



Comparing and contrasting flooded and unflooded forests in Western Amazonia: seed predation, seed pathogens, germination

R. W. Myster

Biology Department, Oklahoma State University, Oklahoma City, OK, 73107 USA; E-mail myster@okstate.edu,
 Web-page: www.researchgate.net/profile/Randall_Myster

Keywords: Ecuador, Igapó, Palm, Peru, *Terra firme*, Várzea, White sand.

Abstract: Because of the importance of the Amazon to our shared human future and because we need to understand how its forests regenerate, I set out seeds for a week in igapó, palm, *terra firme*, várzea and white sand forests and then collected them, scoring seed losses to predators, seed losses to pathogens and seeds that germinated. I found (1) *terra firme* forest, white sand forest, várzea forest and igapó forest under water 1 month every year, were significantly different for seed mechanisms and tolerances, *terra firme* forest, palm forest, várzea forest and igapó forest under water 1 month per year, were significantly different among species, and the interaction term was significant for all forests except for the two most flooded igapó forests, (2) in *terra firme* forest seed predators took most seeds regardless of species, (3) in palm forest species were different regardless of seed mechanism and tolerance, (4) in white sand forest seed predators took most seeds regardless of species, (5) in várzea forest seed predators took most seeds but with some species differences and (6) in igapó forest under water 1 month per year, there were differences in predation, pathogens and germination, and in species variation. I conclude that seed predation losses strength as forests become more stressed either by loss of soil fertility or by flooding with nutrient-poor water. Conversely seed pathogens become more important with water-logged soils and with flooding. Seed loss variation among species within forests was always a secondary factor.

Nomenclature: Gentry (1996).

Introduction

The Amazonian rainforest covers over 6 million square kilometers (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 CO₂ through photosynthesis, but also as a “source” when, for example, its plants decay or burn. Across the Amazonian rainforest landscape are unflooded forests with structural similarities to unflooded rainforests throughout the rest of the Neotropics (Kalliola et al. 1991, Everham et al. 1996, Pitman et al. 2001, Myster and Santacruz 2005, Myster 2009, 2016a,b) but with important differences which may be largely due to soil characteristics (e.g., *terra firme* forests on clay or loam soils, white sand forests on soils with large amounts of quartz, palm forests on permanently waterlogged soils: Tuomisto et al. 2003, Honorio 2006). The Amazon also has extensive flooded forests (Junk 1997, Parolin et al. 2004) mainly derived from the nutrient rich “white” water from the Andes (generally called várzea forests) and from the nutrient poor “black” water from forest runoff (generally called igapó forests: Prance 1979). In addition to these flooded forests differing in water quality, they also differ in frequency, duration, depth, and spatial

variation of flooding, creating complex and diverse forests throughout the Amazon basin (Myster 2009).

The factors controlling the recruitment and regeneration of these forests is key to our understanding of them where the fate of the seed rain has long been seen as particularly important (Grubb 1977). Indeed post-dispersal (Myster 2017) seed mechanisms (seed predation, seed pathogens) and tolerances (germination) play a critical role in determining plant-plant replacements and their resulting plant community patterns (e.g., biodiversity: Myster 2012b). This study was motivated by the importance of understanding the dynamics of forests in Western Amazonia and, in particular, the heterogeneity of their seed processes. Therefore I investigated experimentally post-dispersal seed mechanisms and tolerances in three common unflooded forests (*terra firme*, palm, white sand-varillal), in one forest flooded by white-water (várzea), and in three forests flooded by black-water (igapó), all located in the Western Amazon. I then used those results to test these three hypotheses:

- Most seeds will be lost to seed predators (Myster 2014, 2015d).
- Seed losses to predators and pathogens will decrease as forests become more stressed by loss of soil fertility (*terra firme* → palm → white sand-varillal), or by flooding with nutrient-poor water (várzea → igapó: Paine and Beck 2007).

- If a seed can survive predators and pathogens, it will probably germinate (Myster 2014, 2015d).

