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## RESEARCH ARTICLE

# Flooding × tree fall gap interactive effects on blackwater forest floristics and physical structure in the Peruvian Amazon

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To better understand how flooding and tree fall structure forests in the Amazon, I sampled vegetation plots within three blackwater forests (least flooded, medium flooded, highest flooded) and their tree fall gaps in the Peruvian Amazon. I found (1) increased flooding decreased family richness in the closed-canopy forests but increased it in their gaps, with no trends for no. of unique species, (2) flooding decreased stem size everywhere as did the number of stems as size increased especially for larger stems, (3) Green's index showed clumping only for least-flooded forests with the closed-canopy forest showing more than its tree fall gap, and (4) both flooding and tree fall gap creation decreased canopy coverage perhaps as an additive effect. Further among the stem size classes, only the smallest stems were significantly affected by openness and by type of forest, with a significant interaction term where flooding significantly decreased the number of these smaller stems in all forests and their gaps, except those with the highest level of flooding. Also tree fall gaps had significantly more, smaller stems than their forests in the two most-flooded forests, but not in the least-flooded forest. I conclude that flooding is a greater stressor and influence on the structure of these forests than tree fall, and so, in these forests, gradients and disturbances overlap in their traditional roles.

**Keywords:** LTER; Peru; restinga; tahuampa

### Introduction

Plants respond to both abiotic and biotic factors in the environment which are often organized along gradients (Walter 1973; Whittaker 1975) and after disturbances (Gleason 1926; Pickett & White 1985). Common gradients include precipitation, elevation, and temperature. Disturbances range from the very severe (e.g. landslides [Myster 1997]) to the less severe (conversion to agriculture [Myster 2007b], tree fall [Everham et al. 1996]) where biomass lost may be their currency (Tilman 1988; Myster 2003). Humans have been part of the vast forest–river system of the Amazon basin for many thousands of years, and there is some paleoecological data of their land use. This influence could have significant for much of the Holocene, for example, in occupation of lakeside sites and the cultivation of maize (Weng et al. 2002). The vegetation mosaic of any landscape is, therefore, largely determined by gradients and historical disturbances (Turner & Dale 1991; Myster 2001), and, consequently, examination of an ecosystem's gradients and disturbances – and the responses of their plants to them – is critical to understanding its structure, function, and dynamics.

In the Amazon basin, flooding forms major gradients – varying in frequency, duration, depth, and local spatial variation – which explain much of plant distribution, composition, association, and abundance (Junk 1989; Lamotte 1990). Whereas the unflooded Amazonian rainforest may resemble rainforests in other areas in the Neotropics (Lopez & Kursar 1999; Myster & Santacruz

2005; Myster 2012a), flooded forests have a unique biology and ecology (Kalliola et al. 1991). For example, common plant adaptations to flooding include (1) seed structures, so that seeds can escape predation from both terrestrial mammals and fish in order to germinate where fish may also disperse seeds, (2) seedling strategies of growing fast in order to have their leaves above the next 'high tide' or being able to endure extended submersion, and (3) special root structures, such as aerenchyma tissue, to facilitate gas exchange under water needed in part because of reduction in oxygen solubility in water under high temperatures (Junk 1989; Lopez & Kursar 1999; Parolin et al. 2004). The most common forest disturbance in the vast areas of the Western Amazon that have not been logged or converted to agriculture (Myster 2007b) is natural tree fall (Everham et al. 1996; Myster 2009), and the resulting gap dynamics in flooded forests should also have unusual aspects (Lamotte 1990).

