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Patterns of Plant Phenology in Amazonian Seasonally Flooded and Unflooded Forests

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1 **Abstract**

2 Few studies have successfully monitored community-wide phenological patterns in

3 seasonally flooded Amazonian *várzea* forests, where a prolonged annual flood pulse arguably

4 generates the greatest degree of seasonality of any low-latitude ecosystem on Earth. We

5 monitored the vegetative and reproductive plant phenology of *várzea* (VZ) floodplain and

6 adjacent *terra firme* (TF) forests within two contiguous protected areas in western Brazilian

7 Amazonia, using three complementary methods: monthly canopy observations of 1,056

8 individuals (TF: 556, VZ: 500), twice monthly collections from 0.5-m^2 litterfall traps within

9 two 100-ha plots (1 TF, 1 VZ; 96 traps per plot), and monthly ground surveys of residual

10 fruit-fall along transect-grids within each 100-ha plot (12 km per plot). Surveys encompassed

11 the entire annual flood cycle, and employed a floating trap design to cope with fluctuating

12 water-levels. Phenology patterns were generally similar in both forest types. Leaf fall peaked

13 during the aquatic phase in *várzea* forest, and the dry-season in *terra firme*. Flowering

14 typically followed leaf fall and leaf flush, extending into the onset of the terrestrial phase and

15 rainy season in *várzea* and *terra firme*, respectively. Abiotic seed dispersal modes were

16 relatively more prevalent in *várzea* than *terra firme*; the main contrast in fruiting seasonality

17 was more likely a result of differences in community composition and relative abundance of

18 seed dispersal modes than differences within individual genera. We emphasize the difficulty

19 in distinguishing the role of the flood pulse from other seasonal environmental variables

20 without multi-annual data or spatially replicated studies across the spectrum of Amazonian

21 forest types.

22

23 ***Key words:*** Dispersal modes; Floodplain forest; Fruit traps; Litterfall; Phenophase;

24 Seasonality; *Terra firme*; *Várzea*.

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1 **Resumo**

2 Poucos estudos monitoraram com sucesso a fenologia de toda a comunidade de plantas em

3 florestas de *várzea* na Amazônia, onde um pulso anual de inundação bastante prolongado

4 gera um dos padrões de sazonalidade mais intensos em quaisquer ecossistemas terrestres de

5 baixa latitude. Nós monitoramos a fenologia vegetativa e reprodutiva de plantas lenhosas em

6 florestas de *várzea* (VZ) e *terra firme* (TF) em duas áreas protegidas contíguas na Amazônia

7 brasileira ocidental, através de três métodos complementares: observações mensais das copas

8 de 1.056 árvores e cipós lenhosos (TF: 556, VZ: 500), coletas quinzenais através de

9 armadilhas de serapilheira (0,5 m^2) inseridas em duas parcelas de 100-ha (1 TF, 1 VZ, 96

10 armadilhas por parcela), e levantamentos mensais da queda residual de frutos no solo ao

11 longo de uma grade de transectos dentro de cada parcela de 100-ha (12 km por parcela). Estas

12 abordagens abrangeram todo o ciclo anual de inundação, empregando um desenho inovador

13 de armadilhas flutuantes para lidar com as flutuações no nível da água. Os padrões

14 fenológicos destes tipos de florestas geralmente se semelharam. A queda de folhas atingiu um

15 pico durante a fase aquática na floresta de *várzea*, enaquanto que na *terra firme* isto occoreu

16 na época seca. As florações tipicamente seguiram a queda de folhas maduras e o

17 rebrotamento de folhas novas, estendendo-se até o início da fase terrestre e a estação chuvosa

18 na *várzea* e *terra firme*, respectivamente. Modos abióticos de dispersão de sementes foram

19 mais predominantes na *várzea* do que na *terra firme*; o principal contraste na sazonalidade de

20 frutos entre os dois tipos florestais provavelmente resulta de diferenças na composição

21 florística do que diferenças entre populações no mesmo gênero. Destacamos a dificuldade em

22 distinguir o papel do pulso anual de inundação de outras variáveis ambientais sazonais na

23 ausência de dados supra-anuais ou estudos replicados espacialmente em todo o espectro de

24 tipos de floresta na Amazônia.