Study sites

The first study site, Sabalillo Forest Reserve (SFR: 3° 20' 33"S, 72° 18' 6" W: Frederickson et al. 2005, Moreau 2008), was established in 2000 and is operated by Project Amazonas (www.projectamazonas.org). SFR is located on both sides of the upper Rio Apayacu, 172 km east of Iquitos, Peru. The reserve is part of 25,000 acres set aside over the last decade. It is comprised of low, seasonally inundated river basins of the upper Amazon. The substrate of these forests is composed of alluvial and fluvial Holocene sediments from the eastern slopes of the Andes. Annual precipitation has been measured as 3297 mm per year (Choo et al. 2007). Within the SFR, *terra firme* forest is common as well as palm forest and white-sand forest, with black-water igapó forest-types of differing frequency, duration, and maximum water column height. The rainy season is between November and April.

The second study site is the Yasuni Research Station (YRS: 0° 41' S, 76° 24' W), operated by the Pontificia Universidad Católica of Ecuador and located within the Yasuni National park of eastern Ecuador (Svenning 1999, Duivenvoorden et al. 2001, Myster and Santacruz 2005, Metz et al. 2008, Myster 2012a, 2013, 2014, 2015a). Most of the YRS is *terra firme* forest which has been classified as low-land tropical rainforest (Holdridge 1967). The mean annual rainfall is 3081 mm with the wettest months April to May and October to November. August is the driest month and the mean monthly temperature varies between 22°C and 35°C. Soils in the National park have been described as clayey, low in most cations but rich in aluminium and iron, whereas soils at the station in *terra firme* forest are acidic and rich in exchangeable bases with a texture dominated by silt (Tuomisto et al. 2003). The park has low topographic variation with a mean elevation of approximately 200 m above sea level. The station is the site of a long-term 50 ha vegetation plot in *terra firme* forest, maintained by the Smithsonian Tropical Research Institute (Losos and Leigh 2004), parts of which have been sampled (e.g., Valencia et al. 2004). Also found at YRS is várzea floodplain forest located next to the nutrient rich whitewater Tiputini River, which is inundated a few weeks between the months of October and April to a maximum depth of 3 m.

The third study site is the Area de Conservación Regional Comunal de Tamshiyacu-Tahuayo (ACRCTT: www.perujungle.com: Myster 2007, 2009, 2010, 2013, 2015b,c) located in Loreto Province, 80 miles southeast of Iquitos, Peru (~2° S, 75° W) with an elevation of ~100 m asl. The reserve is part of one of the largest protected areas in the Amazon, containing wet lowland tropical rainforest (Holdridge 1967) of high diversity (Daly and Prance 1989). It is comprised of low, seasonally inundated river basins of the upper Amazon and named for two of the major white-water rivers (the Tahuayo and the Tamshiyacu) which form boundaries to the north and west, creating large fringing floodplains. The substrate

of these forests is composed of alluvial and fluvial Holocene sediments from the eastern slopes of the Andes. Annual precipitation ranges from 2400 – 3000 mm per year, and the average temperature is relatively steady at 26°C. Within the ACRCTT are areas of black-water runoff which create igapó forests of differing frequency, duration, and maximum water column height, where the rainy season is between November and April (Kalliola et al. 1991).

Methods

At SFR I choose two primary *terra firme* forests, two primary palm forests, and two primary white sand-varillal forests in June of 2013. In each forest I selected 5 microsites with closed-canopies, at least 15 m apart. On each microsite in each forest, I randomly placed a plastic petri dish (9 cm in diameter: Hulme 1994) for each of four test species: *terra firme* (*Cecropia* sp., *Miconia* sp., *Duroid* sp., *Pourouma* sp), palm (*Euterpe precatoria*, *Hevea nitida*, *Mauritia flexuosa*, *Virola paronis*) and white-sand-varillal (*Caraipa punctulata*, *Hevea nitida*, *Pachira brevipes*, *Virola paronis*). Each dish had 10 seeds, and the seeds were collected, using gloves, locally off one individual tree the same day they were put out. In addition seeds were hand-sorted, again using gloves, visually inspected for damage, cleaned of fruit by hand and then floated to further exclude nonviable seeds.

