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Comparing and contrasting flooded and unflooded forests in the Peruvian Amazon: seed rain

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Abstract

Background: In order to understand how the seed rain differs among Amazonian forests, I sampled the seed rain in six different forest types across the Amazonian landscape.

Methods: I set up seed traps and took seed samples in three unflooded forests (*terra firme*, white sand-varillal, palm) and three white-water flooded forests (high restinga, low restinga, tahaumpa) in Peru over a period of one year.

Results: I found (1) all forest types had dispersed seed of many unique species, with a few species in common, (2) total seed load peaked in the early part of the year – near the end of the rainy season – and then decreased monotonically over the remainder of the year for all forest types, (3) species richness was greater in unflooded forests compared to flooded forests and the largest number of species were found in *terra firme*, (4) seeds were more evenly distributed among species in the unflooded forests compared to the flooded forests, and (5) Fisher's α diversity of seeds was greater in high and low restinga compared to tahaumpa.

Conclusions: I conclude for the unflooded forests that seed species number and richness increased with soil fertility but for the flooded forests seed species number and richness decreased with months under water. Furthermore, when taken together, results suggest that for forests across the Amazonian landscape differences in flooding regime may have a greater effect on both seed rain load and seed species richness than differences in availability of soil nutrients.

Keywords: High restinga; Low restinga; Palm; Tahuampa; *Terra firme*; White sand

Background

The Amazonian rainforest covers over 6 million square kilometres (Walter 1973; Myster 2009) and is the most productive (Daly and Prance 1989) and diverse terrestrial ecosystem on earth, containing more than 10% of its species (Pires and Prance 1985). This rainforest influences the entire world's weather patterns and climate (Keller et al. 2004), interacting intimately with its carbon cycle both as a "sink" by taking in large amounts of CO_2 through photosynthesis, but also as a "source" when, for example, its plants decay or burn. Within the Amazonian rainforest landscape are unflooded forests with structure similar to unflooded rainforests throughout the rest of the Neotropics (Kalliola et al. 1991; Everham et. al. 1966; Pitman et al. 2001; Myster and Santacruz 2005; Myster 2009) but with some differences which may be largely due to soil characteristics (e.g., *terra firme* on clay or loam

soils, white sand on soils with large amounts of quartz, palm on permanently waterlogged soils: Tuomisto et. al. 2003; Honorio 2006).

Also defining the Amazonian rainforest are extensive flooded forests (Junk 1997; Parolin et. al. 2004) mainly derived from the nutrient rich "white" water from the Andes (generally called várzea) with the rest flooded by nutrient-poor forest runoff (generally called igapó: Junk 1984). Along with the variation in soils, flooding differences in factors such as water quality, frequency, duration, depth, and spatial variation (the flooding regime: Myster 2001) help create complex and diverse forest associations throughout the Amazon basin (Myster 2009).

Among the many factors controlling the regeneration of tropical forests, the seed rain has long been seen as key to understanding recruitment (Mesquita et. al. 2001; Muller-Landau et. al. 2008) because recruitment from the seed bank is low (Loiselle et. al. 1996) and root and stump sprouting is rare, even in forest clearings (Gorchov et. al. 1993). In addition, the seed rain plays a

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Table 1 Number and species of seeds taken from seed traps located in unflooded forests (*terra firme*, white sand varillal, palm) and flooded forests (high restinga, low restinga, tahuampa) of Peru

Species	Terra firme	White sand varillal	Palm	High restinga	Low restinga	Tahuampa
Attalea butyracea	–	–	–	20	–	–
Campsiandra augustifolia	–	–	–	–	–	10
Caraipa punctulata	–	20	–	–	–	–
Casha moeria	33	–	–	–	–	–
Dicymbe puncticulosa	–	14	–	–	–	–
Drypetes amazonia	–	–	–	21	–	–
Eschweilera coriacea	30	–	–	–	–	–
Eschweilera bracteosa	36	–	–	–	–	–
Euterpe precatoria	–	–	20	–	–	–
Guarea macrophylla	–	–	–	–	6	–
Haploclathra paniculata	–	12	–	–	–	–
Hevea nitida	–	34	19	–	–	–
Iryanthera juruensis W.	–	–	–	5	–	8
Leonia glycycarpa	–	–	–	19	–	–
Macrolobium acifolium	–	–	–	51	67	–
Maquira coriacea	22	–	–	13	6	6
Mauritia flexuosa	–	–	25	–	–	–
Miconia tripliuaria	15	–	–	–	2	–
Minguartia guianensis	10	–	–	–	–	–
Miristhicaceae (family)	–	–	–	–	–	4
Ocotea sp.	20	–	–	–	–	–
Oenocarpus batana	4	–	–	–	–	–
Oxandra espintana	2	–	–	–	–	–
Pachira brevipes	–	15	–	–	–	–
Pourouma acurinata	–	–	–	–	12	–
Pouteria caimito	5	–	–	–	–	–
Qualea paraensis	–	–	–	25	–	–
Schefflera sp.	19	–	–	–	–	–
Virola paronis	22	19	12	–	10	–
Unknown	39	15	19	–	–	–