25

PLANT PHENOLOGY, THE TIMING OF PLANT VEGETATIVE AND REPRODUCTIVE CYCLES,

TYPICALLY DISPLAYS STRONG PERIODICITY IN BOTH TROPICAL AND TEMPERATE ZONES (van

Schaik *et al.* 1993, Newstrom *et al.* 1994, Ting *et al.* 2008), and is increasingly relevant to a

wide range of applied issues (Morisette *et al.* 2009). However, we still lack information on

local variation within tropical forest macromosaics consisting of different forest types. A case

in point is the variation between flooded and unflooded forests across lowland Amazonia,

which are subjected to strikingly distinct environmental gradients despite often occurring

side-by-side and experiencing similar climatic conditions.

Phenological patterns in unflooded *terra firme* forests, where dry-season water stress

is more demarcated, are primarily understood to be driven by radiation, photoperiod and

precipitation (Borchert *et al.* 2005, Zimmerman *et al.* 2007, Bradley *et al.* 2011). Extensive

lowland floodplain forests (*e.g.* in the Amazon, Congo, and Mekong river basins), however,

are subjected to an additional annual force, in the form of a predictable 'flood pulse' (Junk *et al.* 1989). For example, white-water Amazonian floodplain forests, known as v*árzea* forests

(Prance 1979), are typically inundated to a depth of up to 7.5 m for up to 230 days per year

(Junk *et al.* 2011). 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 deposition on leaves, and

low water conductance which paradoxically results in water deficits in the tree crown

(Parolin *et al.* 2004a).

The regularity of this powerful flood pulse is expected to influence many ecological

processes within *várzea* forests, including phenological strategies (Schöngart et al 2002,

Parolin *et al.* 2004b, Ferreira *et al.* 2010). In addition to the timing of fruiting, further

adaptations to seasonal inundation are expected to include other plant life-history traits

(Parolin *et al.* 2004b), including seed dispersal modes that take advantage of the prolonged

1   flood pulse. Animal-dispersed plants bearing fleshy fruits are well represented in Amazonian

2   forests, and tropical humid forests in general (Fleming & Kress 2011), while abiotically

3   dispersed plants are typically more common in dry forests (Griz & Machado 2001). In

4   seasonally-inundated forests such as *várzea*, a higher proportion of plants is also expected to

5   bear seeds dispersed by abiotic agents, in particular water, which is expected to be one of the

6   main dispersal vectors (Kubitzki & Ziburski 1994, Oliveira & Piedade 2002, Parolin *et al.*

7   2010b, 2013). However, this is likely to be tempered to some extent by the importance of fish

8   in seed dispersal in flooded forests (Horn *et al.* 2011). Examining the relative importance of

9   different seed dispersal modes between *terra firme* and *várzea* forests may help interpret the

10   communities of vertebrate frugivores found in these two adjacent forest types (Hawes &

11   Peres 2014).

12   Despite accounting for >400,000 km^2 (Junk *et al.* 2011, Melack & Hess 2010), *várzea*

13   forests are one of the most poorly studied Amazonian forest types (Parolin *et al.* 2010a). In

14   particular, few quantitative assessments of community-wide plant phenology are available,

15   with most studies located in close proximity to Manaus and focusing on a select few tree

16   species (Table S1). With the exception of one study (Haugaasen & Peres 2005), which also

17   compares *várzea* to *igapó* (black-water flooded forests), there is a distinct lack of direct

18   comparisons between *várzea* (VZ) and *terra firme* (TF) forests.

19   We redress this regional imbalance using a landscape-scale approach to explicitly

20   compare adjacent *terra firme* and *várzea* forests of the Juruá floodplain in a remote part of

21   western Brazilian Amazonia. Here, we present community-wide phenology patterns from

22   *terra firme* and *várzea* forests, including both reproductive and vegetative characters,

23   recorded using three complementary field methods (canopy observations, litterfall traps, and

24   residual fruit-fall surveys). We tested the hypotheses that the additional influence of the flood

25   pulse in *várzea* forest will induce (i) vegetative and reproductive phenological patterns,

1   including the timing of peak fruiting, to differ between the two forest types; and (ii) abiotic

2   dispersal modes (including anemochory and hydrochory) to be relatively more important than

3   in adjacent *terra firme* forests. In addition to community-wide patterns we also include a

4   comparison of dominant plant genera present in both forest types.