This procedure was repeated for two white-water várzea flooded forests at YRS (underwater 1 month per year) in June 2009 and for six black-water igapó flooded forests at ACRCTT (two underwater 1 month per year [igapó1], two underwater 3-4 months per year [igapó3-4], two underwater at least 6 months per year [igapó6]) in December 2013. The four test species for várzea were (*Cecropia sciadophylla*, *Guarea macrophylla*, *Ochroma pyramidale*, *Turpinia occidentalis*), for igapó underwater 1 month per year (*Attalea butyracea*, *Drypetes amazonia*, *Macrolobium acifolium*, *Qualea paraensis*), for igapó underwater 3-4 months per year (*Brosimum* sp., *Ormosia* sp., *Socratea exorrhiza*, *Terminalia oblonga*) and for igapó underwater at least 6 months per year (*Campsiandra augustifolia*, *Iryanthera jurensis*, *Maquira coriacea*, *Virola elongata*). Each species used in the field experiments was either common in the seed rain or in local plot sampling (Myster 2013, 2015a,b). In addition *Cecropia* sp./*Cecropia sciadophylla*, *Hevea nitida* and *Virola paronis* were used in more than one experiment in different forests. The yearly and seasonal climate variation in the Amazon is relatively small compared to other Neotropical forests (Myster 2009).

After one week in the field, the percentage of seeds remaining in each petri dish, which were not partially eaten and (when examined) still looked viable, was scored as eaten by predators. Evidence of seed predation was observed while collecting this data (e.g. chewed seeds and husks, small mammal feces) and 10 small, colored, plastic seed mimics were placed in each of the dishes to test for possible wind or rain splash removal of seeds. The mimics were counted also after one week in the field and found not to have been removed.

Table 1. F statistic summary table for the two-way ANOVA. P-values are indicated as “*” which means $0.05 > p > 0.01$, “**” which means $0.01 > p > 0.001$ and “***” which means $0.001 > p$. Black-water flooded forest: under water for 1 month per year is indicated as igapó1, under water for 3-4 months per year is indicated as igapó3-4, and under water for 6 months per year is indicated as igapó6.

Effect	terra firme	palm	white sand	várzea	igapó1	igapó3-4	igapó6
seed mechanism/ tolerance (smt)	15.6***	2.9	11.6***	9.5**	4.9*	1.7	1.5
species (sp)	3.7	5.3*	1.1	6.3*	5.9*	2.5	0.9
smt × sp	13.3***	6.5*	8.9**	12.0***	9.2**	3.9	4.2

Given this evidence, I made the assumption that the seeds had been eaten by animals and/or rendered non-viable in some other way associated with the action of an animal agent.

This assumption is common in the literature (see VanderWall et al. 2005 for a recent paper) and no study has yet produced results to question it. Indeed attempts to track seeds in the field after animals take them may, themselves, lead to side effects which has not been discounted (VanderWall et al. 2005). Researchers need to show that recruitment after seed removal by animals is a significant part of a plant’s recruitment and that a seed-following methodology is non-invasive, before this assumption can be revisited (Myster 2015d).

Seeds not removed by predators were then incubated in SFR, YRS and ACRCTT on-site shade houses on moist paper in sealed Petri dishes for 3 weeks. Seeds were then examined and placed in three categories: seeds that germinated, seeds that did not germinate and had extensive fungal damage, and other. After graphing results by individual forest (igapó, palm, *terra firme*, várzea, white sand) and finding them to be normally distributed, percent seed loss data were analyzed using a two-way analysis of variance (ANOVA: SAS 1985) with seed mechanism/tolerance – seed predation, seed pathogens, germination – as one main effect (degrees of freedom [df] = 2) and species as the other main effect (df = 3). For igapó, palm, *terra firme*, várzea and white sand, there were 4 species and 10 microsites for a total of 280 petri dishes, and 2800 seeds, set out. Because interaction terms are more meaningful than main effects (SAS 1985), they were graphed if significant. In addition, means tests were conducted to determine which levels drove significance (SAS 1985).