There were 10 traps sampled six times for each of the six forest type.

critical role in determining plant-plant replacements and, therefore community patterns such as diversity (Myster 2012b). Consequently, the seed rain is critical to explaining the structure, function, and dynamics of tropical forests.

This study was motivated by the importance of Amazon forests and the lack of seed rain studies known to be key to its dynamics. In addition I wanted to better understand the spatial heterogeneity (six different forest types common in the Amazonian landscape) and temporal heterogeneity (over a one year period) of the seed rain throughout the Amazon. Therefore I sampled seed rain in three unflooded forests and in three flooded forests of the Western Amazon in Peru. I address these questions: (1) What species of seed are dispersed in these common Amazon forest types, and are there species in common?, (2) How does the number of seeds vary over a one year time period within the three unflooded forests, within the three flooded forests, and between the unflooded forests and the flooded forests?, (3) Does the seed rain of common unflooded forests in the Amazon differ significantly in total number of seeds, species richness, species evenness, and Fisher's α diversity over a one year sampling?, (4) Does the seed rain of common flooded forests in the Amazon differ significantly in total number of seeds, species richness, species
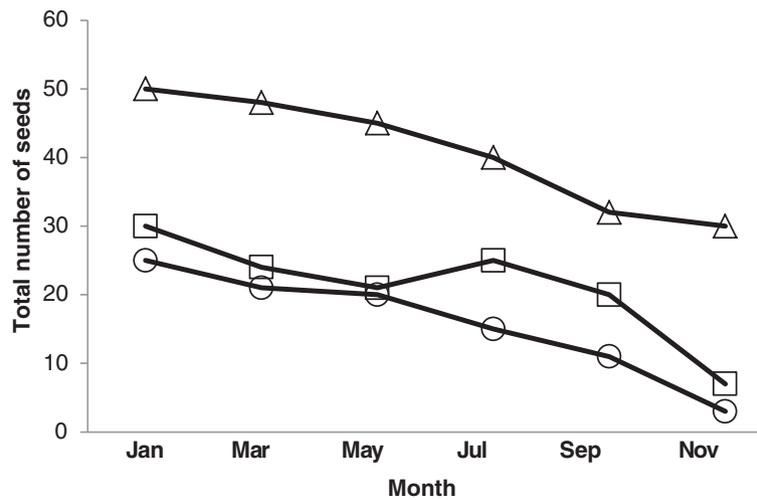
Figure 1 Mean number of seeds (over the 10 traps in each forest type) plotted over the one year collection period by month for the three unflooded forests: *terra firme* (triangle), white sand – varillal (rectangle), and palm (circle).

evenness, and Fisher's α diversity over a one year sampling?, and (5) Does the seed rain of the unflooded forests taken together, and the seed rain of the flooded forests taken together, differ significantly in total number of seeds, species richness, species evenness, and Fisher's α diversity over a one year sampling?

Methods

The study site was the Centro de Investigacion de Jenaro Herrera (CIJH) biological station operated by the Instituto de Investigaciónes de la Amazónia Peruana (www.iiap.org.pe/jenaro.htm) located 2.5 km from the town of Jenaro Herrera and 200 km south of Iquitos on the east margin of the Ucayali River in the Province of Requena, Department of Loreto, Peru (4° 54' S, 73° 40' W: Spichiger et. al. 1996;