5

6   **METHODS**

7   STUDY SITE. — This study was conducted within two contiguous sustainable use forest

8   reserves in the state of Amazonas, Brazil, encompassing nearly 0.9 Mha: the Médio Juruá

9   Extractive Reserve (*ResEx Médio Juruá*, 253,227 ha) and the Uacari Sustainable

10   Development Reserve (*RDS Uacari*, 632,949 ha) (Fig. S1). These two reserves border the

11   Juruá river, a major white-water tributary of the Solimões (=Amazon) river, and contain large

12   expanses of upland unflooded *terra firme* forest (80.6% of combined reserve area) and

13   seasonally-flooded *várzea* forest (17.9%) closer to the main river channel (Hawes *et al.* 2012).

14   The Médio Juruá region has a wet, tropical climate with marked seasonal variation in

15   rainfall, temperature, humidity and floodwaters (Fig. 1). There is a mean annual temperature

16   of 27.1°C and annual rainfall, based on daily records over three consecutive years (2008-

17   2010) at the Bauana Ecological Field Station (BEFS; 5°26'19" S, 67°17'12" W), averaging

18   3,679 mm/yr. Additional rainfall data were obtained from Eirunepé meteorological station

19   (315 km from the study area, 2000-2010, source: INMET). Water-level data were recorded

20   locally at BEFS (Oct 2009 – April 2010) and also obtained from the Juruá river at Porto

21   Gavião, Carauari (90 km from the study area, 1972-1994 and 2008-2010, source: Petrobrás

22   S.A.). Although hot and humid throughout the year, the hottest months are August-November,

23   and humidity peaks in January-April. The precipitation pattern (rainy season: November-

24   April, dry season: May-October) is asynchronous with the flood pulse, so that the river and

25   floodplain water-level lags approximately 6 weeks behind rainfall (aquatic phase: January-

5

1　June, terrestrial phase: July-December) (Fig. 1). Climatic variables during the study period

2　relate closely to records from the previous decade, while the flood-pulse displays a slightly

3　delayed fall in water-level compared to long-term trends (Fig. 1).

4　　　The elevation range within the study area is 65-170 m asl and all sites surveyed

5　consisted of undisturbed primary forest. *Terra firme* soils are typically heavily leached and

6　nutrient poor in comparison to the eutrophic soils of *várzea* forests (Furch 1997), which are

7　renewed with a fresh layer of pre-Andean alluvial sediments every year. Fabaceae,

8　Lecythidaceae, and Sapotaceae were the most abundant tree families in both *terra firme* and

9　*várzea*. Chrysobalanaceae and Moraceae were particularly abundant in *terra firme* compared

10　to *várzea*, whereas Annonaceae and Malvaceae were comparatively more abundant in *várzea*.

11

12　CANOPY OBSERVATIONS. — We conducted monthly crown inspections from the ground for

13　twelve consecutive months (April 2009 – March 2010) along eight 1-km transects (April: 2

14　TF, 2 VZ; May-June: 3 TF, 3VZ; 4 TF, 4 VZ July-March), divided equally across *terra firme*

15　and *várzea* forests on either bank of the Juruá river (Fig. S1). We utilized a selection of

16　available pre-existing transects, either along the opposite edges of two 100-ha plots or near

17　the starts of longer 5-km transects, which were distributed evenly across the wider landscape

18　avoiding large streams and lakes (see Hawes & Peres 2014 for details). Mean elevation

19　(SRTM; Jarvis *et al.* 2008) was 100-106 m and 86-92 m in *terra firme* and *várzea* transects,

20　respectively, with mean flood depths measured directly along *várzea* transects from high-

21　water level marks visible on tree trunks of 192-304 cm (Hawes *et al.* 2012, Hawes unpubl.

22　data).

23　　　All live trees ≥30 cm in diameter at breast height (DBH), and all live woody lianas or

24　hemi-epiphytes ≥10 cm, within 5 m either side of each transect were measured (above

25　buttress roots where required), aluminium tagged, and identified. Palms (Arecaceae) are not

1   best assessed by DBH but only understory palms were present along our transects, which

2   were not included in our sample. Within a total survey area of 8 ha (eight 1000-m x 10-m

3   transects; 4 ha per forest type), we examined a total of 1,056 live stems (TF: 556, VZ: 500;

4   874 trees, 182 lianas) comprised of 120 genera from 45 families (Table S2).

5   The phenophase of each stem was recorded for each plant part at monthly intervals,

6   using a pair of 10x40 binoculars: leaves (new, mature, shedding), flowers, and fruits

7   (immature, mature). Dehiscent fruits were defined as mature when they visibly opened.