Results

Percent seed loss was significantly different among the seed mechanisms and tolerances for *terra firme*, white sand, várzea and igapó1 individually (Table 1). For igapó1, *terra firme*, várzea and white sand, more seeds were lost to predators than to pathogens or that germinated. Percent seed loss was significantly different among species for the forest-types palm, várzea and igapó1 (Table 1). In palm forest *Euterpe precatória* lost the most seeds to predators, *Mauritia flexuosa* lost the most seeds to pathogens and *Hevea nitida* seeds germinated the most. In várzea forest *Guarea macrophylla* lost the most seeds to predators, *Ochroma pyramidale* lost the most seeds to pathogens and *Turpinia occidentalis* seeds germinated the most. In igapó1 forest *Drype tes amazonia*

lost the most seeds to predators, *Macrolobium acifolium* lost the most seeds to pathogens and *Qualea paraensis* seeds germinated the most.

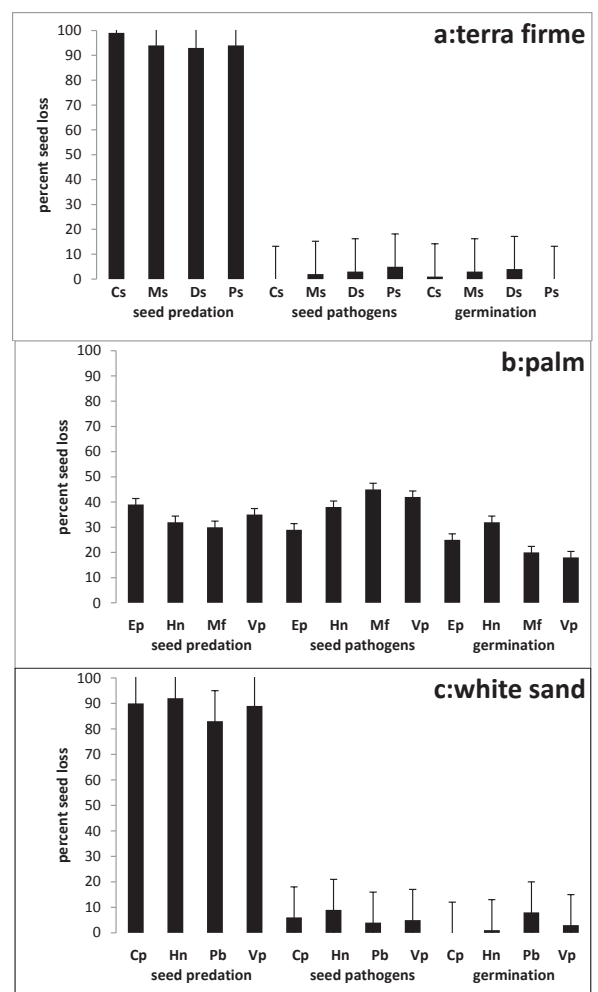


Figure 1. Percent seed loss means and standard errors of the interaction term for the unflooded (a) *terra firme* forest (seed species: *Cecropia* sp. [Cs], *Miconia* sp. [Ms], *Duroid* sp. [Ds], *Pourouma* sp. [Ps]), (b) palm forest (seed species: *Euterpe precatória* [Ep], *Hevea nitida* [Hn], *Mauritia flexuosa* [Mf], *Virola paronis* [Vp]) and (c) white sand-varillal forest (seed species: *Caraipa punctulata* [Cp], *Hevea nitida* [Hn], *Pachira brevipes* [Pb], *Virola paronis* [Vp]).

