Brazilian Central Plateau which borders the Amazon basin to the south. Their waters have transparencies of $>150 \text{ cm}$, low amounts of suspended sediment and dissolved solids, variable pH (between 5 and 8), and water and substrate of low to moderate fertility, with transparent to greenish shades. Finally, white-water rivers (e.g. Solimões/Amazonas, Juruá, and Madeira rivers) have their headwaters in the Andean foothills, transporting large volumes of suspended and dissolved sediments, and thus being rich in nutrient content. Water transparencies are low, between 20 and 60cm, and pH nearly neutral. The large sediment loads give them a characteristic whitish-brown color.

Sioli's classification was later supported by botanical studies such as from Prance 1979 and Kubitzki 1989, which attributed the ecogeographic differentiation among floodplain forests to water chemistry. Nutritional conditions imposed by the different water types lead to ecological and structural differences between várzea and igapó forests. In both forest types, tree species richness tends to increase with decreasing flood height and duration, i.e. with reduced intensity of the environmental filter imposed by the flood (Wittmann et al. 2010b). However, in várzea forests tree densities decrease as flood duration and height decrease along the flood gradient, while in igapó forests the opposite occurs - tree densities increase with the decreasing stress caused by flooding

(Wittmann et al. 2010b). The oligotrophic status of waters and soils in igapó floodplains are also responsible for much slower tree radial growth. For example, the same tree species (*Macrolobium acaciifolium*, Leguminosae), subject to the same flooding regime in different environments, had an average diameter increment of 3.04 ± 0.76 mm year⁻¹ in the igapó, while its radial growth was on average 5.32 ± 1.34 mm year⁻¹ in the várzea (Schöngart et al. 2005). Above-ground woody biomass can be as large in igapó forests (227-304 Mg ha⁻¹) as in várzea forests (230-270 Mg ha⁻¹) (Schöngart et al. 2010), but the annual productivity of várzeas is approximately three times higher (Schöngart et al. 2010; Worbes 1997).

About 75% of these várzeas are covered by forests, while 25% of the remaining areas correspond to water bodies (channels, rivers and lakes), herbaceous vegetation, and non-vegetated sandy bars (Melack and Hess 2010). The combination of annual variation in water levels along the Solimões River (7-13 meters) and the essentially flat topography results in an active floodplain that can span from 20 to 100 km away from the main channel, favoring the establishment of várzea ecosystems (Goulding et al. 1995; Melack and Hess 2010).

The flood pulse is a theoretical concept relating the flood regime of river-floodplain systems with the distribution and dynamics of the associated biota and biogeochemical processes. Junk et al. 1989 define the regular annual “pulse” of river discharge as the major force controlling these systems, governing the lateral exchange and recycling of nutrients and causing biotic responses that ultimately lead to morphological, anatomical, physiological, and phenological/behavioral adaptations. Each location in a floodplain is positioned along a flood gradient, and distinct plant species will have their “optimum” along the gradient, so that local plant communities are assembled according to the flood regimes. Although this “optimum” can be modulated by other factors such as stability, structure, and fertility of the substrate, groundwater table height, and biotic processes (Junk et al. 1989), the spatial heterogeneity of flood duration is the most important factor for forest differentiation in várzeas, having a crucial influence on floristic composition and species diversity (Assis et al. 2015; Luize et al. 2015; Wittmann et al. 2010b, 2006a).

Prolonged flooding imposes constraints on gas exchanges in plants. The diffusion resistance of most gases in the water is about 10,000 times greater than in the air and there is a *c.a.* 30-fold reduction in oxygen concentration between the gaseous and dissolved states (Mitsch and Gosselink 2015). Oxygen depletion under inundation may be even more severe in the tropics, as higher temperatures enhance the microbial oxygen demand and reduces its solubility, which is of about 14 mg l⁻¹ at 0°C and about 7 mg l⁻¹ at 35°C (Parolin et al. 2010). In Amazonian várzea forests, sedimentation rates are an additional cause for oxygen depletion in the rhizosphere. In areas close to the river mainstems, the annual floods can lay up to 19.8 cm year⁻¹ of sediments (Wittmann et al. 2004), rapidly leading to anoxia in the root system and, consequently, to a decline in the energy supply of roots, eventually interrupting CO₂ assimilation (Junk and Piedade 2010; Parolin 2000).

The modulating effect of flooding on carbon assimilation in várzea forests is known for many tree species (Parolin 2000; Parolin et al. 2010; Parolin and Wittmann 2010; Schöngart et al. 2010). However, landscape-scale estimates of carbon stocks and net primary productivity that take into account the spatial heterogeneity of várzea forests and its different hydrological regimes are

still missing. This spatial heterogeneity of várzea forests in carbon stocks and productivity has not been considered in the estimates of carbon fluxes for the Amazon basin, nor in dynamic global vegetation models that are coupled to biogeochemical and climate models (Cox 2001; Galbraith et al. 2010; Joetzjer et al. 2013; Marengo et al. 2012; Prentice et al. 2007; Sitch et al. 2013; Zhang et al. 2015).