8   During the aquatic phase, transects in *várzea* forest were surveyed using dugout canoes.

9   Phenophase activity was estimated as the proportion of individual stems (and genera) bearing

10   a given phenophase in each forest type. For vegetative phenology we used observations of

11   leaf condition to classify each stem as displaying leaf fall, leaf flush or leaflessness. For fruit

12   availability we calculated the Fruit Availability Index (FAI), multiplying a monthly fruit

13   production score of 0-5 for each stem (Fournier 1974) by its basal area (Develey & Peres

14   2000), which is a strong predictor of fruit crop size in trees (Chapman *et al.* 1992). This value

15   was summed for all trees per transect to derive a density estimate of fruit production (FAI/ha).

16   Basal area is not a strong predictor of fruit crop size in high-climbing lianas (Chapman *et al.*

17   1994) so we excluded all lianas and hemi-epiphytes (representing only 17.2% of stems) from

18   this measure.

19

20   LITTERFALL TRAPS. — We used square traps constructed of polyester mesh with PVC tubing

21   support (Stevenson & Vargas 2008). Each trap had a collection area of 0.5 m^2 (0.71 x 0.71 m)

22   and was supported 1 m above the ground. To cope with the seasonal fluctuation of

23   floodwaters in *várzea* forest, we added buoyancy to this basic design using four empty,

24   water-tight 2-litre plastic bottles at each corner of the trap, to maintain the polyester mesh

25   above water. Traps were also tied loosely to the upper branches of surrounding vegetation to

1   stabilize the trap position within a vertical column, as they rose above their supports with the

2   floodwater (Fig. S2).

3   Litterfall traps were employed for twelve consecutive months (May 2009 – April

4   2010) within two 100-ha plots (1 TF, 1 VZ), each plot consisting of a grid of 1-km transects

5   at 200-m intervals (Fig. S1). Traps were located along all transects at 100-m intervals,

6   resulting in a total of 96 traps per plot (total collection area = 48 m^2). All material was

7   collected from traps twice monthly (by canoe during the aquatic phase in *várzea*), dried in

8   direct sunlight during the hottest time of day (09.00h – 15.00h) to a constant weight over at

9   least 72 h, and separated by plant part into fruits and seeds, flowers, leaves, and

10 twigs/branches (maximum diameter not defined). Each fraction was then dry-weighed

11 separately (using a 0.01 g resolution electronic scale) and all fruits and seeds were retained

12 for collection and identification. Mean monthly litterfall collections were estimated as Mg/ha

13 and trap collections were summed to provide annual estimates, standardizing for any

14 variation in number of days per collection period and the occasional omission of individual

15 damaged traps.

16

17 RESIDUAL GROUND SURVEYS. — We conducted monthly ground surveys for residual fruit-fall

18 within three 100-ha plots (2 TF, 1 VZ), as described above. Surveys were completed

19 between April 2008 and July 2010 (TF: total 18 months, 15 consecutive; VZ: total 26 months,

20 13 consecutive). All transects were surveyed slowly over four days (3 transects per day) each

21 month, recording all patches of fallen fruit detected along a 1-m wide strip (total transect

22 length and survey area per plot = 12 km and 1.2 ha). For each fruit patch encountered we

23 recorded its position along the transect, and sampled a specimen for our reference fruit

24 collection. In each case we also located the source fruiting stem, and measured its DBH and

25 perpendicular distance from the transect. During the aquatic phase in *várzea* forest, floating

1 fruits/seeds were also recorded, but unless their source crowns could be located overhead,

2 these were assumed to have originated outside the transect and were therefore excluded from

3 analyses.

4

5 TREE AND FRUIT IDENTIFICATION. — Number-tagged phenology trees were identified to the

6 highest possible level of taxonomic resolution (species 10.6%, genus 82.3%, family 15.0%)

7 by a trained herbarium technician from the Botany Department of the Instituto Nacional de

8 Pesquisas da Amazônia (INPA, Manaus). Additional tree and fruit identification was aided by

9 van Roosmalen (1985), Gentry (1993), Ribeiro *et al.* (1999), Cornejo & Janovec (2010), and

10 Wittmann *et al.* (2010a), which also assigned each species/genus recorded to the appropriate

11 seed dispersal mode: anemochory, hydrochory, barochory/boleochory, synzoochory or