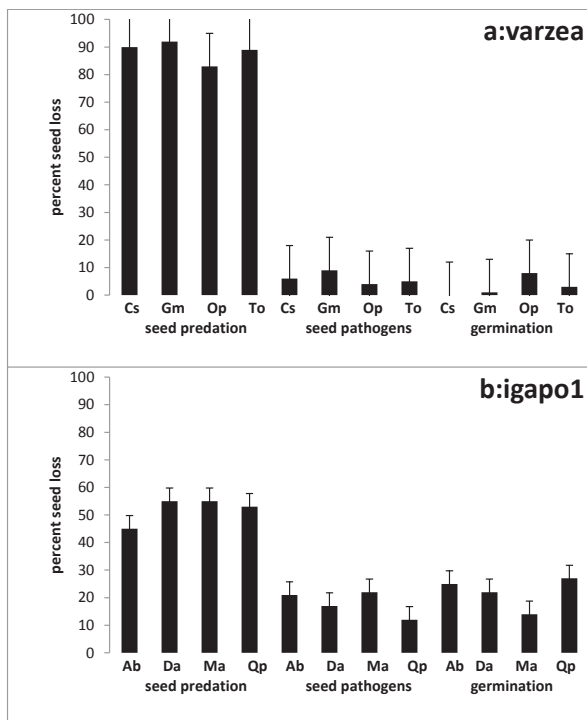


Figure 2. Percent seed loss means and standard errors of the interaction term for the flooded (a) várzea forest (seed species: *Cecropia sciadophylla* [Cs], *Guarea macrophylla* [Gm], *Ochroma pyramidale* [Op], *Turpinia occidentalis* [To]), and (b) igapó1 forest underwater 1 month per year (seed species: *Attalea butyracea* [Ab], *Drypetes amazonia* [Da], *Macrolobium acifolium* [Ma], *Qualea paraensis* [Qp]).

The interaction term was significant for igapó1, palm, *terra firme*, várzea and white sand (but not for igapó3-4 or igapó6: Table 1). Examination of the interaction term for *terra firme* forest shows that seed predators took most seeds regardless of species (Fig. 1a: means testing showed seed predation levels strongly different for all species). Examination of the interaction term for palm forest shows that species were different (Fig. 1b: means testing showed modest differences among species regardless of seed mechanism and tolerance). Examination of the interaction term for white sand forest shows, as in *terra firme*, that seed predators took most seeds regardless of species (Fig. 1c: means testing showed seed predation levels strongly different for all species but at lower levels than *terra firme*). Examination of the interaction term for várzea forest shows that seed predators took most seeds but with some species differences (Fig. 2a: means testing showed seed predation levels and species moderately different). Examination of the interaction term for igapó1 forest-type shows that seed mechanisms and tolerances, and species variation was present (Fig. 2b: means testing showed moderate differences among both seed mechanisms and tolerances and species).

Discussion

There was support for all three hypotheses. Predation was the major seed mechanism of forest recruitment and regen-

eration (Myster 2014, 2015d) for igapó1, *terra firme*, várzea and white sand. Pathogens can play an important role, and most seeds germinated, if they could survive predators and pathogens (Myster 2015d). This suggests that it is the variation in how seed predation works – for example among species, under litter, at different times of the year – that largely determines recruitment and regeneration in the Amazon.

The dryer forests (*terra firme* and white sand) lost more seeds to predators than pathogens, than the wetter palm forest that lost more seeds to pathogens than predators. The higher plant species richness and complexity of *terra firme* forest (Valencia et al. 2004) may have led to more seed predators and, thus more seed predation. Species-rich flooded forests (white-water várzea) had more predation than the species-poor flooded forests (black-water igapó) at the same inundation time period perhaps for the same reason. Within black-water flooded forests, more flooding led to less predation just as the palm forest had less predation than the *terra firme* forest. The lower species diversity found in flooded forest, may be due to adaptations in flooded trees which are a subset of remnants of pre-adaptations from the non-flooded *terra firme* forest species where floodplain trees originated (Parolin et al. 2004). Results suggest that seed predation may be reduced by loss of soil fertility more than by increased flooding. For pathogens, standing water in the palm forest led to the greatest losses, but increased flooding in igapó forest can also lead to increasing loss of seeds to pathogens.

