Interactive effects of flooding and treefall gap formation on *terra firme* forest and *várzea* forest seed and seedling mechanisms and tolerances in the Ecuadorean Amazon

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Abstract: The influence of white-water flooding and treefall gap formation on terra firme forest regeneration was investigated in Yasuni National Park of western Ecuador. I set up seed traps, collected seed rain and soil samples, and set out seeds and seedlings in unflooded terra firme forest (dry) and its gaps, and in nearby white-water floodplain várzea forest (wet) and its gaps. I found that (1) total number of dispersed seeds was greatest in the dry gaps with more seeds and greater richness in the gaps than the forest for both forest types, (2) the greatest number of seedlings germinated from wet gap soils with the least from the dry forest with gaps having more seedlings compared to their respective forests, (3) on average 30% of seeds remained after two weeks in the field and species seed losses were significantly different in all but one of the four sites, (4) more large seeds than small seeds were lost to pathogens and those losses were greater in the forests than the gaps, (5) as seed mass increased seedlings survival rates also increased but growth rates declined, and (6) more seedlings survived in gaps compared to closed forests where they grew faster with a larger leaf area ratio. Past sampling has shown that species composition differed between forest types, and present results show that the greatest seed and seedlings losses and the slowest growth rates were in intact terra firme forest, there were medium losses and medium growth rates in terra firme gaps and in the intact várzea forest, and the smallest losses and fastest growth rates were found in várzea gaps.

Introduction

The Amazon is the world's largest tropical rainforest encompassing over 700,000,000 hectares (Holdridge 1967, Walter 1979, Lamotte 1990). It is also the most productive and most diverse terrestrial ecosystem on earth (Daly and Prance 1989), influencing world-wide precipitation and weather patterns as well as the Carbon cycle (Keller et al. 2004). *Terra firme* is the most common kind of forest in the Amazon. Most of that terra firme forest has not been subjected to extensive logging or agriculture (Myster 2007b), so that the most common disturbance is natural tree-fall (Myster 2009). Those resulting gaps are critical to terra firme forest regeneration, forest structure (e.g., diversity: Denslow 1987) and forest function (e.g., decomposition: Zhang and Zak 1995).

Interacting with gap formation in Amazon forests is a flooding dynamic – defined by flooding frequency and timing, flooding duration, water depth and composition – which forms major gradients (Whittaker 1975) and greatly affects plant species distribution, abundance, and association (Junk 1989, Lamotte 1990). Whereas the unflooded terra firme rainforest in the Amazon resembles rainforests elsewhere in the Neotropics (Everham et. al. 1996, Junk 1989, Lopez and Kursar 1999, Kalliola et al. 1991), these flooded forests have a unique biology and ecology (Kalliola et al. 1991). For example, (1) the dispersed seeds of many species in flood-ed forests must escape predation from both terrestrial and aquatic animals (Junk 1989) in order to germinate; (2) after germination seedlings must either tolerate flooding (Parolin 2002) or grow fast enough to maintain some leaves above the water surface when the flood waters come (Parolin et al. 2004); and (3) growing plants often contain special root structures, such as aerenchyma tissue, to facilitate gas exchange under water (Junk 1989, Lopez and Kursar 1999, Parolin et al. 2004), due in part to the reduction in oxygen availability in water because of low solubility and respiratory demands by microorganisms. The most common kind of flooding in the Amazon is by whitewater, creating *várzea* forests which differ from terra firme in floristic composition and physical structure (Myster 2013b).

In this study, I expand on past studies of the Amazon rainforest by examining how the interacting influences of flooding and tree-fall gap formation affect its seed and seedling mechanisms and tolerances (also see Myster 2007a, 2010). The goal of this study is to explore experimentally the seed rain, seed bank, seed predation, seed pathogenic attack, germination, seedling survivorship, seedling growth and seedling allocation: (1) among common early and mid-successional tree species in the Amazon, (2) between forests that never flood (terra firme) and those that are under whitewater seasonally (várzea), (3) between these intact, closed-canopy forests (terra firme, várzea) and their natural treefall gaps, and

(4) in all their interactions between the prime forest structuring forces of whitewater flooding and treefall gap formation.

I will be testing two specific hypotheses:

- Hypothesis I: Gap formation (intact closed-canopy forest → treefall gap) will decrease seed mechanisms and tolerances more than whitewater flooding (terra firme → várzea: Denslow 1987, Everham et. al. 1996, Schupp and Frost 1989, Zhang and Zak 1995).

- Hypothesis II: Whitewater flooding (terra firme → várzea) will decrease seedling mechanisms and tolerances more than gap formation (intact closed-canopy forest → treefall gap: Whittaker 1975, Junk 1989, Lamotte 1990).

Study area

The study site is the Yasuni Research Station (YRS: 0º41' S, 76º24' W), operated by the Pontificia Universidad Catolica of Ecuador and located within the Yasuni National Park of western Amazonian Ecuador (Valencia et al. 2004, Myster and Santacruz 2005, Myster 2012a, 2013b). The mean annual rainfall is 2826 mm, with August the driest month, and the mean monthly temperature varies between 22ºC and 34ºC (Valencia et al. 2004). Soils in the national park have been described as clayey, kaolinitic and aluminium-rich, whereas soils at the station in terra firme forest are acidic and rich in exchangeable bases with a texture dominated by silt (Coomes and Grubb 1998, Parolin et al. 2004, Tuomisto et al. 2003). Terra firme forest – never underwater and found throughout tropical America (Pitman et al. 1999; Pitman et al. 2001) – has been categorized as lowland tropical rainforest (Holdridge 1967). The elevation of the entire park is approximately 200 m above sea level and the station itself is the site of a long-term 50 ha vegetation plot, maintained by the Smithsonian Institution (Valencia et al. 2004).

Also at YRS, and located next to the nutrient rich whitewater Tiputini River, is floodplain várzea forest which is underwater off and on between the months of October and April to a maximum depth of 3 m. Treefall is the most common disturbance in both forest types (Svenning 2000), but flooding may have similar effects as gap formation because it also destroys and relocates biomass (Myster 2003, Salo and Kalliola 1990). I have measured the spatial and temporal variation of light in both terra firme forest and várzea forest at YRS and found a mean value for intact terra firme forest of 6.55 μmol/m²/s, for intact *várzea* forest of 8.82 μmol/m²/s, for terra firme gaps of 50.45 μmol/m²/s and for várzea gaps of 62.11 μmol/m²/s (Myster 2012a; author unpub. data). Elsewhere in Peru, I found a value of 10.22 μmol/m²/s for a forest under black water for a longer time than the YRS várzea forest and a value of 65.65 μmol/m²/s for its gaps (Myster 2007a, Myster 2010). Dominant tree species in terra firme include *Matisia oblongifolia*, *Rinorea lindeniana*, *Matisia malacocalyx*, *Iriartea deltoidea*, and *Brownea grandiceps*, and in *várzea* forest *Phytelephas tenuicaulis*, *Coussarea macrophylla*, *Quararibea wittii*, *Rinorea lindeniana* and *Sorocea steinbachii* (Balslev et al. 1987, Duivenvoorden et al. 2001, Valencia et al. 2004, Myster 2013b) The várzea forest also

had less tree stems, less species and was more open compared to the *terra firme* forest, both sampled at YRS (Myster 2013b).