Therefore, the present study aims to advance our understanding of how spatial heterogeneity in terms of different forest subtypes and flood patterns of várzea forests controls three key ecological aspects: carbon stocks, litterfall production and dynamics, and net primary productivity.

The present study is divided in four main chapters, each one addressing specific questions of the above goal. Chapter 2, published in Ferreira-Ferreira et al. 2015, uses multitemporal synthetic aperture radar (SAR) remote sensing imagery combined with object-based image analysis, and field data to derive vegetation structure and flood duration classes in the study area. This chapter provides the basis to assess the spatial heterogeneity in terms of distribution of vegetation and spatial patterns of inundation. In Chapter 3, we go a step further in spatial inundation characterization, moving from flood duration classes to temporally continuous and pixel-based estimation of flood duration. In this chapter we used the same SAR imagery as the previous chapter and a logistic model to develop an empirical flood modeling method which allow us to extend current capabilities in predict spatial patterns of flooding. Chapter 4 address two questions: (i) How much and in which direction aboveground carbon stocks vary depending on forest subtypes and flood regimes? And (ii) which of the factors influencing AGC are most affected by flood duration? We answered these questions using field inventory methods combined with results from previous chapters. Monitoring one full year of litterfall, in Chapter 5 we ask three scientific questions: (i) Does fine litterfall production and dynamics differ among forest subtypes and flood regimes? (ii) Do distinct forest types and flood regimes reveal different community-level signals of varying plant investment strategies into reproductive organs versus photosynthetic organs? (iii) Assuming that litterfall production can be used as a proxy for forest total NPP, what we can infer about how the primary productivity of várzea forest could respond to hydrological variability and changes? In this chapter, we estimate net primary productivity from litterfall production and discuss how it varies in space. Finally, in Chapter 6 we emphasize the main remarks of the complete study and relate them to form a more comprehensive picture of how the present work advances our understanding of the ecology and carbon biogeochemistry of várzea forests.

Chapter 6

SYNTHESIS AND CONCLUSION

Considering that forests comprise 85.5% (397,800 ha) of the total area of the Mamirauá Sustainable Development Reserve mapped by us (468,000 ha; Chapter 2), and taking into account the mean AGC found by us of $114.01 \pm 11.63 \text{ Mg C ha}^{-1}$, which is consistent with the $107.17 \text{ Mg C ha}^{-1}$ reported by Schöngart et al. 2010 for the same region, we then estimate a mean total carbon stock of $45.35 \pm 4.63 \text{ Tg C}$ for the studied area. We estimated mean carbon stocks per forest subtype as 25.32 ± 2.14 , 11.20 ± 2.02 , and $5.94 \pm 0.88 \text{ Tg C}$ for low várzeas, high várzeas and chavascal forests, respectively. As AGC values in our dataset are primarily differentiated by forest subtype, we can use our forest type mapping (Figure 2.5) to determine the approximate distribution of forest AGC across the mapped area.

We show that while low várzea forests have relatively higher aboveground carbon stocks, it was comparatively less productive than high várzeas per unit of area. This result in lower carbon residence times in high várzeas. Assuming our forest stands are in a quasi-equilibrium state, we can calculate the aboveground C residence time as the ratio of AGC to aboveground NPP (ANPP) (Malhi et al. 2004). For the sake of comparison of C residence times among forest subtypes, we can assume that 50% of total NPP is allocated to ANPP (Aragão et al. 2009). This results in mean aboveground C residence times of 13, 10, and 7 years for low várzea, high várzea and chavascal, respectively. Schöngart et al. 2010 also characterize várzea forests as highly dynamic ecosystems, with C residence times in the long-term carbon pool of aboveground coarse wood live biomass (AGWB) of only 26 years, compared to a mean 56-80 years in terra firme forests (Malhi et al. 2004). Since we are also considering short-lived components (canopy), our C residence times are much lower.

Up-scaling our NPP estimates per unit area for the year 2017, we can estimate an annual carbon assimilation of c.a $4.00 \text{ Tg C year}^{-1}$, distributed in 1.97 ± 0.63 , 1.15 ± 0.82 , $0.87 \pm 0.33 \text{ Tg C year}^{-1}$ for low várzea, high várzea and chavascal forests, respectively. Although we report higher NPP rates per unit area in high várzea forests instead of low várzeas, high várzea forests cover only 18.7% of the total mapped area, while low várzea forests cover 37.7% of the area, thus resulting in a higher amount of carbon assimilation per year in low várzeas.