Honorio 2006). CIJH comprises an area of 4,336 km² with forest types relatively close to each other (Honorio 2006). The mean annual temperature is 26.0°C with a range between 25.1°C and 26.5°C and the mean annual rainfall is 2724 mm with a rainy season between the months of November and April (Kalliola et al. 1991). Dominating the unflooded portions of the CIJH are broad leaf forest (*terra firme*), white sand-varillal forest and low terrace palm forest. Common genera in the *terra firme* forest include *Eshweilera*, *Pouteria*, *Oenocarpus*, *Miconia*, and *Protium*, common genera in white sand-varillal forest include *Pachira*, *Haploclathra*, and *Macrolobium* and common species in palm forest include *Mauritia flexuosa*, *Oenocarpus bataua*, *Euterpe precatoria* and *Socratea exorrhiza* (Honorio 2006).
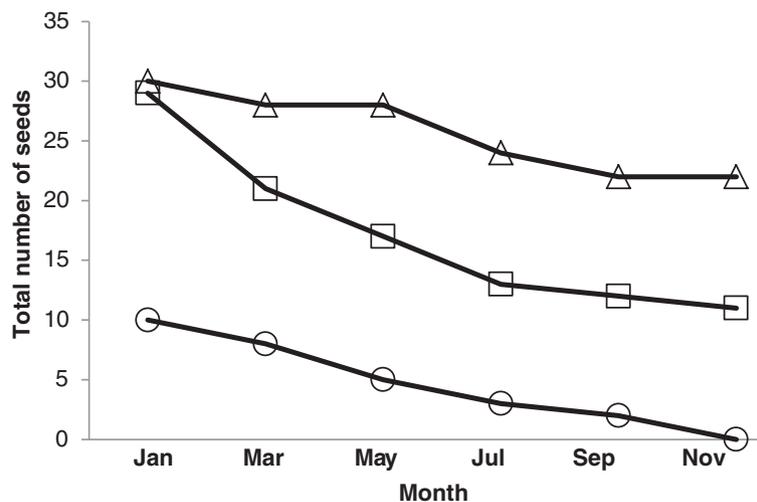
Figure 2 Mean number of seeds (over the 10 traps in each forest type) plotted over the one year collection period by month for the three flooded forests: high restinga (triangle), low restinga (rectangle), and tahnampa (circle).

Figure 3 Mean number of seeds (over the 30 traps in the three unflooded forests and the 30 traps in the flooded forests) plotted over the one year collection period by month for the unflooded forests (triangle) and the flooded forests (rectangle).
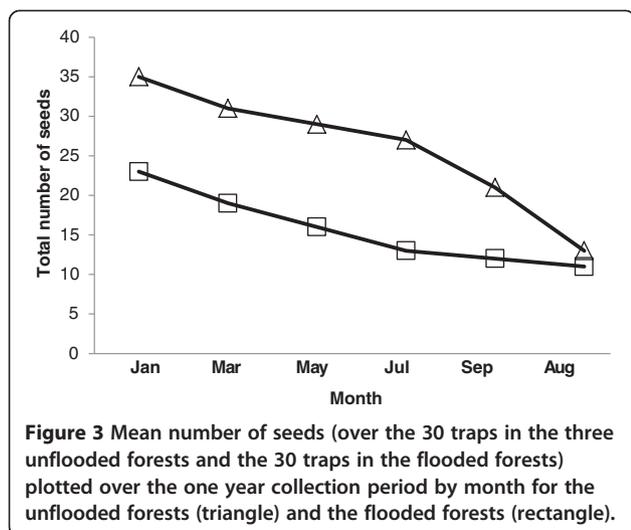
Clay soils dominate *terra firme* forest and white sand forest soils consist mainly of quartz with individual trees having slender boles and roots concentrated at the soil surface (Klinge et al. 1990). Palm swamps occur in depressions or low-lying patches with poor drainage (Montufar and Pintaud 2006).

There are also forests that border CIJH white-water rivers and flood during the rainy season. These include forests which are underwater on average 1–2 months per year (called here high restinga), forests which are underwater on average 3–5 months per year (called here low restinga), and forests which are underwater at least 6 months per year (called here tahuampa). Common tree genera in Peru high restinga forests are *Chorisia, Eschweilera, Hura, Spondias,* and *Virola*, and common tree species in Peru low restinga forests and tahuampa forests include *Calycophyllum spruceanum, Ceiba samauma, Inga* spp., *Cedrela odorata, Copaifera reticulata, Phytelephas macrocarpa* with understorey palms such as *Scheelea* spp., *Guazuma rosea*, and *Piptadenia pteroclada* (Myster 2007a; Myster 2010).