Methods

Within each of the two forest types (which, for ease of presentation, will be referred to as dry [terra firme] and wet [várzea]), 10 representative areas were randomly selected in June of 2004, each at least 75 m apart: five of primary forest and five fresh, average-sized (all between 100-300 m² in area: Brokaw 1982) treefall gaps. The forests themselves were 200 m apart. In the center of each forest area and each gap area, seed traps were established and soil samples were taken in late June 2004 (Augspurger and Franson 1988) for a total of 20 microsites (2 forest-types [terra firme vs. várzea] × 2 openness-types [gap vs. non-gap/intact forest] × 5 replicates). Seed rain was collected using standard 1 m² area seed traps (see Myster and Sarmiento 1998) placed in the center of microsite and identified to species for a total sampling area of 20 m². The traps were constructed with wire mesh (5 cm² square) on top, cloth underneath for collecting the seeds, and suspended on 1 m slippery plastic poles for keeping the traps off the ground to reduce predation.

In order to investigate the seed bank, three soil samples were collected near each seed trap by insertion of a standard soil sampling probe of 6 cm diameter into the soil to a depth of 10 cm (a total sampling area of over 753 cm²), because recruitment is typically limited to these uppermost soil layers (Vazquez-Yanes and Orozco-Segovia 1993). At a shadehouse located at YRS, soil samples at each seed trap site were combined by spreading them on top of sterile potting mix at a 1 cm thickness in a small plastic pot. Each pot was then covered with thin plastic with a few holes poked through and watered weekly. After one year in the field (for the seeds in seed traps collected monthly and then pooled) or six months germinating in an on-site shadehouse (for the seedlings from soil samples), individuals were identified to species or genus using Vasquez-Martinez (1997), Romoleroux et al. (1997) and Gentry (1993) as taxonomic sources, but on-site taxonomists (see Valencia et al. 2004) also consulted the web site of the Missouri Botanical Garden <www.mobot.org>.

Tree seeds were also set out in each of the above 20 microsites in early July 2004. Ripe fruits were first hand-collected (using gloves) locally from one individual of two common (Valencia et al. 2004) early successional trees (*Cecropia sciadophylla* [0.0003 g/seed and bird/bat dispersed], *Ochroma pyramidale* [0.09 g/seed and wind dispersed]) and one common mid-successional/subcanopy tree (*Turpinia occidentalis* [0.51 g/seed and bird dispersed]) with obviously damaged and/or empty seeds discarded in the field (Dalling et al. 1998). Seeds were then hand-sorted (again using gloves) in the laboratory, visually inspected for damage under a dissecting microscope, and then floated to further exclude nonviable seeds (as in Myster 1997, 2004). Finally ten seeds of each of the three species were separately placed in sets of four plastic 9 cm diameter petri dishes spaced 30 cm apart, at each microsite: (1) a control dish, (2) a dish with tanglefoot (Forestry-

suppliers:Jackson, Mississippi) spread on the inside to deter insects, (3) a dish covered with 2 cm² chicken wire mesh to deter mammals, and (4) a dish with both exclusion treatments (see Myster 1997). This makes a total of 240 dishes (3 species × 4 treatments × 20 microsites) and 2400 seeds. Heavy plastic seed mimics were also placed in each dish.

After two weeks in the field, seed loss was scored in each dish, which was assumed to be due to action by an animal – not wind or splashing rain – because (1) evidence of animals was observed while collecting this data (e.g., chewed seeds and husks, small mammal feces) and (2) duplicate plastic seed mimics were not lost. I also made the assumption that seeds carried away were eaten and/or rendered nonviable in some other way associated with the action of an animal agent (Notman and Gorchov 2001), that is seeds did not germinate later after being removed by an animal. This assumption has been discussed in the literature for several years (Myster 2007b, 2013a) but to date no study has produced statistically significant results to question its validity. Indeed, attempts to track seeds in the field after animals take them – using, for example, fish line glued to seeds or tagging seeds using radioactive isotopes, magnets, and fluorescent dyes – may lead to experimental side effects of their own, which has not been examined. Only when germination after seed removal by animals has been shown to be statistically significant and a "seed-following" methodology has been proved to be non-invasive, should this assumption be reexamined.

The remaining seeds were collected for incubation (same protocol as in Myster 1997) and any empty seed hulls were discarded. Insect predators probably included ants, while mammal predators probably included mice and small rats (Emmons 1990, Myster 1997, Myster 2004). Seed were incubated in a YRS shadehouse on moist paper in sealed plastic petri dishes. After three weeks, seeds that germinated, seeds that did not germinate and had extensive fungal infection (lost to pathogenic attack where contact with the soil is not necessary for infection: Myster 1997, Gallery et. al. 2010), and "other" seeds were scored after viewing under a dissecting microscope.

Two tree seedlings of each of two common early successional trees (*Cecropia ficifolia*, *Ochroma pyramidale*) and one common mid-successional/sub-canopy tree (*Clidemia dimorphica*: Valencia et al. 2004) were collected locally from a few gaps and forest understories with their root systems largely intact and with some original soil attached. Seedlings of *Ochroma* sp. and *Turpinia* sp. were not available for study. All seedlings were approximately 10 cm in height at time of collection. These seedlings were planted in each of the same 20 microsites used earlier in early July 2004 for a total of 120 seedlings (2 replicates × 3 species × 20 microsites). To facilitate comparison between seed and seedlings mechanisms and tolerances, the same genus was used for both the seed and the seedling experiment in two out of three cases. Based on past experience in transplanting tree seedlings in the Neotropics (Myster 2004) and on discussions with other YRS researchers about the hardiness of these species, seedling death due to stress associated with transplantation was probably rare.

After six months in the field, individual seedlings were first scored for survivorship and, for those seedlings that survived, scored for height and for basal diameter. Then surviving seedlings were collected and taken to the laboratory where total leaf area for each seedling was scored by placing each leaf against a plastic template divided into 1cm² squares and total leaf biomass, total stem biomass, and total root biomass was scored by weighting after one month of air-drying at room temperature. I then computed total biomass for each seedling as the sum of total leaf biomass, total stem biomass and total root biomass. From that data I computed, for each seedling, three growth parameters (1) relative growth rate (RGR = ln(final height) – ln(initial height [=10 cm])/0.5 yr, (2) leaf area ratio (LAR = total leaf area/total biomass which is a better predictor of relative growth rate than physiological parameters: Kitajima 1994, Poorter et al. 1990), (3) specific leaf area (SLA = total leaf biomass/total leaf area), and the allocation parameter (1) leaf mass ratio (LMR = total leaf biomass/total biomass).

Because individual samples of the seed rain and the seed bank were pooled over forest and gap types, standard errors could not be computed. For each of the seed and seedling mechanisms and tolerances, data were analyzed for the main effect of species, the main effect of forest-type, and the main effect of openness-type using three-way analysis of variance blocked for forest-type (ANOVA: SAS 1985). Where significant effects were found, the Ryan-Einot-Gabriel-Welsch multiple range test (Myster 1997, SAS 1985) was used to investigate which levels of the variables were most important in determining those effects. All ANOVA's variance assumptions were tested and found well justified. In addition, the sequential Bonferroni test was employed (Rice 1989), but did not suggest that any significant results be viewed with suspicion.