Plot sampling in these forests (Myster 2013, 2014, 2015a) show only a modest correspondence between the results and the trees that actually grow there. This suggests that other mechanisms or other sources of variation in the workings of the seed mechanisms and tolerances may play major roles in rainforest recruitment and regeneration (Muller-Landau et al. 2008). Indeed the complexities of forest recruitment are a major challenge for modelers who wish to predict plant-plant replacements (Myster 2012b).

Results are consistent with other primary Amazon forest studies that found up to 90% seeds lost to predators total with 60% after 16 days (Russo 2005) and in another study seeds taken were mainly large and by mammals with at most 12% scatter-hoarded but even those were eaten later (Paine and Beck 2007). Other Amazon studies suggest further complexity and future experiments by showing that (1) larger seeds get taken by pathogens more than smaller seeds, germination was ~43% and pathogen loss was up to 75% depending on species (Pringle et al. 2007), (2) secondary dispersal is low (Culot et al. 2009), (3) seed predation was reduced under litter (the thicker the better: Cintra 1997), and (4) after bat defecation seeds were eaten 8% per week with possible satiation (Romo et al. 2004). Finally tree seeds in flooded forests may suffer secondary dispersal by fish (Parolin et al. 2004).

I conclude that seed predation losses strength as forests become more stressed either by loss of soil fertility or by flooding with nutrient-poor water. Conversely seed pathogens become more important as soil become more waterlogged and with flooding. Seed loss variation among species is always a secondary factor. Understanding the fate of seeds

after they disperse into a forest allows us to understand its regeneration and dynamics, and leads to potential methods of management and conservation. Managers may want to increase predation or pathogen attack for some tree species and decrease it for others. Methods for increasing (decreasing) it might be to increase (decrease) animals or fungi, or changing the water dynamics.

Acknowledgements: I thank D. Graham, P. Beaver, J. Varica and H. Navarette for their help in the logistics of this research. I also thank J. Jernstedt, K. Gross, V. Pillar, I. Turner, T. Pons, A. Langefors and E. Bruna for commenting on a previous version of the manuscript. Finally I thank the Fulbright Foundation for three teaching/research awards in Ecuador and Peru.