In May 2010, I established a 50 m transect in each of six unlogged unflooded forests (two *terra firme* forests, two white sand-varillal forests, two palm forests) and in each of six unlogged flooded forests (two high restinga forests, two low restinga forests, two tahaumpa forests). Every 10 m along each transect I placed a cloth seed trap of 1 m² collecting area and 0.5 m depth, for a total of 5

traps per forest. Setting traps on transects at regular intervals, rather than in subjectively chosen microsites, better capture the variation in forest floor conditions that determine recruitment after dispersal, such as light, litter, and water availability (Dalling et. al. 1998; Myster 2012a). The traps were constructed with 5 cm² wire mesh on top, cloth underneath for collecting the seeds, and suspended on 1 m plastic poles for keeping the traps off the ground to reduce predation. This design has proven effective in several past Neotropic seed rain studies (e.g., Myster 2004; Myster 2007b) and predation is very rare for seed traps of this size (Muller-Landau et. al. 2008). No seed traps were flooded during the sample period.

Seeds were collected in July 2010, September 2010, November 2010, January 2011, March 2011 and May 2011. All seeds of trees and shrubs were removed from each trap during a collection period and no evidence of seed decay was observed. The design allowed an investigation into both the natural temporal heterogeneity of the seed rain over time and the natural spatial heterogeneity of the seed rain along the forest floor. Seeds were identified to species, or to genus in rare cases, using Gentry (1993), Romoleroux et al. (1997) and the on-site CIJH herbarium.

For each forest type (10 traps x 6 sampling periods per forest type), total number of seeds, species richness (total number of seed species), and seed species evenness (using Pielou's J index: Ludwig and Reynolds 1988) were calculated. Because richness trends could have been undermined by dissimilar densities (i.e., some plots could have had more species solely due to the larger number of seeds sampled there), Fisher's α diversity (Fisher et al. 1943) - an index independent of sample size and suggested for species-rich forests including those in the Amazon (Valencia et al. 1994; Valencia et al. 2004) - was also computed, using the iterative procedure described in Rosenzweig (1995).

These data were then used for one-way analysis of variance (ANOVA: SAS 1985) tests for each of the four seed community parameters (1) among the three unflooded forest types using all seed traps (10 microsites x 6 sampling periods = 60 replicates for each of the three forest types), (2) among the three flooded forest types using all seed traps (10 microsites x 6 sampling periods = 60 replicates for each of the three forest types) and (3) between all unflooded forests vs. all flooded forests (180

Table 2 F statistic summary table for the one-way ANOVAs using the response variables of total number of seeds, species richness (total number of seed species), seed species evenness (using Pielou's J index: Ludwig & Reynolds 1988) and Fishers α diversity

	Total number of seeds	Species richness	Species evenness	Fishers α diversity
Among unflooded forests	40.29***	5.63*	1.34	1.76
Among flooded forests	26.73***	0.11	1.98	7.58**
Unflooded forests vs. flooded forests	8.55**	6.01*	4.43*	2.19