Results

Dry forest traps had, on average, 3.5 seeds/m²/month, dry gap traps had 33.9 seeds/m²/month, wet forest traps had 3.7 seeds/m²/month, and wet gap traps had 6.9 seeds/m²/month (Table 1). The total number of seeds was greatest in the dry gaps mainly because of the contribution of seeds from *Ficus maxima* (Table 1). The number of dispersed seeds was very similar between dry and wet forest, with more seeds falling in the gaps for both forest types. Richness was also greater in the gaps compared to the intact closed-canopy forest, regardless of forest type (Table 1) while wet forest had more species than dry forest. *Iriartea deltoidea* was the only species found in all four sites. *Brownea graniceps*, *Euterpe precatoria*, and *Inga auristellae* were the only species found in both forests. *Matisia* sp. and *Cecropia sciadophylla* were the only species found in both gaps

After five months of germination, dry forest had 15 seedlings emerge from its soil samples, dry gap had 24, wet forest had 34, and wet gap had 43 (Table 2). The greatest number of seedlings came from the wet gap with the least from the dry forest. Gaps had more seedlings than their respective forests, but numbers of species were very similar across forest types and their gaps. *Elcho pityrogramma* and *Cecropia*

Table 1. Tree seeds collected from traps taken from and summed over forest and gap microsites both in *terra firme* (dry) and floodplain (wet) rainforest. Nomenclature for Table 1, Table 2, and the test species is at http://www.theplantlist.org/tpl/record/kew-313975.

Species	dry forest	dry gap	wet forest	wet gap
Brownea grandiceps		32	14	
Grias neuberthii		24		
Matisia sp.	9			12
Cecropia sciadophylla		161		120
Ficus maxima		422		
Iriartea deltoidea	29	40	15	12
Oenocarpus bataua	18			18
Euterpe precatoria	42		11	
Inga auristellae	62		58	
Aspidosperma sp.		69		
Prestoea schultzeana		56		
Coussapea orthomera		81		
Mouriri grandiflora		32		
Asteraceae		138		
Prunus sp.		8		
Dicranostiles sp.			47	13
Astrocaryum murumuru			30	
Pepemacrustaa sp.				21
Hasseltia floribunda				15
Clusia sp.				17
Piptadenia sp.				27
Virola peruviana			39	31
Icasinacea sp.				1
Gustavia sp.			11	
Pseudolmedia laevis			23	
Total number of seeds	160	1087	212	292
Total seed richness	5	12	9	12

Table 2. Tree seedlings germinated from soil samples taken from and summed over forest and gap microsites both in *terra firme* (dry) and floodplain (wet) rainforest.

Species	dry forest	dry gap	wet forest	wet gap
Elcho pityrogramma	8	13	27	38
Ossaea boliviensis	1	7	4	
Phylodendron sp.	1			
Cecropia membranacea	5	3	3	4
Asteraceae		1		
Commelinaceae				1
Total number of seedlings	15	24	34	43
Total seedling richness	4	4	3	3

membranacea were the only species found in all four microsites. *Ossaea boliviensis* was the only species found in both forests. *Cecropia membranacea* and an unnamed member of the family Asteraceae were the only species, genera or family found in both the seed rain and the seed bank. Whereas in the seed rain *Cecropia* spp. were found only in gaps, in the seed bank they were found in all microsites. However Asteraceae was only found in the dry gap for both seed rain and seed bank (Table 2).

Table 3. F statistic summary table for percent tree seeds remaining in petri dishes. The P value of each significant test is indicated as: * for a P value between 0.05 and 0.01, ** for a P value between 0.01 and 0.001, and *** for a P value less than 0.001. Main effects are species, exclude invertebrates, and exclude vertebrates.

	Dry forest	Dry gap	Wet forest	Wet gap
Species (S)	14.27**	37.90***	7.53*	1.30
Exclude Invertebrates (EI)	97.56***	286.33***	30.53**	28.95**
Exclude Vertebrates (EV)	51.16***	169.88***	47.17**	43.38**
S * EI	8.37*	1.25	0.82	0.12
S * EV	2.39	2.29	1.94	0.01
EI * EV	3.05	1.68	3.21	0.38
S * EI * EV	2.73	3.62	0.35	1.15

Table 4. F statistic summary table for percent tree seeds taken out of petri dishes. The P value of each significant test is indicated as: * for a P value between 0.05 and 0.01, ** for a P value between 0.01 and 0.001, and *** for a P value less than 0.001. Main effects are species, forest-type (dry vs. wet), and openness-type (intact forest vs. gap).

|	Predation	Pathogens	Germination
Species (S)	14.36**	19.66**	3.53
Forest type (FT)	0.81	0.03	4.43*
Openness (O)	0.26	5.53*	0.40
S * FT	0.57	0.19	1.12
S * O	1.69	2.93	1.40
FT * O	0.07	0.56	2.29
S * FT * O	1.93	0.15	0.72

Table 5. F statistic summary table for seedling survivorship, growth, and allocation. The P value of each significant test is indicated as: * for a P value between 0.05 and 0.01, ** for a P value between 0.01 and 0.001, and *** for a P value less than 0.001. Main effects are species, forest-type (dry vs. wet), and openness-type (intact forest vs. gap). Replication was too low to compute the three way interaction term for relative growth rate (RGR), leaf area ratio (LAR), leaf mass ratio (LMR) and specific leaf area (SLA).

|	Survivorship	RGR	LAR	LMR	SLA
Species (S)	18.36***	9.66**	15.53***	1.11	7.02**
Forest type (FT)	2.81	5.02*	6.43*	2.45	5.66*
Openness (O)	6.26*	5.53*	7.40*	0.76	3.02
S * FT	0.57	0.19	1.12	0.55	1.23
S * O	1.69	4.93*	4.80*	1.59	1.67
FT * O	0.07	5.56*	17.29***	2.02	0.45
S * FT * O	0.05	-----	-----	-----	-----

The majority of seeds were lost to predators, with approximately 45% of the seeds remaining after 2 weeks in the field (Table 3. Figures 1a, 1c, 1d). Species were significantly different in all but one of the four sites (Table 3). More seeds remained of *Turpina* – which had larger seeds – in all cases

where species were significantly different, but more *Ochroma* seeds survived in the dry forest compared to dry gap and wet forest. Both exclusion treatments were highly effective in all four sites in deterring predators, with 95-100% survival in dishes having both exclusion treatments, however more seeds were taken by invertebrates (81%) compared to vertebrates