Our flood modeling approach proved promising, although further development is needed to reduce uncertainties. We can use our flood duration predictions to provide a first degree approximation of how heterogeneous NPP

distribution can be when taking into account the role of flood duration as well as forest subtypes. Figure 6.1 shows forest NPP as a linear function of flood duration (see Figure 5.14a), while Figure 6.2 shows the spatial distribution of NPP when predicted by flood duration, controlling for forest subtype (ANCOVA; Figure 5.14b). The flood duration model predictions were biased toward values of maximum flood duration, and since flood duration was inversely related to flood duration, our predicted NPP was biased towards low values. When controlling for forest subtype, the spatial prediction of NPP was mostly distributed within intermediate values, between 17 and 30 Mg C.

Even with large uncertainties, these maps highlight the remarkable heterogeneity expected from NPP in várzea forests, and stresses the importance of considering the role of flood duration and forest subtypes in estimates of carbon dynamics in the Amazon floodplains. The influence of flood duration on carbon stocks and fluxes is still one of the largest sources of uncertainty in these studies. Moreover, the effectiveness of bilateral and multilateral policies for reduction of greenhouse gas emissions, such as REDD+ (Reducing emissions from deforestation and forest degradation) require more accurate estimations of carbon stocks and assimilation capacity (Salimon et al. 2011). These sources of error can be minimized by improving and extending *in situ* monitoring of different forest formations under different hydrological regimes with remote sensing and modeling approaches such as conducted in this study, enabling to capture both vegetation structure and flooding under the forest canopy. With the expected new generation of synthetic aperture radar platforms, such as NISAR and BIOMASS, and advancements in SAR processing and machine learning methods, such approaches will be applicable at a basin-level scale.

Predicting how the carbon balance of Amazonian várzeas and Amazonian wetlands in general will respond to climatic and hydrological changes requires a more detailed and mechanistic understanding of carbon cycling and its relationship to ecohydrological factors, including the spatially explicit mapping of relevant wetland characteristics. This study advances our understanding by fulfilling these requirements.