The p-value is indicated as *if 0.05 < p < 0.01, as **if 0.01 < p < 0.001, and as ***if p < 0.001.
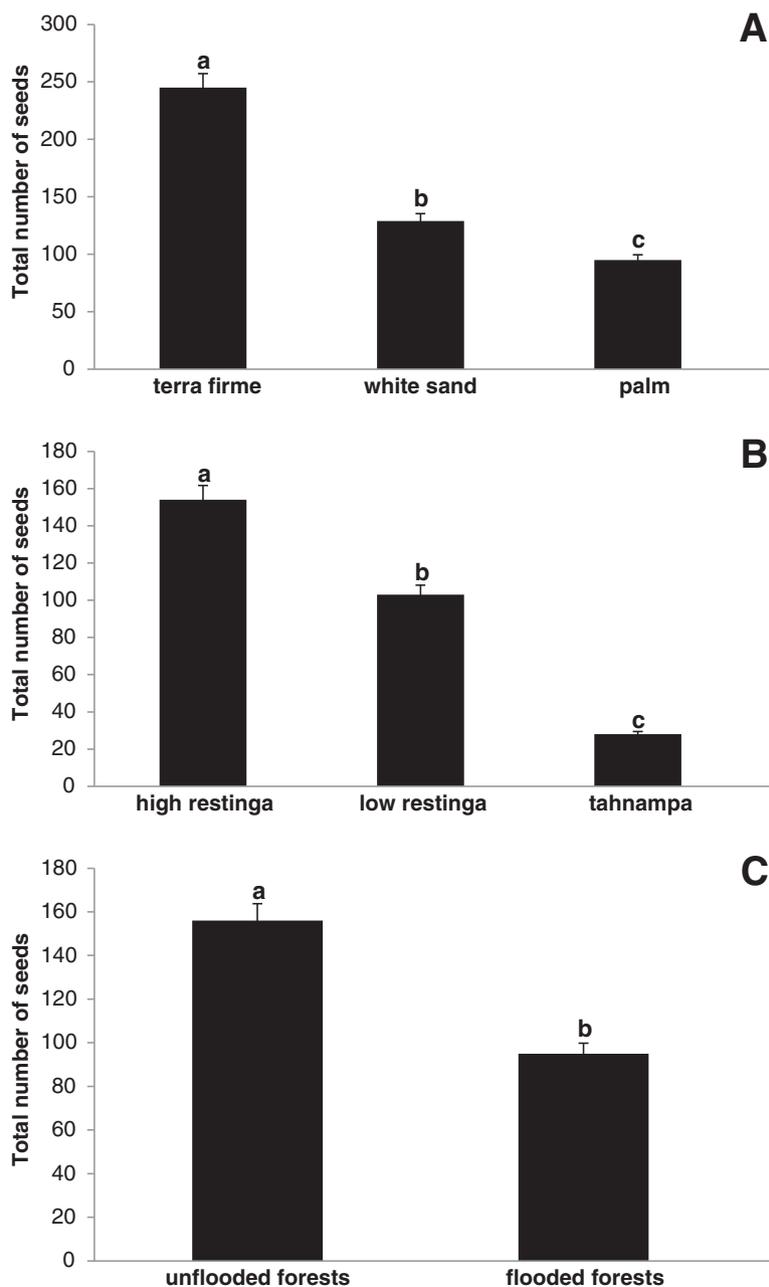
Figure 4 Mean and standard error bar graphs for the significant results from Table 2 involving total number of seeds (A) among unflooded forests, (B) among flooded forests, and (C) unflooded vs. flooded forests. Means testing results are indicated by lowercase letters which are different, if groups were significantly different, as given in Table 2.

replicates for flooded forests and 180 replicates for unflooded forests). Because seed traps were emptied completely after each collection period, and therefore could not influence the next sample collected in the same trap, repeated measure ANOVA was not necessary. If significance was found, means tests were conducted with the Tukey procedure (SAS 1985). All data were examined and found to be normally distributed.

Results

All forest types had dispersed seed of tree species that were not found in any of the other forest types: *terra firme* (*Casha moeria, Eschweilera coriacea, Eschweilera bracteosa, Minguartia guianensis, Ocotea* sp.*, Oenocarpus batana, Oxandra espintana, Pouteria caimito*), white sand (*Caraipa punctulata, Dicymbe puncticulosa, Haploclathra paniculata, Schefflora* sp.*, Pachira brevipes*),
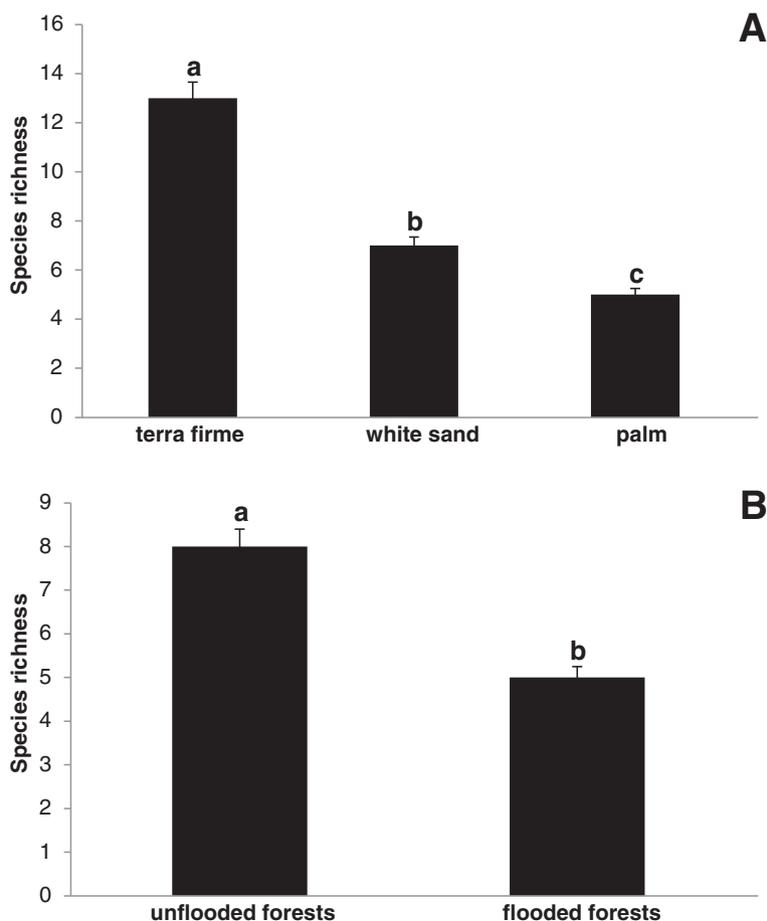
Figure 5 Mean and standard error bar graphs for the significant results from Table 2 involving species richness (A) among unflooded forests and (B) unflooded vs. flooded forests. Means testing results are indicated by lowercase letters which are different, if groups were significantly different, as given in Table 2.