(63%) unlike another terra firme study that used larger seeds (Notman and Gorchov 2001). The species × exclude insects interaction suggests that insect preferences drove the significant seed species effects more than mammal preferences (Figure 1b) and that the insect preferences were strongest at the smaller seed sizes.
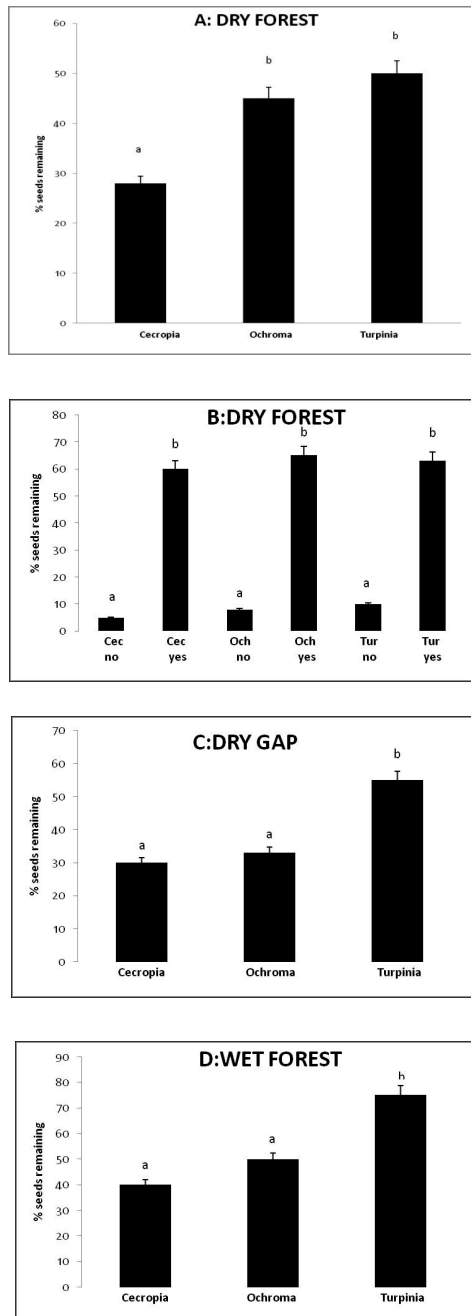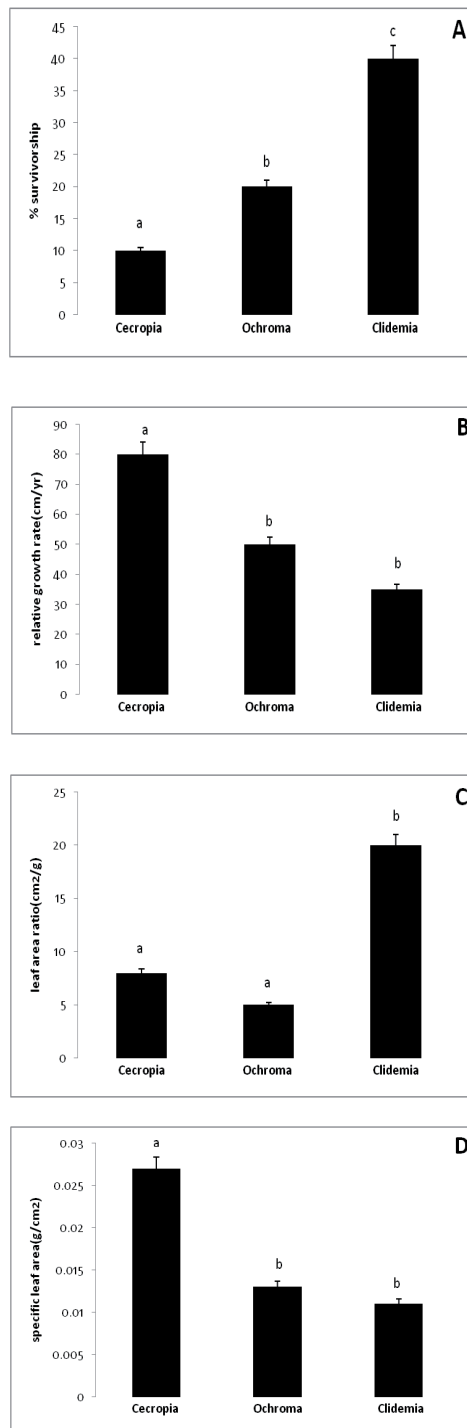

Figure 1. Means and standard errors of significant effects on percent tree seeds remaining (A) in dry forest by species, (B) in dry forest by species x excluding invertebrates (no = no exclusion, yes = exclusion), (C) in dry gap by species, and (D) in wet forest by species. Species are ordered by increasing seed fresh mass. Means testing results are indicated by lowercase letters which are different, if groups were significantly different, as given in Table 3.
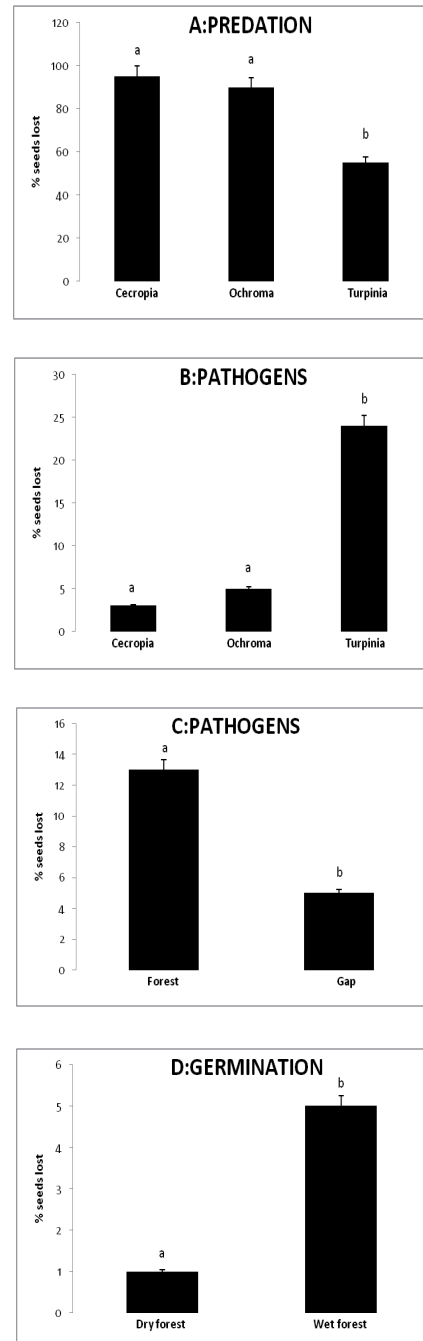
Figure 2. Means and standard errors of significant effects on percent tree seeds lost (A) to predators by species, (B) to pathogens by species, (C) to pathogens by openness, and (D) to germination by forest type. Species are ordered by increasing seed fresh mass. Means testing results are indicated by lowercase letters. If groups were significantly different, as given in Table 4, then letters are different.
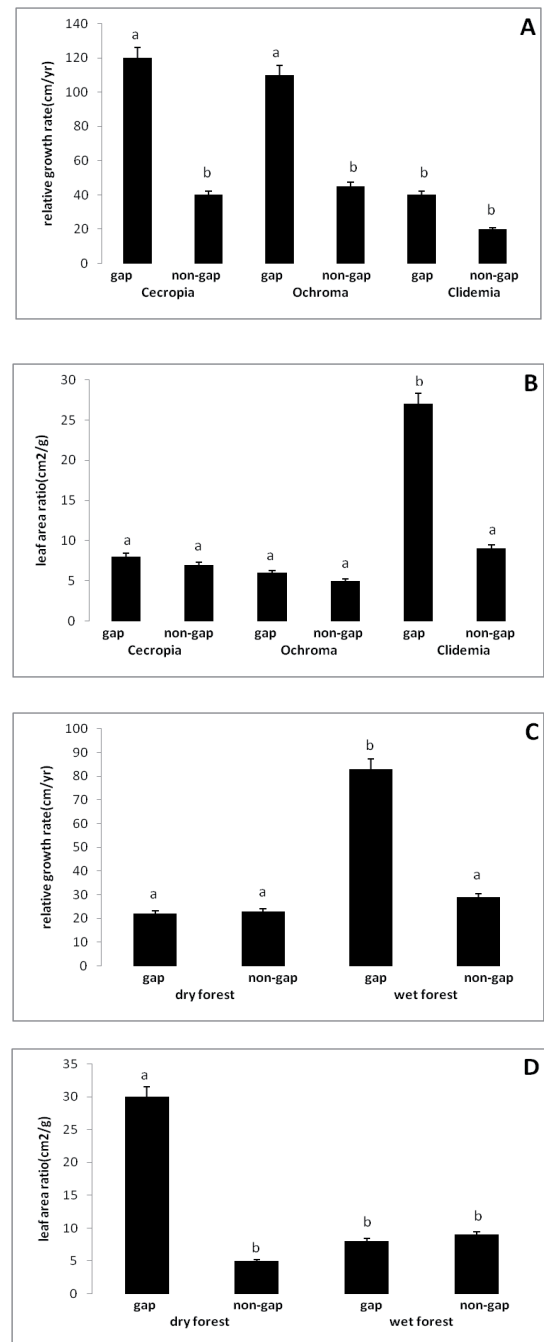
The domination of species effects (Figure 2a) continued when seeds were scored for losses due to pathogens (Table 4), with larger seeds (i.e., *Turpina*) suffering more losses (Figure 2b). Pathogenic losses were also greater in the forest com-