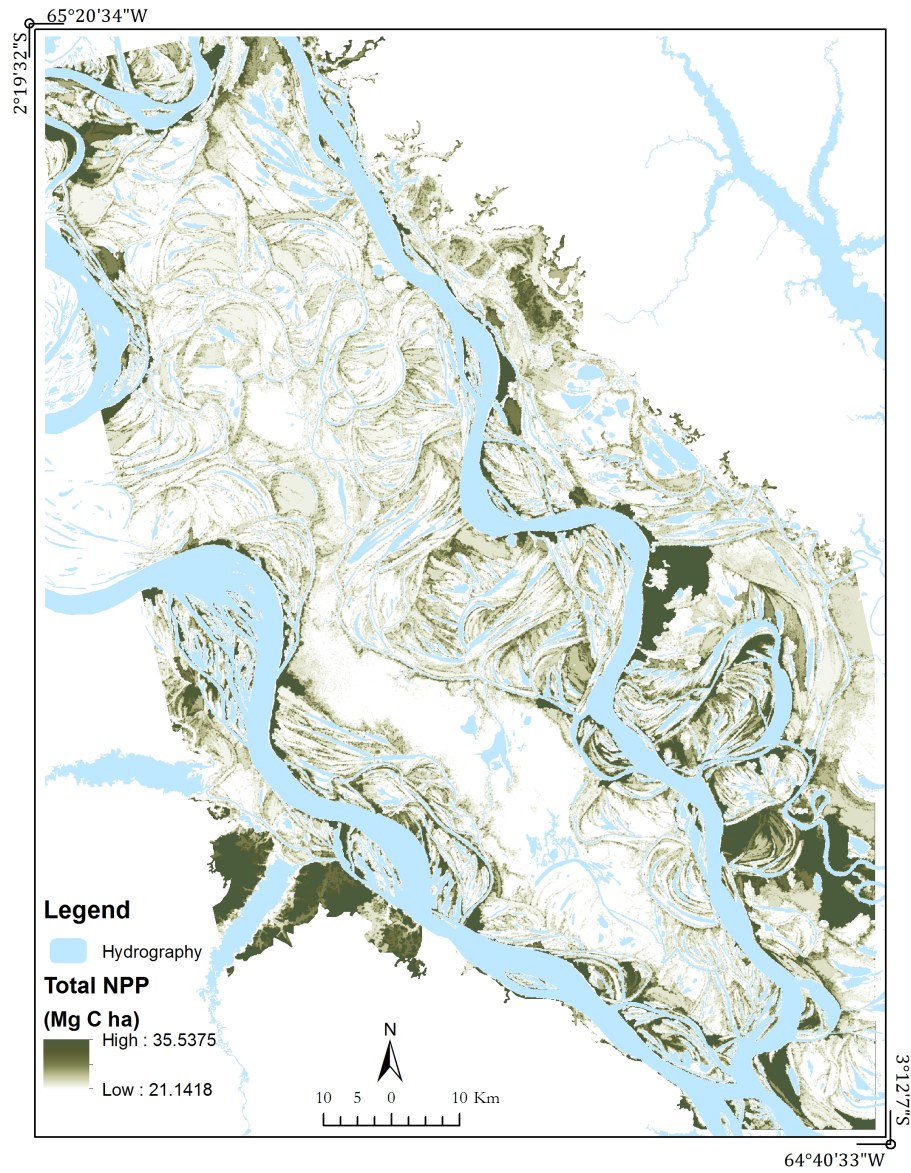


Figure 6.1: Spatial distribution of net primary productivity (NPP) in the várzeas forests of Mamirauá Sustainable Development Reserve (Central Amazon, Brazil). The NPP was predicted by a linear model using flood duration as predictor variable (see Figure 5.14a). The spatial distribution of flood durations were predicted using the logistic model for the year 2017, as in the Figure 3.4.

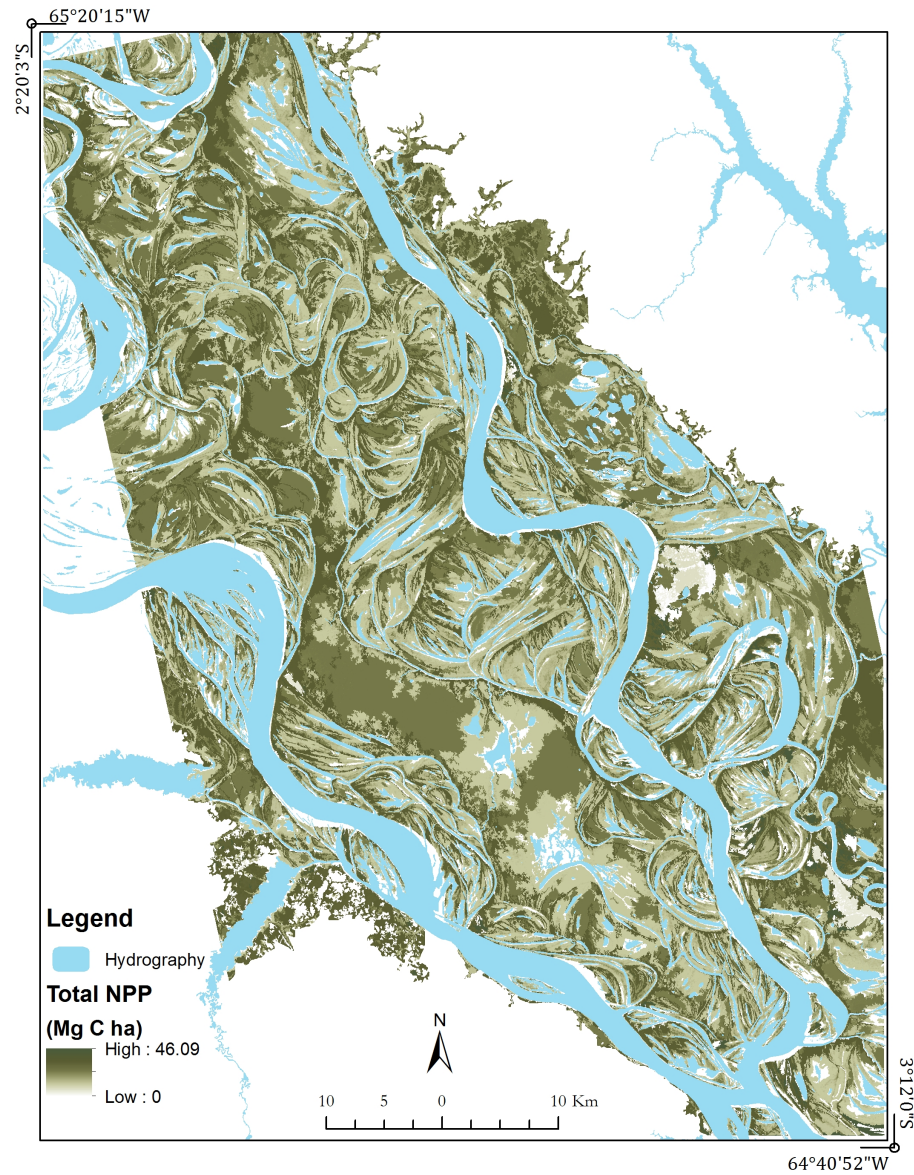


Figure 6.2: Spatial distribution of net primary productivity (NPP) as a function of flood duration controlling for forest subtype in the várzeas forests of Mamirauá Sustainable Development Reserve (Central Amazon, Brazil). The spatial distribution of flood durations were predicted using the logistic model for the year 2017, as in the Figure 3.4.

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