palm (*Euterpe precatoria, Mauritia flexuosa*), high restinga (*Attalea butyracea, Drypetes amazonia, Leonia glycycarpa, Qualea paraensis*), low restinga (*Guarea macrophylla, Pourouma acurinata*) and tahuampa (*Campsiandra augustifolia* and seeds of the family Miristhicaceae*: Table 1). There were few seed species shared among forest types. No species was found in all six forest types. The most common species were *Maquira coriacea* and *Virola paronis*, which were found in four of the six.

Total seed load peaks in the early part of the year and decreases monotonically over time for all forest types (Figures 1, 2 and 3). Within that general pattern, *terra firme* forest had significantly more seeds than the other unflooded forests (Table 2, Figure 4A), high restinga and low restinga had significantly more seeds than tahuampa (Table 2, Figure 4B) and unflooded forests had significantly more seeds than flooded forests (Table 2, Figure 4C).

Species richness was also significantly different among unflooded forests, and also between unflooded vs.

flooded forests (Table 2). *Terra firme* forest had significantly more seed species as the other unflooded forests (Figure 5A) and unflooded forests had significantly more seed species than flooded forests (Figure 5B). The distribution of seed abundances among the species (species evenness) was significantly more in the unflooded vs. the flooded forest (Figure 6A). Finally, Fishers α diversity was significantly greater in high and low restinga compared to tahuampa (Figure 6B).

Discussion

The seed rain sampling was similar to other Neotropical seed rain studies (e.g. Dalling et. al. 2002; Muller-Landau et. al. 2008) in showing only a modest correspondence between the seed rain sampled in a forest and the trees sampled close by in 1 ha permanent plots (Myster 2013, Myster in press). This suggests that rare species, seed rain in other years, and/or other regeneration mechanisms and tolerances (Myster 2012b, Myster 2014) may play major roles in forest regeneration (Muller-Landau
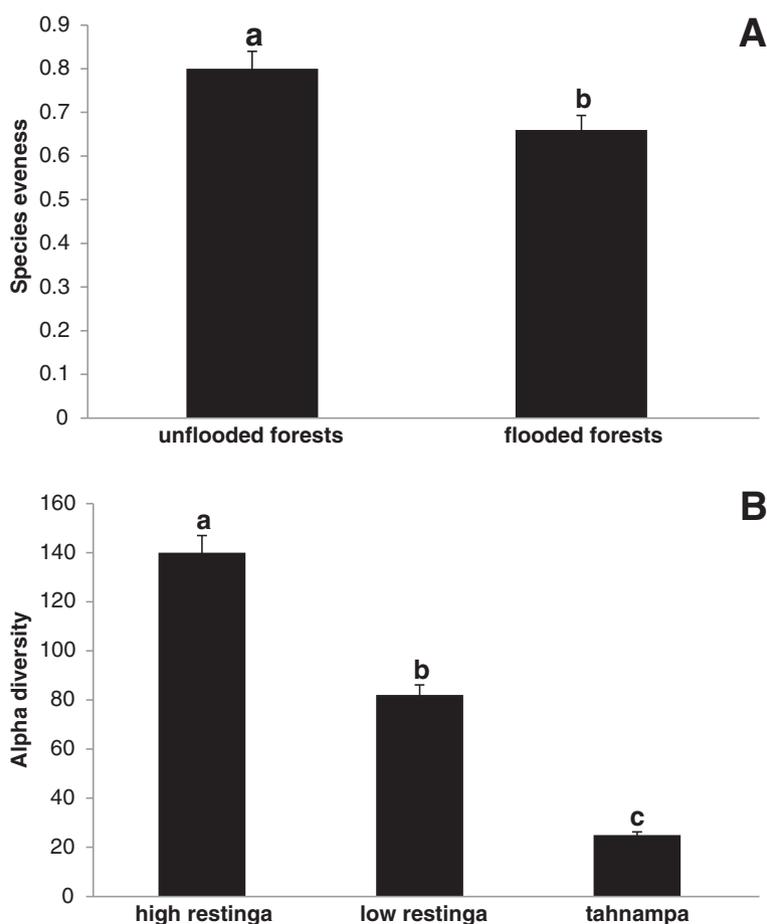
Figure 6 Mean and standard error bar graphs for the significant results from Table 2 involving species evenness (A) unflooded vs. flooded forests, and involving Fishers α diversity (B) among flooded forests. Means testing results are indicated by lowercase letters which are different, if groups were significantly different, as given in Table 2.