pared to the gap sites (Figure 2c) and more seeds germinated in the wet forest compared to the dry forest (Figure 2d).

Species effects were also seen when seedling survivorship and growth were examined (Table 5). As seed mass increased, seedlings survival increased (Figure 3a) but growth slowed (Figure 3b). The mid-successional *Clidemia* had the

Figure 3. Means and standard errors of significant effects of species on (A) seedling survivorship, (B) seedling relative growth rate, (C) seedling leaf area ratio, and (D) seedling specific leaf area. Species are ordered by increasing seed fresh mass. Means testing results are indicated by lowercase letters which are different, if groups were significantly different, as given in Table 5.

Figure 4. Means and standard errors of significant interaction effects of (A) species and openness on seedling relative growth rate, (B) species and openness on seedling leaf area ratio, (C) forest type and openness on seedling relative growth rate, and (D) forest type and openness on seedling leaf area ratio. Species are ordered by increasing seed fresh mass. Means testing results are indicated by lowercase letters which are different, if groups were significantly different, as given in Table 5.

largest leaf area ratio (Figure 3c) and the smallest seeded species *Cecropia* had the largest specific leaf area (Figure 3d). There was also faster growth in the wet forest compared to the dry forest (RGR in dry forest = 23 cm/yr vs. 68 cm/yr in wet forest), a smaller leaf area ratio (LAR in dry forest = 18 cm^2/g vs. 9 cm^2/g in wet forest) and a larger specific leaf area (SLA in dry forest = 0.01 g/cm^2 vs. 0.018 g/cm^2 in wet forest). More seedlings survived in gaps compared to closed forests (survivorship in gaps = 60% vs. 35% in intact forest) where they also grew faster (RGR in gaps = 60 cm/yr vs. 35 cm/yr in intact forest) with a smaller leaf area ratio (LAR in gaps = 18 cm^2/g vs. 35 cm^2/g in intact forest). Finally, significant interaction effects (Table 5) helped to clarify the main effects. Relative growth rate was highest in gaps for the two smallest-seeded species *Cecropia* and *Ochroma* (Figure 4a) and those gaps were in wet forest (Figure 4c). Alternatively, leaf area ratio was greatest in gaps for the larger-seeded *Clidemia* (Figure 4b) and those gaps were in dry forest (Figure 4d).

Discussion

There was support for both hypothesis I and hypothesis II because the most common effects were gap formation affecting seeds and flooding affecting seedlings. Species differences, however, were also important, especially for seed predation and seed pathogens.

Comparison to other Neotropic studies

Seed numbers in the traps were within ranges sampled in other Neotropical terra firme forests, low compared to some Neotropical gaps (1.1-12 seeds/m2/month in intact forest and 72-234/m^2/month for gaps: Schupp 1990, Young et al. 1987) and Ecuadorian old fields (166/m^2/month: Myster 2004) but not others (1.3/m^2/month load in gaps and 9.5/m^2/month in forest: Loiselle et al. 1996). Seed rain in other tropical floodplain forest in the Amazon also contained the species *Iriartea deltoidea* and the genus *Virola* (Clark et al. 1999). *Cecropia* sp. levels were in the ranges of other studies (Alvarez-Buylla and Martinez-Ramos 1990).

As in Panama lowland terra firme forest and gaps, most of the seed rain was from animal-dispersed species, but more wind-dispersal species were found in the gaps compared to the forests (Augspurger and Franson 1988). Seeds were again mainly from species-rich families such as Melastomataceae, Piperaceae, and Rubiaceae. However, the study was done in the wet season when flooding is more likely and there may be more bird-dispersed seeds available compared to wind-dispersed seeds with the reverse true at the end of the dry season earlier in the year (Denslow and Diaz 1990, Kubitzki and Ziburski 1994). In addition with these seeds, secondary dispersal is common by fish and by water.

Seedlings emerging out of the seed bank were rare which is usually true in tropical systems (Vazquez-Yanes and Orozco-Segovia 1993). However, *Cecropia* sp. were present and they are known to persist in the terra firme soil for more than a year (Brokaw 1998) and in floodplain soil for at least

two months (Parolin et al. 2004). The number of seeds and seedlings in the gap seed rain and seed bank is similar to recovering agricultural fields and landslides in upland forest in Ecuador (Myster and Sarmiento 1998, Myster 2004), but with very few species in common. Because there were more seedlings in gaps than in forests, seed banks may be more important as a regeneration mechanism in these gaps compared to these forests (Dalling et al. 1998). Finally correlations between seed rain and seedling densities can be difficult to find (Swamy et. al. 2011).

As found in several other Neotropical *terra firme* studies, predators took a large majority of seeds (Schupp 1988, Dalling et al. 1998, Everham et al. 1996, Notman and Gorchov 2001, Romo et al. 2004, Wenny 2000), and there were large seed losses in Amazonian floodplain forest (Romo et al. 2004). This study showed high predation in all microsites but no significant differences between gaps and intact *terra firme* forest (Wenny 2000) where other studies have shown both more (Schupp and Frost 1989) and less predation in gaps (reviewed in Notman and Gorchov 2001) compared to the forest. Seeds survived at the same levels or higher for all three test species in the wet forest compared to the dry, so flooding may have reduced predation (Wurm 1998) or perhaps predators were less abundant in the flooded forest. Most significant effects were due to species differences (Notman and Gorchov 2001) reflecting the preferences of insects and rodents (which may be an interaction of seed odors and the olfactory capabilities of predators: Schupp 1988). Trends are consistent with rodents preferring the medium and larger seeds and insects preferring small seeds (Notman and Gorchov 2001), and seeds being preferred by vertebrates or invertebrates but not both (Notman and Grochov 2001). For example, 86% of *Cecropia monostachya* predation in an old field located in an Ecuadorian upland forest was from insects rather than mammals (Myster 2004). Finally in the flooded forest and gaps, larger mammals such as tapirs could be significant seed dispersers on seeds larger than those used in this study (Fragoso and Huffman 2000).