References

- Choo, J.P.S., R.V. Martinez and E.W. Stiles. 2007. Diversity and abundance of plants with flowers and fruits from October 2001 to September 2002 in Paucarillo Reserve, Northeastern Amazon. *Peru Revisited Peru Biology* 14:25–31.
- Cintra, R. 1997. Leaf litter effects on seed and seedling predators of the palm *Astrocaryum murumura* and the legume tree *Dipteryx micrantha* in Amazonian forest. *J. Trop. Ecol.* 13:709–725.
- Culot, L., M. Huuynen, P. Gerard and E.W. Heymann. 2009. Short-term post-dispersal fate of seeds defecated by two small primate species (*Saguinus mystax* and *S. fuscicollis*) in the Amazonian forest of Peru. *J. Trop. Ecol.* 25:229–238.
- Daly, D.C. and G.T. Prance. 1989. Brazilian Amazon. In: *Floristic Inventory of Tropical Countries*. NY Botanical Garden, Bronx, NY. pp. 401–426.
- Duivenvoorden, J.F., H. Balslev, J. Cavelier, C. Grandez, H. Tuomisto and R. Valencia. 2001. *Evaluacion do recursos vegetales no maderables en la Amazonia noroccidental*. The Netherlands Centre for Geo-ecological Research (ICG), The Netherlands.
- Everham, E.M. III., R.W. Myster and G. VanDegnachte. 1996. Effects of light, moisture, temperature, and litter on the regeneration of five tree species in the tropical montane wet forest of Puerto Rico. *Amer. J. Bot.* 83:1063–1068.
- Frederickson, M.E., M.J. Greene and D.M. Gordon. 2005. ‘Devil’s garden’ bedeviled by ants. *Nature* 437:495–496.
- Gentry, A.H. 1966. *A Field Guide to the Families and Genera of Woody Plants of Northwest South America*. Univ. Chicago Press, Chicago.
- Grubb, P.J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biol. Rev. Cambridge Phil. Soc.* 52:107–111.
- Holdridge, L.R. 1967. *Life Zone Ecology*. Tropical Science Center, San Jose, CR.
- Hulme, P.E. 1994. Post-dispersal seed predation in grassland: its magnitude and sources of variation. *J. Ecol.* 82:645–652.
- Honorio, E.N. 2006. Floristic relationships of the tree flora of Jenaro Herrera, an unusual Area of the Peruvian Amazon. M.Sc. thesis, University of Edinburgh, Edinburgh, UK.
- Junk, W.J. 1997. *The Central Amazon Floodplain – Ecology of a Pulsing System*. Springer, Berlin. Ecological studies 126.
- Kalliola, R.S., M. Jukka, M. Puhakkaa and M. Rajasilta. 1991. New site formation and colonizing vegetation in primary succession on the western Amazon floodplains. *J. Ecol.* 79:877–901.
- Keller, M., A. Alencar, A. Asner et al. 2004. Ecological research in the large-scale biosphere atmosphere experiment in Amazonia: Early results. *Ecol. App.* 14:S3–S16.
- Losos, E.C. and E.C. Leigh. 2004. *Forest Diversity and Dynamism: Findings from a Network of Large-scale Tropical Forests Plots*. University of Chicago Press, Chicago.
- Metz, M.R., L.S. Comita, Y.Y. Chen, N. Norden, R. Condit and S.P. Hubbell. 2008. Temporal and spatial variability in seedling dynamics: a cross-site comparison in four lowland tropical forests. *J. Trop. Ecol.* 24:9–18.
- Moreau, C.S. 2008. Unraveling the evolutionary history of the hyperdiverse ant genus *Pheidole* (Hymenoptera: Formicidae). *Mol. Phys. Evol.* 48:224–239.
- Muller-Landau, H.C., S.J. Wright, O. Calderon, R. Condit and S.P. Hubbell. 2008. Interspecific variation in primary seed dispersal in a tropical forest. *J. Ecol.* 96:653–667.
- Myster, R.W. 2007. Interactive effects of flooding and forest gap formation on composition and abundance in the Peruvian Amazon. *Folia Geobot.* 42:1–9.
- 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 and temporal heterogeneity of light and soil water along a *terra firme* transect in the Ecuadorian Amazon. *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. 2013. The effects of flooding on forest floristics and physical structure in the Amazon: results from two permanent plots. *Forest Res.* 2:112.
- Myster, R.W. 2014. Interactive effects of flooding and treefall gap formation on *terre firme* forest seed and seedling mechanisms and tolerances in the Amazon. *Community Ecol.* 15:212–221.
- Myster, R.W. 2015a. *Várzea* forest vs. *terra firme* forest floristics and physical structure in the Ecuadorean Amazon. *Ecotropica* 20:35–44.
- Myster, R.W. 2015b. Comparing and contrasting eight different flooded and non-flooded forests in the Peruvian Amazon: seed rain. *New Zealand J. For. Sci.* 45:5.
- Myster, R.W. 2015c. Flooding x tree fall gap interactive effects on black-water forest floristics and physical structure in the Peruvian Amazon. *J. Plant Interactions* 23:12–25.
- Myster, R.W. 2015d. Seed predation, pathogens and germination in primary vs. secondary cloud forest at Maquipucuna Reserve, Ecuador. *J. Trop. Ecol.* 31:375–378.
- Myster, R.W. 2016a. The physical structure of Amazon forests: a review. *Bot. Rev.* 82:407–427.
- Myster, R. W. 2016b. Black-water forests (igapó) vs. white-water forests (várzea) in the Amazon: floristics and physical structure. *The Biologist (Lima)* 13:391–406.
- Myster, R.W. 2017. Does the seed rain limit recruitment, regeneration and plant community dynamics? *Ideas Ecol. Evol.* 10:1–12.
- Myster R.W. and P.G. Santa Cruz. 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 Yasuni, Ecuador. *Revista Pontanti Universidad Católica* 76:111–124