Therefore, in order to better understand how Amazonian rainforests are structured, and to collect data urgently needed in the Neotropics for sound, sustainable management efforts, I used data from forest and gap plots in each of these three forest types found in northeastern Peru: blackwater forest that floods 1–2 months per year (called dry here for ease of presentation), blackwater forest that is under water 3–5 months per year (called wet), and blackwater forest which is under water for at least 6 months out of the year (called very wet). I used those data to test the interactive effects of blackwater forest type (dry, wet, very wet) × forest openness (closed-canopy, tree fall gap) on floristics

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(family richness, no. of unique species) and physical structure (mean stem size, stem size distribution, dispersion, canopy coverage). Two previous analyses of this data-set (Myster 2007a, 2010) focused on species richness, genera richness, average height, maximum height, basal area, stem density, above-ground biomass, turnover, and Fisher's alpha.

## Materials and methods

### Study site

The study site is the Area de Conservacion Regional Comunal de Tamshiyacu-Tahuayo (ACRCTT: [www.perujungle.com](http://www.perujungle.com); Gottdenker & Bodmer 1998; Myster 2007a, 2009, 2010) located in Loreto Province, 80 miles southeast of Iquitos, Peru ( $\sim 2^{\circ}\text{S}$ ,  $75^{\circ}\text{W}$ ) with a mean elevation of 106 m. The reserve is part of one of the largest (270,654 ha) protected area in the Amazon, containing wet lowland tropical rainforest (Lugo & Lowe 1995; Myster & Santacruz 2005; Myster 2012a) of high diversity (Daly & Prance 1989; Daly & Mitchell 2000). It is comprised of low, seasonally inundated river basins of the upper Amazon and named for the Tahuayo and Tamshiyacu rivers which form boundaries to the north and west. The substrate of these forests is composed of alluvial and fluvial Holocene sediments from the eastern slopes of the Andes. Annual precipitation ranges from 2.4 to 3.0 m per year, and the average temperature is relatively steady at  $26^{\circ}\text{C}$ .

This rainforest is divided into distinct communities defined by their flooding regime (Wittmann et al. 2004) where the rainy season is between November and April (Kalliola et al. 1991). These include blackwater forest which floods 1–3 months per year, blackwater forest which floods 4–6 months of the year, and blackwater forest which floods at least 6 months of the year. Maximum level of flooding was not measured in this study but is correlated with flooding duration (Randall W. Myster, pers. obs.). Blackwater is a local forest runoff containing tannins leached from litter, making the water acidic and low in nutrients (Myster 2009). Common trees in these forests include those of genera *Chorisia*, *Eschweilera*, *Hura*, *Spondias*, and *Virola*, and species such as *Calycophyllum spruceanum*, *Ceiba samauma*, *Inga* spp., *Cedrela odorata*, *Copaifera reticulata*, *Phytelphas macrocarpa* with understory palms such as *Guazuma rosea*, and *Piptadenia pteroclada* (Prance 1979; Daly & Prance 1989; Puhakka et al. 1992; Myster 2007a).

### Blackwater flooded forest plots

Within each of these three forest types, five areas of similar topography were selected in May 1999. These areas were primary, unlogged blackwater forest and had fresh, average-sized (100–300 m<sup>2</sup>; Brokaw 1982) gaps within them. Information gathered at the reserve from past scientific research and from local people working at the reserve was used to find these forest types and their

young gaps (<3 years old). In each forested area, and also in the center of an average-sized gap found in the area, a 5 m  $\times$  5 m (25 m<sup>2</sup>) plot was established as suggested for gaps of this size (Thompson et al. 1999). This was replicated five times within each forest type. Each of these 30 plots (3 forest types [dry, wet, very wet]  $\times$  2 forest openness types [closed-canopy, tree fall gap]  $\times$  5 replicates) was sampled during May 1999, 2000, 2001, and 2002. This included identifying each tree (the complete species list is in Myster 2007a) that was at least 1 cm diameter at breast height (dbh), measuring that dbh, and estimating its height using a tangent height gauge for tall trees. The dbh measurement was taken at the nearest, lowest point where the stem was cylindrical, and for buttressed trees it was taken above the buttresses.