et. al. 2008). This result, along with studies of forest seed predation and seedling competition (e.g., conducted on site at CIJH: Notman et. al. 1996, author unpub. data), shows the complexities of forest recruitment and the major challenge for modelers who wish to predict the plant-plant replacements (Myster 2012b) which result in forest community patterns. As an example of this complexity, this is the first major sampling of the seed rain in flooded forests where secondary dispersal by fish is common (Parolin et. al. 2004).

Results agree with these other studies: (1) *terra firme* has much larger numbers of seed compared to the more open and less diverse white sand and palm forests (Honorio 2006), (2) less flooded forests have larger numbers of seeds compared to the more flooded – and open but less diverse – forests (Myster 2007a; Myster 2010) and (3) seed rain peaked after the start of the rainy season (Parolin et. al. 2004). Results also show, however, how different these forests are in seed species composition when compared to other Neotropical forests. For example,

there were no species or genera in common with one sampling of a large plot in Panama (Dalling et. al. 2002) or Costa Rica (Loiselle et. al. 1996) and only a few similar genera with another Panama sampling (Muller-Landau et. al. 2008). Seed rain density was only slightly less in this *terra firme* forest compared to the same forest type in Panama.

There were much less seeds in areas recovering from agriculture both in Ecuador and Puerto Rico (Myster 2004; Myster 2007b), especially wind-dispersed tree species. After logging on site (CIJH: Gorchov et. al. 1993) there were also large declines in seed load from forest to center of logging strips with many tree succession genera also seen after agriculture (e.g., *Cecropia, Miconia, Piper* : Myster 2004). Lower montane *terra firme* forest in Puerto Rico and Ecuador has similar number of seeds, but less species with *Miconia* sp. and *Guarea* sp. found in common. Fisher's α diversity and species richness trends were very similar to past sampling in these kinds of forests (Myster 2010).

Whereas species diversity is lower in flooded forests compared to unflooded, adaptations in flooded trees may be remnants of preadaptions from the unflooded *terra firme* species where floodplain trees originated (Parolin et. al. 2004). Results show that increased flooding and decreased soil fertility both lead to reductions in seed rain which reflect loss of forest diversity and complexity (Myster 2007a; Myster 2010), and results further suggest that seed rain may be more reduced by loss of soil fertility than by increased flooding. Because differences among unflooded forests are due mainly to soil fertility (Tuomisto et. al. 2003; author unpub. data), results may help illustrate these two major structuring forces in Amazonian forests: flooding and soil fertility.

Conclusions

I conclude for the unflooded forests that seed species number and richness increased with soil fertility but for the flooded forests seed species number and richness decreased with months under water. I also conclude that seed rain peaks right after the start of the rainy season. Finally, when taken together, results suggest that for forests across the Amazonian landscape differences in flooding regime may have a greater effect on both seed rain load and seed species richness than differences in availability of soil nutrients.

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