- Paine, C.E.T. and H. Beck. 2007. Seed predation by Neotropical rainforest mammals increases diversity in seedling recruitment. *Ecology* 88:3076–3087.
- Parolin, P., O. Desimobne, K. Haase K. et al. 2004. Central Amazonian floodplain forests: tree adaptations in a pulsing system. *Bot. Rev.* 70:357–380.
- Pires, J.M. and G.T. Prance. 1985. The vegetation types of the Brazilian Amazon. In: G.T. Prance and T.E. Lovejoy (eds.), *Amazonia*. Pergamon Press, Oxford. pp 109–145.
- Pitman, N.C., J.W. Terborgh, M.R. Silman, P.V. Nunez, D.A. Neill, C.E. Ceron, W.A. Palacios and M. Aulestia. 2001. Dominance and distribution of tree species in upper Amazonian *terra firme* forests. *Ecology* 82:2101–2117.
- Prance, G.T. 1979. Notes on the vegetation of Amazonia III. The terminology of Amazonian forest types subject to inundation. *Brittonia* 31:26–38.
- Pringle, E.G., P. Alvarez-Loayza and J. Terborgh. 2007. Seed characteristics and susceptibility to pathogen attack in tree seeds of the Peruvian Amazon. *Plant Ecol.* 193:211–222.
- Romo, M., H. Tuomisto and B.A. Loiselle. 2004. On the density-dependence of seed predators in *Dipteryx micrantha*, a bat-dispersed rain forest tree. *Oecologia* 140:76–85.
- Russo, S.E. 2005. Linking seed fate to natural dispersal patterns: factors affecting predation and scatter-hoarding of *Virola calophylla* seeds in Peru. *J. Trop. Ecol.* 21:243–253.
- SAS 1985. User's Guide: Statistics, Ver. 5. SAS Institute Inc. Cary, NC. 956 pp.
- Spichiger, R., P. Loizeau, C. Latour and G. Barriera. 1996. Tree species richness of a South-Western Amazonian forest (Jenaro Herrera, Peru, 73°40'W/4°54'S). *Candollea* 51:559–577.
- Svenning, J.C. 1999. Microhabitat specialization in a species-rich palm community in Amazonian Ecuador. *J. Ecol.* 87:55–65.
- Tuomisto, H., K. Ruokolainen, A.D. Poulsen, R.C. Moran, C. Quintana, G. Canas and J. Cell. 2002. Distribution and diversity of Pteridophytes and Melastomataceae along edaphic gradients in Yasuni National Park, Ecuadorian Amazonia. *Biotropica* 34:516–533.
- Tuomisto, H., K. Ruokolainen and M. Yli-Halla. 2003. Dispersal, environment and floristic variation of Western Amazonian forests. *Science* 299:241–244.
- Valencia, R., R.B. Foster, G. Villa, T.R. Condit, J. Svenning, C. Hernandez, K. Romoleroux, E. Losos, E. Magard and S.L. Balslev. 2004. Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. *J. Ecol.* 92:214–229.
- VanderWall S.B., K.M. Kuhn and M.J. Beck. 2005. Seed removal, seed predation, and secondary dispersal. *Ecology* 86:801–806.
- Walter, H. 1973. *Vegetation of the Earth and the Ecological Systems of the Geo-Biosphere*. Springer, Berlin.

Received August 22, 2015
 Revised September 14, 2017
 Accepted October 12, 2017