Significant species differences were also found for pathogenic attack with the largest seeds (*Turpinia*) losing the most seeds, with a 10% loss on average for all three species. This compares well to a 15% loss of *Cecropia monostachya* seeds in Ecuadorian old fields (Myster 2004). Fungicide reduced mortality to 33% for *Cecropia insignis* in another terra firme study (Dalling et al. 1998), but some of those seeds may have been able to germinate. Not surprisingly, more seeds were lost to fungus in the moist forest understory than in the relatively dry gaps. Average germination rates were 3% lower than in other studies (9% in Ellison et al. 1993), which did not include seeds that survived predation and pathogens. For example, germination rates for *Cecropia schreberiana* were 21.2% in the high light conditions of a natural gap in wet upland rainforests (Everham et al. 1996) and may be up to 90% under favorable conditions (Silander and Lugo 1990). *Cecropia latiloba* seeds are still viable after passing through Amazon fish (Kubitzki and Ziburski 1994). Perhaps because of the need for large amounts of water for germination, seeds germination rates were higher in the várzea forest compared

to terra firme forest. Finally, seed germination results may mirror growth differences in planted seedling with different shade requirements (Raich and Khoon 1990).

An experiment done in the Puerto Rican rainforest showed *Cecropia schreberiana* survival was 12.5% under high light and 0% under low light (Everham et al. 1996), very close to the results here in gaps and the understory. However, *Cecropia* survivorship was higher at 34% after agriculture in upland Ecuadorean rainforest (Myster 2004). In addition the growth rate for *Cecropia* was very similar to growth examined elsewhere (Brokaw 1998). There was a trend for the larger-seeded species to survive more (but see Jones et al. 1988) but, as before, species differences in survival were very large (Swaine 1996).

Results support previous studies that showed small-seeded species have very low RGR in the understory, but high RGR in gaps whereas larger-seeded species have low RGR in the understory but only slightly greater RGR in gaps (e.g., Swaine 1996). Results suggest an inverse relationship between RGR and survival, as larger seeds generate larger seedlings and greater survival in the understory (Swaine 1996). In addition, seed size may affect initial seedling height and the ability to avoid flooding (Lopez 2001). LAR corresponds well with RGR and *Cecropia* had higher LAR than *Clidemia* in gaps. Results also confirm that species differences in LAR are small in the understory, but much larger in gaps. We must keep in mind, however, that both seed and seedling results were based on a small number of species. Consequently confirmation of the results depends on expanded experiments in the future.

Hypotheses I and II

Results show most of the mechanisms and tolerances investigated supported Hypothesis I and Hypothesis II (e.g., seed dispersal, seed predation, seed disease, seedling survivorship, seedling allocation) while some others did not (e.g., seed bank, seed germination, seedling growth). Also dispersed seeds, seedlings germinating from soil samples, and planted seedlings all had greater diversity in gaps compared to floodplain forest. All of these mechanisms and tolerances greatly affect the resulting forest structure (Terborgh 2012) through the tree-tree replacement process (Myster 2012b) and sampled Amazon trees showed in another study that while canopy structure was determined by gap dynamics, canopy diversity depended on forest type with the flooded forests having the highest diversity (Myster 2007a, 2010).

Implications for the Amazon

Whereas forest-type differences imply effects of different water availability, and degree of openness differences imply effects of light availability, forest-type × opened-type interactive effects may be showing how these two key resources relate to regeneration in these forests and to the biology of the tree species involved. Indeed the life-histories of these trees, if we knew them, may include a tradeoff between flood tolerance and shade tolerance (Junk 1989) because flood tolerance

is inversely related to seed size (Lopez and Kursar 1999) and shade tolerance is directly related to seed size (Denslow 1980, Brokaw 1982). The tolerance of seedlings to flooding is critical in determining adult distribution and abundance (Grubb 1977, Parolin et. al. 2004) and results do show that floodplain forests had the highest germination rates but the lowest survival, compared to more dry sites (Balslev et. al. 1987).

In general, results show variation in regeneration mechanisms between forests as well as in their gaps (Chazdon and Pearcy 1991, Lieberman and Lieberman 1989). In other Amazonian gaps where there was a low seed rain and a poor seed bank, most recruitment came from tree stump strouting (Thompson et. al. 1998). Also the increased levels of light and nutrients after tree-fall should be key factors producing intense competition within gaps (Denslow 1980) with the smallest stems hit the hardest, and herbivory taking many stems (Swaine 1996). Flooding may offer, however, some release from competition and facilitation may be more likely in flooded forests compared to terra firme (Balslev et. al. 1987).

Conclusions

If these results turn out to be generally true in the Amazon, then the high biodiversity of these areas may be maintained in part by the existence, and interaction, of flooded forest and gaps (but see Wittmann et. al. 2010). In that case, the variation in mechanisms and tolerances found in this study can help in the conservation and management of these forests and – by extension – the Western Amazon. This includes the sustainability of the future forest products, and the wider ecosystem goods and services that both local and global people depend on.

If flooding acts like a disturbance in these forests by removing biomass (Myster 2003) – especially of seeds and seedlings – then flooding might be expected to magnify the effects of gap formation, where terra firme has the greatest losses of seeds and seedlings, the smallest losses and fastest growth rate will be in the flooded gaps, and the terra firme gaps and the intact flooded forest will have intermediate loss and growth levels (Parolin et. al. 2004, Peres 1997). This would be due in part because plant biomass is removed both by flooding and by gap formation, and because intact terra firme forest has the most diverse and largest animal/fungi populations and the least light available (Everham et. al. 1996, Schupp 1988).

References

Alvarez-Bulla, E. and Martinez-Ramos, M. 1990. Seed bank versus seed rain in the regeneration of a tropical pioneer tree. *Oecologia* 84:314-325.

Augspurger, C.K. and Franson, S.E. 1988. Input of wind-dispersed seeds into light gaps and forest sites in a Neotropical forest. *J. Trop. Ecol.* 4:239-252.

Balslev, H., Luteyn, J., Ollgaard, B. and Holm-Nielsen, H.B. 1987. Composition and structure of adjacent unflooded and floodplain forest in Amazonian Ecuador. *Opera Bot.* 92:37-57.

Brokaw, N.V.L. 1982. The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica* 11:158-160.

Brokaw, N.V.L. 1998. *Cecropia schreberiana* in the Luquillo Mountains of Puerto Rico. *Bot. Rev.* 64: 91-120.

Chazdon, R.L. and Pearcy, R.W. 1991. The importance of sunflecks for forest understory plants. *Bioscience* 41:760-766.