Trees were identified to species, or to genus in a few cases, using Gentry (1993), Vasquez-Martinez (1997), and Ruokolainen and Tuomisto (1998) as taxonomic sources. We also consulted the Universidad Nacional de la Amazonia Peruana (UNAP) herbarium and these two websites: the Missouri Botanical Garden ([www.mobot.org](http://www.mobot.org)) and for specific surveys done in the Peruvian Amazon ([www.iiap.org.pe](http://www.iiap.org.pe)). Finally, in a few instances when plants could not be identified to species, common morphospecies were collected and deposited in the UNAP herbarium. These data are housed in the archives of the Long-Term Ecological Research (LTER) site in Puerto Rico (LTERDBAS #150) and may be accessed through their website ([luq.lternet.edu](http://luq.lternet.edu)).

### Data analysis

The 2002 data were used in an analysis of variance (ANOVA; split-plot design) using the means testing procedure Ryan-Einot-Gabriel-Welsh (SAS 1985). There were two main effects: forest type (dry vs. wet vs. very wet with two degrees of freedom)  $\times$  openness (closed-canopy forest vs. tree fall gap with one degree of freedom). I also investigated the interaction term (with two degrees of freedom) where significant interaction terms are graphed, because they are the most meaningful (SAS 1985). Finally, because of the multiple ANOVAs, the sequential Bonferroni test was employed (Rice 1989) but did not suggest that any significant results were unreliable.

I then pooled the data by combining the replicates together to generate two floristic parameters (family richness, no. of unique species) and four physical structures (mean stem size, stem size distribution classes, dispersion, canopy closure). The stem dispersion pattern was computed by comparing plot data to Poisson and negative binomial distributions using chi-square analysis and then generating Green's index (Ludwig & Reynolds 1988; Myster & Pickett 1992) which is based on the variance to mean ratio where 0 indicates a random distribution and 1 indicates maximum clumping. Canopy closure is expressed as a percentage of total plot coverage, using the formula in Buchholz et al. (2004).

## Results

The family richness for the dry forest (closed-canopy = 18, tree fall gap = 8) was summed over all five plots. The family richness for the wet forest (closed-canopy = 13, tree fall gap = 16) was summed over all five plots. The family richness for the very wet forest (closed-canopy = 9, tree fall gap = 11) was summed over all five plots.

The unique species for the dry forest, closed-canopy were *Lonchocarpus* sp., *Lecythis* sp., *Quararibea bracteolosa*, *Ormosia* sp., *Miconia grandifolia*, *Potalia amara*, *Lonchocarpus guilleminianus*, *C. reticulata*, *Ficus* sp., *Bixa orellana*, *Maytenus* sp., *Trophis racemosa*, *Simarouba* sp., *Duguetia quitarensis*, and *Protium* sp. for a total of 15, also summed over all five plots. The unique species for the dry forest, tree fall gap were *Lepidocarium* sp., *Cajanus cajan*, *Clibadium* sp., *Pourouma bicolor*, *Bauhinia* sp., *Virola cuspidata*, *Lanza caspi*, and *Licania britteniana* for a total of 8, also summed over all five plots. The unique species for the wet forest, closed-canopy was only *Aniba riparia*, also summed over all five plots. The unique species for the wet forest, tree fall gap were *Abuta grandifolia*, *Gnetum* sp., *Palicourea* sp., and *Coccoloba* sp. for a total of 4, also summed over all five plots. The unique species for the very wet forest, closed-canopy were *Astrocaryum murumuru*, *Theobroma subincanum*, *Annona* sp., *Psidium* sp., *Oenocarpus mapora*, and *Chionanthus* sp. for a total of 6, also summed over all five plots. Finally, the unique species for the very wet forest, tree fall gap were *Alchornea* sp., *Erythroxylum* sp., *Anaxagorea* sp., *Heliconia* sp., and *Persea* sp. for a total of 5, also summed over all five plots.

