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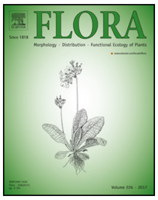

Patterns of floristic diversity and composition in floodplain forests across four Southern Amazon river tributaries, Brazil

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ABSTRACT

Floodplain forests cover extensive areas of the Amazon basin, but the number of tree inventories is low. Vast floodplain regions therefore remain floristically unknown. We present a quantitative inventory of floodplain forests from four Amazon river basins (Jutaí, Juruá, Tefé and Purus), investigate within- and between-basin floristic similarity, and examine patterns of tree species dominance and distribution. Twelve hectares with all trees ≥10 cm dbh were inventoried; three hectares in each river basin. Rarefaction curves were used to compare species richness across study areas. GNMDS was used to investigate within- and between-basin floristic similarity, combined with an analysis of similarity (ANOSIM) to test for significant differences. In total, 7722 stems representing 518 species were recorded. Inventory plots from the same river basin were clearly clustered in the GNMDS ordination and the ANOSIM showed that floristic composition differed significantly both between and within study areas. Fabaceae was the most abundant family and *Eschweilera albiflora* the most abundant species. Only nine species were highly abundant in more than one study area, whereas 220 species were recorded in only one sample plot. Our results demonstrate high levels of beta-diversity in Amazonian floodplain forests. The high number of uncommon species is consistent with other studies.

1. Introduction

Floodplains subjected to long-lasting and monomodal flood pulses cover approximately 760,000 km^2 along the Amazon River and its larger tributaries (Melack and Hess, 2010; Junk et al., 2011). Forests occurring on these vast floodplains might endure inundation up to 230 days per year, as the pronounced periodicity of precipitation, the Andean snow melt and the low declivity of the basin, combine to cause seasonal floods that may reach 10–15 m in amplitude in central Amazonia (Junk, 1989; Wittmann et al., 2004). Many adaptations have been described for plant species that inhabit these environments. They include reductions in photosynthetic activity and growth during flooding (Worbes et al., 1992; Worbes, 1997; Parolin, 2000), anaerobic metabolism (Fernandes-Corrêa and Furch, 1992; Schlüter et al., 1993), adventitious roots (Parolin, 2001), and hydrochoric and ichtyochoric dispersal strategies (Kubitzki and Ziburski, 1994; Lopez, 2001).

Amazonian floodplains were recently re-classified by Junk et al. (2011) as (i) floodplains of high fertility (white-water river floodplains, or *várzea*), (ii) floodplains of low fertility (black- or clear-water river floodplains, or *igapó*) and (iii) floodplains of intermediate fertility (black-water river floodplains on paleo-whitewater substrates, or floodplain *paleo-várzea*). Várzea floodplains are the most extensive and cover approximately 275,000 km^2 (Junk et al., 2011). Their rivers carry large amounts of nutrient-rich Tertiary/Quaternary sediments originating from the Andes or pre-Andean regions. Igapó covers an area of approximately 180,000 km^2 (Melack and Hess, 2010) and occurs along rivers that carry small amounts of ancient Precambrian sediments originating from the Guyana and Central Brazilian Shields. Floodplain paleo-várzeas cover at least 125,000 km^2 and occur on fluvial Andean deposits that have been abandoned by white-water rivers. These floodplains are inundated by small to intermediate black-water rivers that originate in cratonic areas and carry these already once-deposited paleo-sediments (Junk et al., 2011).

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The floristic composition of some Amazonian floodplain forests was described at the beginning of the last century by researchers such as Spruce (1908), Huber (1906, 1910) and Ducke (1913). However, the number of tree inventories in floodplain forest is approximately four times lower than in Amazonian upland forests (hereafter, terra firme; ter Steege et al., 2013). Most floodplain inventories have focused on várzea forest where approximately 100 ha have been inventoried in total (summarized in ter Steege et al., 2013). In igapó and paleo-várzea forest, only about 30 ha of inventories are currently available (e.g. Keel and Prance, 1979; Campbell et al., 1986; Ayres, 1993; Ferreira and Prance, 1998; Haugaasen and Peres, 2006; Montero et al., 2012). These inventories are mainly concentrated along the Amazon river, in the Caquetá/Japurá floodplains or in the Madeira river headwaters (ter Steege et al., 2013). Vast Amazonian floodplain regions therefore remain poorly known floristically (Parolin et al., 2004; Schulman et al., 2007).

It has been shown that tree species diversity and composition vary substantially between and within floodplain types in Amazonia (Worbes et al., 1992; Ayres, 1993; Ferreira and Stohlgren, 1999; Ferreira, 2000; Albernaz et al., 2012; Assis and Wittmann, 2011). Várzea forest generally supports a higher number of species than igapó, and is recognized as the most species-rich floodplain forest worldwide (Wittmann et al., 2006, 2010). High habitat diversity, caused by an extremely dynamic environment and high substrate fertility may promote and sustain this high species richness (e.g. Kalliola et al., 1991; Wittmann et al., 2002, 2004). Habitat heterogeneity has also been indicated as the main driver of the high beta-diversity at a local scale in várzea, while geographic gradients coupled with differences in flooding regimes and substrate fertility appear to be more important at larger scales across the Amazon floodplains (Wittmann et al., 2010; Assis et al., 2015a).