Clark, J.S., Silman, M., Kern, R., Macklin, E. and Hillerislambers, J. 1999. Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology* 80:1475-1494.

Coomes, D.A. and Grubb, P.J. 1998. Responses of juvenile trees to above- and below-ground competition in nutrient-starved Amazonian rain forest. *Ecology* 79:768-782.

Dalling, J.W., Swaine, M.D. and Garwood, N.C. 1998. Dispersal patterns and seed bank dynamics of pioneer trees in moist tropical forest. *Ecology* 79:564-578.

Daly, D.G. and Prance, G.T. 1989. Brazilian Amazon. In: Campbell, D.G. and Hammond, H.D. (eds), *Floristic Inventory of Tropical Countries*. New York Botanical Garden, Bronx, NY. pp 401-426.

Denslow, J.S. 1980. Patterns of plant species diversity during succession under different disturbance regimes. *Oecologia* 46:18-21.

Denslow, J.S. 1987. Tropical rainforest gaps and tree species diversity. *Ann. Rev. Ecol. Syst.* 18:431-451.

Denslow, J.S. and Diaz, A.E.G. 1990. Seed rain to tree-fall gaps in a Neotropical rain forest. *Can. J. For. Res.* 20:642-648.

Duivenvoorden, J.F., Balslev, H., Cavelier, J., Grandez, C., Tuomisto, H. and Valencia, R. 2001. Evaluacion do recursos vegetales no maderables en la Amazonia noroccidental. The Netherlands Centre for Geo-ecological Research (ICG), The Netherlands.

Ellison, A.M., Denslow, J.S., Loiselle, B.A. and Brenes, D. 1993. Seed and seedling ecology of neotropical Melastomataceae. *Ecology* 74: 1733-1749.

Emmons, L.H. 1990. *Neotropical Rainforest Mammals: A Field Guide.* The University of Chicago Press, Chicago, IL, USA

Everham, E.M. III, Myster, R.W. and VanderGenachte, E. 1996. Effects of light, moisture, temperature and litter on the regeneration of five tree species in the tropical montane wet forest of Puerto Rico. *Am. J. Bot.* 83:1063-1068.

Fragoso, J.M.V. and Huffman, J.M. 2000. Seed-dispersal and seedling recruitment patterns by the last Neotropical megafaunal element in Amazonia, the tapir. *J. Trop. Ecol.* 16:369-385.

Gallery, R.E., Moore, D.J.P. and Dalling, J.W. 2010. Interspecific variation in susceptibility to fungal pathogens in seeds of 10 tree species in the neotropical genus *Cecropia*. *J. Ecol.* 98:147-155.

Gentry, A. 1993. *A Field Guide to Woody Plants of Northwest South America (Colombia, Ecuador, Peru)*. Conservation International, Washington, DC.

Grubb, P.J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* 52:107-145.

Holdridge, L.R. 1967. *Life Zone Ecology.* Tropical Science Center, San Jose, Costa Rica.

Jones, R.H., Sharitz, R.R., Dixon, P.M., Segal, D.S. and Schneider, R.L. 1988. Woody plant regeneration in four floodplain forests. *Ecol. Monog.* 64**:** 345-367.

Junk, W.J. 1989. Flood tolerance and tree distribution in central Amazonian floodplains. In: Holm-Nielsen, L.B., Nielsen, I.C. and Balslev, H. (eds), *Tropical Forests: Botanical Dynamics, Speciation and Diversity*. Academic Press, NY. pp. 47-64

Kalliola, R., Jukka, S., Puhakka, M. and Rajasilta, M. 1991. New site formation and colonizing vegetation in primary succession on the western Amazon floodplains. *J. Ecol.* 79:877-901.

Keller, M., Alencar, A., Asner, G.P., Braswell, B., Bustamante, M., Davidson, E., Feldpausch, T., Fernandes, E., Goulden, M., Kabat, P., Kruijt, B., Luizao, F., Miller, S., Markewitz, D., Nobre,. A.D., Nobre, C.A., Filho, N.P., Da Rocha, H., Dias, P.S., Von Randow, C. and Vourlitiis, G.L 2004. Ecological research in the large-scale biosphere atmosphere experiment in Amazonia: early results. *Ecol. Appl.* 14:S3-S16.

Kitajima, K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* 98:419-428.

Kubitzki, K. and Ziburski, A. 1994. Seed dispersal in flood plain forests of Amazonia. *Biotropica* 26:30-43.

Lamotte, S. 1990. Fluvial dynamics and succession in the Lower Ucayali River basin, Peruvian Amazonia. *For. Ecol. Manag.* 33/34:141-156.

Lieberman, M. and Lieberman, D. 1989. Forests are not just Swiss cheese: canopy stereogeometry of non-gaps in tropical forests. *Ecology* 70:550-552.

Loiselle, B.A., Ribbens, E. and Vargas, O 1996. Spatial and temporal variation of seed rain in a tropical lowland wet forest. *Biotropica* 28: 82-95.

Lopez, O.R. 2001. Seed flotation and post-flooding germination in tropical *terra firme* and seasonally flooded forest species. *Funct. Ecol.* 15:763-771.

Lopez, O.R. and Kursar, T. A 1999. Flood tolerance of four tropical tree species. *Tree Physiol.* 19: 925-932.

Myster, R.W. 1997. Seed predation, disease and germination on landslides in Neotropical lower montane wet forest. *J. Veg. Sci.* 8:55-64.

Myster, R.W. 2003. Using biomass to model disturbance. *Community Ecol.* 4:101-105.

Myster, R.W. 2004. Regeneration filters in post-agricultural fields of Puerto Rico and Ecuador. *Plant Ecol.* 172:199-209.

Myster, R.W. 2007a. Interactive effects of flooding and forest gap formation on tree composition and abundance in the Peruvian Amazon. *Folia Geobot.* 42:1-9.

Myster, R.W. 2007b. *Post-agricultural Succession in the Neotropics.* Springer-Verlag, NY.

Myster, R.W. 2009. Plant communities of Western Amazonia. *Bot. Rev.* 75:271-291.

Myster, R.W. 2010. Flooding duration and treefall interactive effects on plant community richness, structure and alpha diversity in the Peruvian Amazon. *Ecotropica* 16:43-49.

Myster, R.W. 2012a. Spatial heterogeneity of light and soil water along a *terra firme* transect in Amazonian Ecuador: effects on tree seedling survivorship, growth, and allocation. *Can. J. For. Res.* 42:1-4.

Myster, R.W. 2012b. Plants replacing plants: the future of community modeling and research. *Bot. Rev.* 78:2-9.

Myster, R.W. 2013a. The role of seed predation in the maintenance of the Cross Timbers ecotone of Oklahoma, USA. *J. Plant Interaction* 8:134-139.

Myster, R.W. 2013b. The effects of flooding on forest floristics and physical structure in the Amazon: results from two permanent plots. *Forest Res.* 2:112.doi:10.4172/2168- -9776.1000112.

Myster, R.W. and Sarmiento, F.O. 1998. Seed inputs to microsite patch recovery on two Tropandean landslides in Ecuador. *Restor. Ecol.* 6:35-43.