The number of stems in stem size class 2 for the dry forest was 20 for closed-canopy and 15 for tree fall gap, summed over all five plots. The number of stems in stem size class 2 for the wet forest was 22 for closed-canopy and 14 for tree fall gap, summed over all five plots. The number of stems in stem size 2 for the very wet forest was 13 for closed-canopy and 8 for tree fall gap, summed over all five plots. The number of stems in stem size class 3 for the dry forest was 8 for closed-canopy and 6 for tree fall gap, summed over all five plots. The number of stems in stem size class 3 for the wet forest was 12 for closed-canopy and 11 for tree fall gap, summed over all five plots. The number of stems in stem size 3 for the very wet forest was 11 for closed-canopy and 7 for tree fall gap, summed over all five plots.

The number of stems in stem size class 4 for the dry forest was 15 for closed-canopy and 3 for tree fall gap, summed over all five plots. The number of stems in stem size class 4 for the wet forest was 6 for closed-canopy and 3 for tree fall gap, summed over all five plots. The number of stems in stem size 4 for the very wet forest was 5 for closed-canopy and 1 for tree fall gap, summed over all five plots. Green's index for the dry forest was 0.75 for closed-canopy and 0.91 for tree fall gap; both of these forests were significantly nonrandom ( $\chi^2$ : 19.332

and 18.666 both >12.592, df = 8,  $p < 0.001$ ) and clumped ( $\chi^2$ : 16.447 and 15.281 both >12.592, df = 8,  $p < 0.01$ ). Green's index for the wet forest was 0.42 for closed-canopy and 0.52 for tree fall gap. Green's index for the very wet forest was 0.26 for closed-canopy and 0.33 for tree fall gap.

There was not a significant difference (1) among forest types when closed-canopy forest and tree fall gap data were pooled within dry forest, within wet forest and within very wet forest, (2) between closed-canopy forests (dry, wet, and very wet forest data pooled) and tree fall gaps (dry, wet, and very wet forest data pooled), or (3) in the interaction between these two main effects, on family richness (Table 1). There were significant differences, however, among forest types when closed-canopy forest and tree fall gap data were pooled within dry forest, within wet forest, and within very wet forest among forest types for no. of unique species, stem size class 1, Green's index and % canopy closure, between closed-canopy forests (dry, wet, and very wet forest data pooled) and tree fall gaps (dry, wet, and very wet forest data pooled) for stem size class 1 and % canopy coverage, and in the interaction between these two main effects, on mean stem size, stem size class 1 and % canopy coverage (Table 1).

For the significant interaction terms, means testing showed that mean stem size decreased significantly as flooding increased and when gaps were formed (Figure 1). In particular, the dry forest and wet forest were similar, the very wet forest was similar to the dry and wet gaps, and the very gap was dissimilar (Figure 1). Means testing also showed that number of stems in the smallest stem class decreased significantly as flooding increased and when gaps were formed (Figure 2). In particular, the dry forest and its gap were similar, the wet gap and the very wet gap were similar, and the wet forest and very wet forest were similar (Figure 2). Finally, means testing showed that % canopy coverage decreased significantly as flooding increased and when gaps were

Table 1. *F* statistic and significant *p*-value summary table for all main and interactive effects, operating on all floristic and physical structure parameters.

Response variable	Main effect (forest type)	Main effect (openness)	Interaction effect
Family richness	2.22	3.33	1.98
No. of unique species	6.06*	2.01	3.33
Mean stem size	3.02	2.76	5.45*
No. of stems	5.55*	5.02*	7.63**
1 < 2 cm dbh			
No. of stems	3.84	4.04	4.55
2 < 4 cm dbh			
No. of stems	3.02	3.33	3.59
4 < 10 cm dbh			
No. of stems at least 10 cm dbh	4.97	2.91	4.72
Green's index	5.43*	2.41	3.02
% canopy coverage	5.06*	4.97*	6.38*

A *p*-value between 0.05 and 0.01 is indicated by \*, a *p*-value between 0.01 and 0.001 is indicated by \*\*.