12 endozoochory. All fruit/seed specimens were deposited at the Herbarium of the Instituto

13 Federal de Educação, Ciência e Tecnologia do Amazonas (IFAM, Manaus).

14

15 DATA ANALYSES. — Phenophase activity was calculated for each of the three methods

16 employed: (1) canopy observations were quantified as the percentage of stems or genera

17 observed in a given phenophase (further partitioned by seed dispersal mode for unripe and

18 ripe fruit), and as the FAI index of fruit production; (2) trap collections were used to derive

19 the monthly mean dry weight (Mg/ha) across all traps and the overall mean per trap across all

20 months; (3) fruit/seed collections from ground surveys were used to estimate the monthly

21 basal area density of all fruiting stems (m^2/ha). Our general focus compared community-

22 wide phenology patterns between *terra firme* and *várzea* forest, including the relationship

23 with seed dispersal modes, but also included an examination of fruiting phenology in

24 individual plant genera present in both forest types (>2 individuals in each) using circular

25 statistics with January being 15° (Morellato *et al.* 2010). All analyses were conducted in R (R

1   Development Core Team 2010); circular statistics were conducted using the CircStats

2   package (Lund & Agostinelli 2012), graphics were produced using the *ggplot2* package

3   (Wickham 2009).

4

5   **RESULTS**

6   VEGETATIVE PHENOLOGY. — Both *terra firme* and *várzea* forests displayed high seasonality,

7   although canopy observations of leaf fall and leaf flush were recorded at low levels

8   continuously throughout the year; leaf fall peaked in both forest types in March-April, while

9   leaf flush peaked in March in *várzea* and was more steady in *terra firme* (Fig. 2). Deciduous

10   species occurred in both forest types, but peaks in leaflessness occurred towards the end of

11   the aquatic phase (June) in *várzea* forest, compared to the end of the dry season (September)

12   in *terra firme* (Fig. 2).

13   Mean total fine litterfall in *várzea* forest was not significantly different from that in

14   *terra firme* (Table 1). Although leaf fall was significantly lower, the amount of

15   twigs/branches, bark and trash was higher. The proportion of total fine litterfall comprising

16   leaves was 80.4% and 74.7% in *terra firme* and *várzea* forest, respectively, with litterfall

17   fractions consisting of fertile material making the smallest contributions (Table 1, Fig. S3).

18   Leaf-fall collections were highest during the middle of the aquatic phase (March-May) in

19   *várzea* forest, compared to the dry season (August) in *terra firme* (Fig. 3).

20

21   REPRODUCTIVE PHENOLOGY. — Canopy observations of flowering reached maximum levels

22   shortly after peaks in leaflessness and leaf flush in both forest types, with peaks in *várzea* and

23   *terra firme* in July-September and October-November, respectively. Flowering in both forest

24   types persisted until December, with subsequent fruit development and maturation appearing

25   much more synchronous between the two forest types than other phenophases (Fig. 2).

1   Production of immature fruits peaked in November-January, whereas that of mature fruits

2   peaked in March-April.

3   Data from litterfall traps correspond closely with canopy observations. Peak flower

4   fall in *várzea* and *terra firme* forest was recorded in June and September-November,

5   respectively but they were not significantly different. Peak fruit-fall was recorded in January

6   for both *várzea* and *terra firme* forest (Fig. 3). There was no significant difference in fruit

7   biomass density between the two forest types. Surveys for residual fruit-fall showed

8   considerable inter-annual variation but suggest a unimodal pattern in *terra firme* forest with a

9   peak associated with maximum rainfall (Fig. 4). In contrast, temporal fruit availability in

10   *várzea* was more complex with the strongest peaks during the aquatic phase, but also

11   secondary peaks during the terrestrial phase (Fig. 4).

12

13   FRUITING SEASONALITY AND SEED DISPERSAL MODES. — The timing of fruiting was relatively

14   consistent within most individual genera occurring in both forest types (Fig. 5) and while the

15   community-wide pattern in fruit production also appeared similar in both *terra firme* and

16   *várzea* forest, there were noticeable differences across seed dispersal modes (Fig. S4). The

17   proportion of plant genera exhibiting abiotic dispersal modes (wind, water and ballistic) was

18   relatively higher in *várzea* forest (TF: 19 genera, 21.1% of genera; VZ: 17 genera, 26.2 % of

19   genera), whereas *terra firme* forest was more dominated by animal-dispersed plants (TF: 71

20   genera, 78.9% of genera; VZ: 48 genera, 73.8 % of genera). Fruiting peaked in *terra firme*

21   forest during the mid-rainy season almost exclusively due to animal-dispersed plants, with

22   wind-dispersed and ballistic genera bearing fruit at a more steady low level. In *várzea* forest,

23   both wind- and water-dispersed genera bore fruits most frequently during the aquatic phase

24   (Fig. S4).