Myster, R.W. and Santacruz, P. G. 2005. Una comparación de campo de insectos de suelo-morar de Amazonas: Tierra firme y bosques de tierras inundadas vs. espacios abiertos en el Parque Nacional Yasuní, Ecuador. *Pontificate Rev. Univ. Cat. Ecu.* 76:111-124.

Notman, E. and Gorchov, D. L 2001. Variation in post-dispersal seed predation in mature Peruvian lowland tropical forest and fallow agricultural sites. *Biotropica* 33:621-636.

Parolin, P. 2002. Submergence tolerance vs. escape from submergence: two strategies of seedling establishment in Amazonian floodplains. *Environ. Exp. Bot.* 48:177-186.

Parolin, P., De Simone, O., Hasse, K., Waldhoff, D., Rottenberger, S., Kuhn, U., Kesselmeier, J., Kleiss, B., Schmidt, W., Piedade, M.T.F. and Junk, W.F. 2004. Central Amazonian floodplain forests: Tree adaptations in a pulsing system. *Bot. Rev.* 70:357-380.

Pitman, N.C.A., Terborgh, J., Silman, M.R. and Percy, N.V. 1999. Tree species distributions in an upper Amazonian forest. *Ecology* 80:2651-2661.

Pitman, N.C., Terborgh, J.W., Silman, M.R., Nunez, P.V., Neill, D.A., Ceron, C.E., Palacios, W.A. and Aulestia, M. 2001. Dominance and distribution of tree species in upper Amazonian *terra firme* forests. *Ecology* 82:2101-2117.

Poorter, H., Remkes, C. and Lambers, H. 1990. Carbon and nitrogen economy of 24 wild species differing in relative growth rate. *Plant Physiol.* 94:621-627.

Peres, C.A. 1997. Primate community structure at twenty western Amazonian flooded and unflooded forests. *J. Trop. Ecol.* 12:381-405.

Raich, J.W. and Khoon, G.W. 1990. Effects of canopy openings on tree seed germination in a Malaysian dipterocarp forest. *J. Trop. For.* 6:205-217.

Rice, W.R. 1989. The sequential Bonferroni test. *Evolution* 43:223-225.

Romo, M., Tuomisto, H. and Loiselle, B.A. 2004. On the density-dependence of seed predation in *Dipteryx micrantha*, a bat-dispersed rain forest tree. *Oecologia* 140:76-85.

Romoleroux, K., Foster, R., Valencia, R., Condit, R., Balslev, H. and Losos, E. 1997. Especies lenosas (dap => 1 cm) encontradas en dos hectareas de un bosque de la Amazonia ecuatoriana. In: Valencia, R. and Balslev, H. (eds), *Estudios Sobre Diversidad y Ecologia de Plantas.* Pontificia Universidad Catolica del Ecuador, Quito, Ecuador. pp. 189-215.

Salo, J.S. and Kalliola, R.J. 1990. River dynamics and natural forest regeneration in the Peruvian Amazon. In: Gentry, A.H. (ed.), *Four Tropical Rainforests.* Yale University Press, New Haven, CO. pp 245-256.

SAS. 1985 User's Guide: Statistics, Version 5. SAS Institute Inc. Cary, NC.

Schupp, E.W. 1988. Factors affecting post-dispersal seed survival in a tropical forest. *Oecologia* 76:525-530.

Schupp, E.W. 1990. Annual variation in seedfall postdispersal predation, and recruitment of a Neotropical tree. *Ecology* 71:504-515.

Schupp, E.W. and Frost, E.J. 1989. Differential predation of *Welfia georgii* seeds in treefall gaps and the forest understory. *Biotropica* 21:200-203.

Silander, S.R. and Lugo, A.E. 1990. *Cecropia peltata* L.: Yagrumo hembra, trumpet tree. In: *Silvics of North America.* Vol. 2: Hardwoods, Agricultural Handbook 654, US Department of Agriculture, Washington, DC. pp. 244-249.

Svenning, J.C. 2000. Small canopy gaps influence plant distributions in the rain forest understory. *Biotropica* 32:252-261.

Swaine, M.D. 1996. *The Ecology of Tropical Forest Tree Seedlings.* Man and the Biosphere: Volume 17. The Parthenon Publishing Group, NY.

Swamy, V., Terborgh, J., Dexter, K.G., Best, B.D., Alvarez, P. and Cornejo, F. 2011. Are all seeds equal? Spatially explicit comparisons of seed fall and sapling recruitment in a tropical forest. *Ecol. Lett.* 14:195-201.

Terborgh,, J. 2012. Enemies Maintain Hyperdiverse Tropical Forests. *Am. Nat.* 179:303-314.

Thompson, J., Protor, J., Scott, D.A., Fraser, P.J., Marrs, R.H., Miller, R.P. and Viana, V. 1998. Rain forest on Maraca Island, Roraima Brazil: artifical gaps and plant response to them. *For. Ecol. Manag.* 102:305-321.

Tuomisto, H., Poulson, A.D., Ruokolainen, K., Moran, R.C., Quintana, C. and Celi, J. 2003. Linking floristic patterns with soil heterogeneity and satellite imagery in Ecuadorian Amazonia. *Ecol. Appl.* 13:352-371.

Valencia, R., Foster, R.B., Villa, G., Condit, R., Svenning, J., Hernandez, C., Romoleroux, K., Losos, E., Magard, E. and Balslev, H. 2004. Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. *J. Ecol.* 92:214-229.

Vazquez-Yanes, C. and Orozco-Seqovia, A. 1993. Patterns of seed longevity and germination in the tropical rainforest. *Ann. Rev. Ecol. Syst.* 24:69-87.

Vasquez-Martinez, R. 1997. *Florula de las Reservas Biologicas de Iquitos, Peru.* Monographs in Systematic Botany Volume 63. Missouri Botanical Garden Press. St. Louis, MO.

Walter, H. 1979. *Vegetation of the Earth and the Ecological Systems of the Geo-biosphere.* 2nd ed. Springer-Verlag. NY.

Wenny, D.G. 2000. Seed dispersal, seed predation, and seedling recruitment of a Neotropical montane tree. *Ecol. Monog.* 70:331-351.

Whittaker, R.H. 1975. *Communities and Ecosystems.* MacMillian, NY.

Wittmann, F., Junk, W.J. and Schöngart, J. 2010. Phytogeography, species diversity, community structure and dynamics of central Amazonian floodplain forest. In: Junk, W.J., Piedade, M.T.F., Parolin, P., Wittman, F. and Schöngart, J. (eds), *Central Amazonian Floodplain Forests: Ecophysiology, Biodivesity and Sustainable Management.* Ecological Studies, Springer Verlag, Heidelberg. pp. 61-102.

Wurm, P.A.S. 1998. A surplus of seeds: high rates of post-dispersal seed predation in a flooded grassland in monsoonal Australia. *Aust. J. Ecol.* 23:385-392.

Young, K.R., Ewel, J.J. and Brown, B.J. 1987. Seed dynamics during forest succession in Costa Rica. *Vegetatio* 71:157-173.

Zhang, Q. and Zak, J.C. 1995. Effects of gap size on litter decomposition and microbial activity in a subtropical forest. *Ecology* 76:2196-2204.