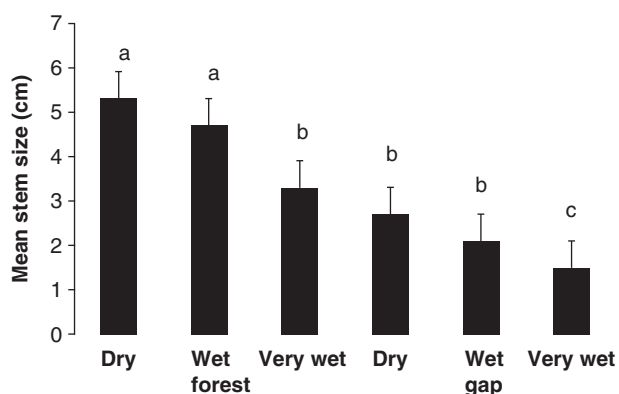


Figure 1. Means and standard errors of mean stem size in all plots grouped by the significant interaction effect between forest type  $\times$  openness. Means testing results are indicated by lowercase letters. If groups were different then the letters are different.

formed (Figure 3). In particular, the dry forest was dissimilar, the wet forest was similar to the very wet forest and the dry gap, and the wet and very wet gaps were similar (Figure 3).

## Discussion

Increased flooding decreased family richness in the closed-canopy forests but increased it in their gaps, with no trends for no. of unique species. Flooding decreased stem size everywhere as did the number of stems as size increased especially for larger stems. Green's index showed clumping only for the least-flooded forests with the closed-canopy forest showing less than its tree fall gap perhaps because flooding removed the smaller stems. Small stems may have been lost because of the force of the flow of water and/or because they are more easily submerged. Finally, both flooding and tree fall gap creation decreased canopy coverage perhaps as an additive effect.

The tree stem size distributions compared well with other Western Amazon flooded forests (see references in

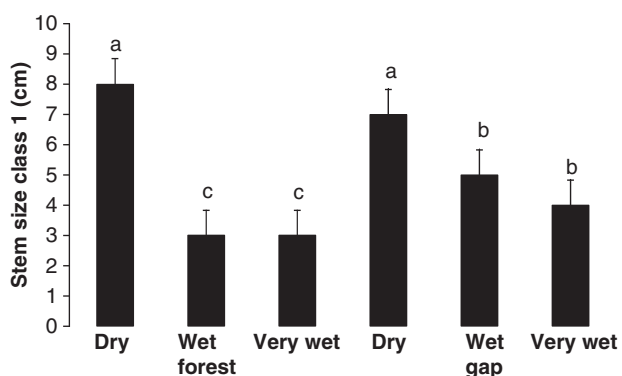


Figure 2. Means and standard errors of no. of stems in size class 1 in all plots grouped by the significant interaction effect between forest type  $\times$  openness. Means testing results are indicated by lowercase letters. If groups were different then the letters are different.

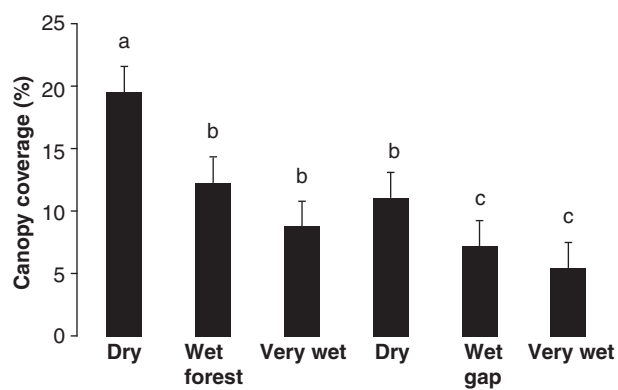


Figure 3. Means and standard errors of % canopy closure in all plots grouped by the significant interaction effect between forest type  $\times$  openness. Means testing results are indicated by lowercase letters. If groups were different then the letters are different.