25

DISCUSSION

Our study reports two important observations: (1) vegetative and reproductive phenological

cycles show strong seasonality in *várzea* and *terra firme* forests although patterns are broadly

similar, including peak fruiting within plant genera occurring in both forest types; and (2)

abiotic seed dispersal modes are relatively more prevalent in *várzea* forest than in *terra firme*

forest, where plants are more heavily dependent upon animal seed-dispersal vectors. Note

that litterfall material could not be oven-desiccated during this study and, in addition to the

definition of branch size categories, may represent a potential source of error to be considered

in the following comparisons with other studies.

VEGETATIVE PHENOLOGY. — Phenological studies often focus on flowers and fruits although

leaf production and abscission are potentially key stages 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 quantified

as a measure of primary productivity. In the *várzea* forests of the Médio Juruá, leaves

comprised 74.7% 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.* 2001).

Absolute values for *várzea* total fine litterfall in our study were intermediate between a

successional stage *várzea* (Schöngart *et al.* 2010) and a 60-year-old stand (Worbes 1997) in

Central Amazonia and, in contrast to regional analyses (Chave *et al.* 2009), we found no

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*.

This supports 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

1 cambial dormancy induced by the onset of the aquatic phase, with peak leaflessness

2 coinciding with the maximum flood pulse. In contrast, leaflessness in *terra firme* peaked

3 during the height of the dry season, although we failed to find evidence for varying degrees

4 of deciduousness between these forest types (but see Parolin 2001, Haugaasen & Peres 2005).

5

6 REPRODUCTIVE PHENOLOGY. — The timing of flowering we recorded concurs with previous

7 findings that peak levels in *várzea* forest occur towards the end of the aquatic phase, but can

8 extend into the terrestrial phase once floodwaters recede (Ayres 1986, Schöngart *et al.* 2002,

9 Haugaasen & Peres 2005). However, while Haugaasen & Peres (2005) report no difference

10 between peak flowering in *terra firme* and *várzea*, we found flowering in *terra firme* to peak

11 two months later than in *várzea*, and continue beyond the dry season into the onset of the

12 rainy season. Small differences in flowering between forest types could reflect an influence

13 of seasonal flooding on the availability of pollinators (van Dulman 2001). Canopy

14 observations also showed community-wide flowering to extend for almost six months,

15 reflecting a wide range of reproductive strategies for individual species.

16   Fruiting in humid tropical forests typically occurs during the early- to mid-rainy

17 season (van Schaik *et al.* 1993, Zhang &Wang 1995). Our data were consistent with this

18 pattern and fruit availability was similar in both *várzea* and *terra firme*, despite small

19 differences in the phenology of leaves and flowers. Likewise, fruiting peaks at Lago Uauaçú

20 were observed in December-March (early-mid rainy season) and January (start of the aquatic

21 phase) in *terra firme* and *várzea* forest, respectively (Haugaasen & Peres 2005). However, on

22 closer inspection, this pattern seems more complex in *várzea* forest than a simple lag behind

23 *terra firme*. While our trap collections indicate a *várzea* peak in December-January (early-

24 rainy season) as in *terra firme*, the amplitude is lower and a more pronounced peak occurs

25 during maximum flood levels in April-May. This is supported by ground surveys for residual

1   fruit-fall, which suggest a bimodal distribution in fruit production in *várzea* forest in contrast

2   to a unimodal pattern in *terra firme*. This is similar to the *várzea* forest at Lago Teiú,

3   Mamirauá (Ayres 1986), where a first fruit peak follows peak rainfall but precedes peak

4   water-levels, and a secondary peak precedes the onset of the rainy season, coinciding with the

5   submergence of low-lying *várzea* (*chavascal*). In our study the secondary peak occurred

6   during the terrestrial phase (onset of the rainy season), and was notably comprised of fleshy

7   fruits such as *Byrsonima* spp. and *Manilkara* spp.