In this paper, we present a quantitative floristic inventory of várzea and paleo-várzea forests located along four Amazon river tributaries of central-western Brazilian Amazonia where little or no previous systematic botanical collections have been implemented. More specifically, we address the following questions: (i) How does tree diversity vary at local and regional scales in Amazonian floodplain forests containing different substrate conditions? (ii) Do floodplain forests with different historic-geographic origins, but situated within the same geographic area, support distinct tree assemblages? (iii) What are the patterns of tree species dominance and distribution at a regional scale? We discuss our results in light of previous floristic inventories across Amazonian floodplain forests.

2. Methodology

2.1. Study areas

Tree inventories were carried out in four central-western Amazonian floodplain forests located along different tributaries of the Solimões (=Amazon) river: Purus (S4°19′; W61°52′), Tefé (S4°9′; W65°6′), Juruá (S3°14′; W66°3′) and Jutaí (S3°22′; W67°28′; Fig. 1). All study areas are located in the lower reaches (in proximity to the confluence with the Amazon river) of each river basin and thus situated at similar latitude, but are separated longitudinally by a minimum and maximum distance of approximately 120 and 600 km, respectively. The Purus and Juruá rivers are white-water rivers carrying large amounts of nutrient-rich sediments from the Andes. Floodplains along these rivers are thus classed as várzea. The Tefé and Jutaí rivers carry paleo-sediments originating from the Andes, and are therefore classed as floodplain paleo-várzeas (Junk et al., 2011).

All four study areas are subjected to a predictable, long-lasting (>5 months), monomodal flood pulse (Fig. 2). Tefé, Juruá and Jutaí experience the flooding peak in April/May and Purus in June. October is the month in which all study areas have the lowest river level. The Purus has the highest flood amplitude, followed by Juruá, Jutaí and Tefé (Fig. 1). The Purus also has the highest flooding average (days/year^{-1}) at 128.3 ± 56.6 days, followed by Jutaí (120.4 ± 38.5), Juruá (114 ± 22.4) and Tefé (97.5 ± 58.5), respectively. Annual rainfall is approximately 2700, 2800, 2600 and 2500 mm, for Juruá, Jutaí, Purus and Tefé, respectively. None of the study areas have more than one month per year with rainfall – <100 mm (Sombroek, 2001).

2.2. Forest inventory

Tree inventories were conducted during the 2009 and 2010 low-water season. In total, 12 ha of floodplain forest were inventoried; three hectares in each river basin. All plots were placed in late-successional forest located far from cities and major settlements (at least 50 km). We therefore considered the forests pristine. Due to floodplain heterogeneity, inventory plots ranged from 0.25-1.0 ha (mean = 0.43 ± 0.15 sd)

Distance between plots within the same basin ranged from 0.5 to 10 km (mean = 4.71 ± 2.31 sd). Details of size and geographic coordinates of the sample plots are presented in the supplementary information (Table S1). All trees ≥10 cm in diameter at breast height (dbh) within each plot were individually tagged and had their dbh measured. Non-timber species (e.g. lianas, epiphytes or hemi-epiphytes) were not included in the inventories. Vouchers were collected from all trees and transported to the herbarium at the National Institute of Amazonian Research (INPA), Manaus, where they were identified to the lowest taxonomic level possible. Specimens not identified to species were assigned to morpho-species. Conforming to herbarium regulations, only fertile material was permanently deposited.

2.3. Data analysis

To investigate patterns of floristic composition we calculated relative abundance (RA), relative frequency (RF), relative dominance (based on basal area) (RD) and importance value index (IVI; Curtis and McIntosh, 1951) for each species in each study area. The family importance value (FIV; Mori et al., 1983) was also calculated for each family. Alpha-diversity was derived using the Fisher's Alpha Index (Fisher et al., 1943) and differences between study areas were tested using Mann-Whitney *U* tests. Differences were considered significant when $p < 0.01$.

In order to remove potential effects of different inventory plot sizes, rarefaction curves were used to compare species richness across study areas. Global Non-metric Multidimensional Scaling (GNMDS; Minchin, 1987) with Bray-Curtis distance measure based on 100 iterations was used to investigate within- and between-basin floristic similarity. An analysis of similarity (ANOSIM) was performed to examine significant differences in species composition between and within study areas. This analysis also uses the Bray-Curtis distances and includes a nonparametric permutations test equivalent to an ANOVA for similarity matrices (Clarke, 1993). All analyses were performed in R version 2.14.1 (R Development Core Team 2011), using the Vegan package (Oksanen, 2005).

3. Results

3.1. Species diversity

A total of 7722 stems representing 518 species (of which 211 are morpho-species), 203 genera and 55 families were recorded in the 12 ha inventoried. The Jutaí supported the highest number of individuals, but Purus contained the highest number of species