Myster 2009). In addition, the least-flooded forest had similar stem densities compared to unflooded forests elsewhere in the Amazon (Ferreira & Prance 1998; Pitman et al. 1999; Thompson et al. 1999). Several structural parameters conformed to the flooding gradient, which is decreasing in complexity as flooding increased, which may be due in part to root burial by sedimentation and oxygen deficiency in flooded forests (Junk 1989; Lopez & Kursar 1999). Other parameters agreed with the more traditional view of tree fall destroying forest structure (Brokaw 1982) which then recovers that structure over time through a development sequence of ground coverage, organized vertical growth, surface arrangement at multiple levels, and crown differentiation. The fact that flooding and tree fall naturally occur together in these forests was captured in the sampling design which allowed an examination of how these forces work in concert. It would seem that flooding acts as a disturbance in these forests (Salo & Kalliola 1990) by removing plant biomass as gaps do (Myster 2001; Myster 2003).

In general, results show that flooding was a greater stressor on the forest than tree fall, with gap effects greatly diminishing as flooding increased. This may be because while tree fall can remove one or a few large trees, flooding destroys many (smaller) stems which can add up to removing more biomass and canopy coverage, increasing its effect. The loss of tree stem density with flooding (Baslev et al. 1987) might best be explained either by the loss of tree stems due to the action of moving water or by the physical damage due to the weight of debris (also seen in temperate forests: Myster & McCarthy 1989). Similarly loss of stems in gaps may be due to the weight of a falling tree, for example, its lianas pulling other trees down as well. The dry conformed to nonflooded forest expectations in having nonrandom, uniform stem dispersion patterns (Picard et al. 2009). Clumping in their gaps was also expected, but it was less (a smaller Green's index value) than that found in larger forest openings recovering from agriculture (Myster & Pickett 1992) which contain perches for

birds to land and disperse seeds. Such clumping may result from dispersal and/or from adaptations helping seeds and seedlings to survive after dispersal (Howe 1989).

Previous analyses of this same data-set showed other structural effects of gap formation on canopy average height, canopy maximum height, basal area, density, above-ground biomass, turnover, and alpha diversity (leading to fewer but larger trees in forest plots compared to gap plots: Myster 2010). Those analysis showed structural effects of and forest type on species richness, genera richness, density, turnover, and alpha diversity (leading to fewer trees, genera, and species as flooding increased: Myster 2010) as well. Finally compositional effects were also seen where common species existing between the wet forest and its gaps and between gaps found in the wet and very wet forest, tree richness being maximum in the dry forest and minimum in very wet gaps, and dominance-diversity curves having more dominance by single species in the dry forest and their gaps (Myster 2007a). Finally, in an on-site 1 ha wet blackwater forest plot (Myster 2013; Myster in press, Randall W. Myster, unpub. data): (1) stems conformed to a reverse J size pattern, (2) total stems when compared to other similar forest samplings with a slightly larger average dbh, (3) trees were clumped at a higher degree than a 1 ha várzea plot (Myster 2013; Randall W. Myster, unpub. data) with 12% canopy closure, and (4) extensive flooding reduced basal area, size of stems, stem densities, and above-ground biomass.

## Conclusion

Future long-term sampling in these plots may reveal that the dynamics of these forests, as for all plant communities, is defined by their plant-plant replacement process (Myster 2007b, 2012b). Results suggest managers concern themselves more with flooding than tree fall as a dominant structuring agent in these forests. Flooding tends to eliminate both vertical and horizontal heterogeneity which affects availability of commonly logged tree species as well as wildlife populations. Thus, flooding may reduce the 'mosaic' structure (Myster & Malahy 2012) caused by tree fall. Future modeling of these forest communities and their stand development should incorporate data on the effects of these two structuring forces, flooding and tree fall. Consequently in Amazonian forests gradients (here flooding) and disturbances (here tree fall gap formation) may overlap in their traditional roles by presenting plants with similar cues under different circumstances and may also have additive effects on forest structure.

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