8   The lack of a difference in fruit biomass between the two forest types is surprising

9   considering the much higher nutrient availability in *várzea* forests (Furch 1997). This may

10   imply that flooding and nutrient availability in the floodplain forest does not affect fruit

11   production. However, this finding fails to take in to account the lower stature and less

12   continuous nature of the *várzea* forest canopy, which suggests that relative fruit production

13   (per stem or per unit of aboveground forest biomass) is actually higher in this forest type,

14   where overall basal area is greater despite similar stem density (Hawes *et al.* 2012). That fruit

15   biomass recorded in litterfall traps was similar despite these differences in forest structure is

16   testament to the high productivity of *várzea* forests.

17

18   FRUITING SEASONALITY AND SEED DISPERSAL MODES. — Our results suggest that any contrast

19   in fruiting seasonality between *várzea* and *terra firme* is more likely a result of differences in

20   community composition and the relative prevalence of various seed dispersal modes than

21   differences within single genera. Our results from *terra firme* were consistent with previous

22   studies, in terms of the maturation of fleshy fruits consumed by vertebrate frugivores during

23   the humid early wet season (Lieberman 1982) and, conversely, the dry-season maturation of

24   fruits and seeds dispersed by abiotic agents (van Schaik *et al.* 1993). The greater prevalence

25   of wind-dispersed trees and lianas within *várzea* forest is likely related to the lower stature

1 and less continuous nature of the canopy, as well as the history of plant colonization of the

2 floodplains from adjacent *terra firme* forest communities (Wittmann *et al.* 2010b). That we

3 failed to detect any hydrochorous plants bearing mature fruits during the *várzea* terrestrial

4 phase is unsurprising, but mature fruits in anemochorous plants in this forest type appear

5 more tightly aligned to the dry season *per se* than to the terrestrial phase.

6   While we documented a surprisingly low proportion of hydrochorous plant genera in

7 *várzea* forest, seed dispersal in several plants classified as anemochorous or zoochorous may

8 in fact also be assisted by the floodwaters. Buoyancy represents just one of many strategies

9 employed by plants with fruits or seeds falling during flood conditions (Ferreira *et al.* 2010).

10 Others alternatively sink, remaining dormant on the forest floor until water-levels recede

11 (Kubitzki & Ziburski 1994) where they provide a food resource for terrestrial frugivores

12 returning to floodplain forests. During the aquatic phase moreover, many zoochorous fruits

13 are consumed and potentially dispersed by fish, rather than mammals or birds (Goulding

14 1980, Kubitzki & Ziburski 1994, Correa *et al.* 2007, Horn *et al.* 2011). As a result, the

15 proportion of tree species in floodplain forests that benefit from floodwaters, either directly or

16 indirectly and even without obvious hydrochoric characteristics, may be underestimated by

17 current classifications of seed dispersal modes.

18

19 PHENOLOGICAL TRIGGERS. — Varying levels of precipitation have often been considered the

20 principal environmental trigger for plant phenology in the tropics (van Schaik *et al.* 1993),

21 with the key proximate cue usually assumed to be the period of water stress (but see Wright

22 & Cornejo 1990). In *terra firme* forest, the period of most intense water stress is the dry

23 season, while within *várzea*, paradoxically, the greatest degree of water stress is a result of

24 anoxia from the extended period of water-logging and deep submersion (Parolin 2009). Other

25 environmental variables, however, may also potentially contribute as proximate triggers

1   (Parolin *et al.* 2010a). Indeed, the role of water stress may not be as important as the

2   seasonality of daily insolation, with this mechanism of photoperiod control now recognized

3   as a factor triggering leaf flush and flowering, even in tropical forests near the equator

4   (Borchert *et al.* 2015). Given the wide variety of plant strategies, different triggers may be

5   relevant for different species in both *terra firme* and *várzea* forests (Wright & Cornejo 1990,

6   Schöngart *et al.* 2002, Parolin *et al.* 2010a). This is shown by the variation in phenological

7   schedules between plants with different seed dispersal syndromes, where fruiting events in

8   wind-dispersed species in *várzea* forest appears more closely related to the dry season than to

9   the flood pulse.

10   Phenological triggers are best identified by examining long-term datasets; the

11   importance of multi-year studies is highlighted by the supra-annual reproductive cycles in

12   many species (Newstrom *et al.* 1994, Haugaasen & Peres 2005, Norden *et al.* 2007) and the

13   inter-annual variation in climatic conditions resulting in substantial oscillations in flood

14   pulses. However, apart from residual fruit-fall, we lacked such multi-year datasets. Further

15   caution in defining the environmental triggers of plant phenology is necessary due to the

16   difference between proximate triggers (environmental events correlated with phenology) and

17   the ultimate factors driving evolutionary scale selection pressures (Hamann 2004). Because

18   of these issues we resist the temptation to over-analyze possible phenological triggers in this

19   study.

20

21   CONCLUSIONS. — Our year-round community-wide assessment along the Rio Juruá

22   represents one of the most extensive efforts conducted to date in Amazonian *várzea* forest,

23   including a large sample area for canopy observations, litterfall traps and ground surveys,

24   making a substantial contribution to understanding phenological patterns and processes

25   within this forest type. Our successful 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 and illustrates the

possibilities for long-term studies in *várzea* and other flooded forests.

The increasingly threatened *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 seasonal habitat.

While recent large-scale advances have been made in digital and remote phenology

monitoring (Pennec *et al.* 2011, Zhao *et al.* 2012), there remains no substitute for field

surveys, especially for reproductive phenophases.

Within any single short-term study, it is difficult to disentangle the relationships

between phenology and environmental variables and, despite the general consistency between

forest types, it remains possible that the annual flood pulse still has an important contributory

role to play in plant phenology in *várzea* forests. Clarification of the relative roles of

environmental triggers in the phenology of flooded forests would be aided, not just by multi-

year studies, but by a systematic effort to increase the geographic distribution of phenology

studies.

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22

1 **TABLES**

2

3 TABLE 1. Annual fine litterfall fractions (Mean ± SD, Mg/ha/yr) sampled by 96 traps in each

4 forest type from April 2009 to March 2010. *P*-values are represented by * $P < 0.05$, ** $P < 0.005$,

5 *** $P < 0.001$.

	Terra firme	*Várzea*	*t*	*P*
Leaves	8.27 ± 0.96	7.43 ± 1.04	−5.76	<0.001 ***
Twigs/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

6

7

1   **FIGURE LEGENDS**

2   FIGURE 1. Seasonal variation in climate and river water-level in the Médio Juruá region of

3   western Brazilian Amazonia. Mean monthly records for (A) temperature, (B) humidity, and (C)

4   rainfall from Eirunepé meteorological station: gray shading represents 95% confidence intervals,

5   solid circles represent study months April 2009 – April 2010 (source: INMET 2000-10); mean

6   daily records for (D) water-level of the Juruá river at Porto Gavião, Carauari: gray fill represents

7   long-term records 1972-94, solid circles represent daily measurements during the study period:

8   April 2009 – April 2010 (source: Petrobrás S.A., 1972-94 and 2009-10).

9   FIGURE 2. Percentage of stems for each phenophase recorded by monthly canopy observations

10   in *terra firme* (open circles, dashed line) and *várzea* forest (shaded circles, solid line).

11   FIGURE 3. Mean monthly values for (A) total fine litterfall (Mg/ha), recorded from twice

12   monthly collections of 96 traps per 100-ha plot in both *terra firme* (open circles, dashed line) and

13   *várzea* forest (shaded circles, solid line), and for individual vegetative and reproductive fractions:

14   (B) leaves, (C) fine woody litter (twigs/branches, bark, trash), (D) flowers, and (E) fruits.

15   FIGURE 4. Fruit production estimates in *terra firme* (open circles, dashed line) and *várzea* forest

16   (shaded circles, solid line) using three complementary sampling methods: canopy observations of

17   (A) unripe and (B) ripe fruit, (C) trap collections of the fruit fraction in litterfall, and (D) ground

18   surveys of residual fruit patches (stem basal area: m^2/ha). Seasonal variation in (E) rainfall: black

19   points represent total monthly values from daily records at the Bauana field station; dotted line

20   represents records from the Eirunepé meteorological station (source: INMET), and (F) water-

21   level: solid circles represent daily measurements at the Bauana field station; gray fill represents

22   daily records obtained at Porto Gavião, Carauari (source: Petrobrás, S.A.).

1   FIGURE 5. Correlation of peak fruiting (mean angle ± circular standard deviation) from canopy

2   observations of 20 plant genera occurring in both *terra firme* and *várzea* forest. Point shading

3   represents seed dispersal modes; dashed lines represent equal angle in both forest types; number

4   codes refer to plant genera listed in Table S3.