FLOODING GRADIENT AND TREEFALL GAP INTERACTIVE EFFECTS ON PLANT COMMUNITY STRUCTURE, RICHNESS, AND ALPHA DIVERSITY IN THE PERUVIAN AMAZON

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Abstract. The Amazon is the most productive and diverse terrestrial ecosystem in the world and among its important structuring forces are flooding gradients and treefall gap dynamics. Consequently, in order to more fully understand Amazonian forests, I sampled Peruvian vegetation plots for five years both in forest and in fresh gaps within each of three forest types (terra firme, varzea, tahuampa) that differed in flooding duration and maximum water depth. I found a significant effect of degree of openness (i.e. treefall gap formation) on canopy average height, canopy maximum height, basal area, density, above-ground biomass, turnover, and alpha diversity, and a significant effect of forest type (i.e. the flooding gradient) on species richness, genera richness, density, turnover, and alpha diversity. In general, there were fewer trees, but they were larger, and more productive in the forest plots compared with the gap plots; and the most flooded plots had fewer trees, species, and genera compared with both the less flooded forest and unflooded forest. Also the greatest amount of turnover was found in the most flooded forests, and the intermediately flooded forest had the greatest richness and alpha diversity. These results taken together support a "mass effects" hypothesis where species from both the unflooded and most flooded forests and their gaps have overlapping ranges in the less flooded forest and gaps, causing continuous immigration which boosts diversity. In summary, (1) canopy structure was determined by traditional gap dynamics, but much of canopy diversity depended on the type of forest, (2) tree density decreased as flooding increased, especially among the smallest stems, and (3) there was evidence to suggest that the high biodiversity of the Amazon may be maintained in part by the existence of moderately flooded forest and gaps. *Accepted 25 October 2009.*

Key words: biodiversity, LTER, mass effects hypothesis, tahuampa, Tamshiyacu-Tahuayo, terra firme, várzea, whitewater.

INTRODUCTION

Scientists have long known that plants respond both to gradients (Walter 1973, Whittaker, 1975) and to disturbances that disrupt the structures laid down on those gradients (Gleason 1926, Pickett & White 1985). Common gradients include rainfall and temperature, and natural disturbances range from the very severe to the less severe where biomass lost may be the currency of disturbance (Tilman 1988, Myster 2003). Thus the vegetation mosaic of any landscape is a function of both environmental variation in gradients and historical disturbances (Risser 1987, Turner & Dale 1991, Myster *et al.* 1997) where gradients may be viewed as plant pattern variation in space and disturbances as plant pattern variation in time (Myster 2001).

Because fundamental ecosystem structures, functions, and processes are often plant-based (plants being the major conduits for energy and nutrient dynamics), a prime ecological focus needs to be on plant responses to gradients and disturbances (Watt 1947, Myster 2007b). In the Amazon basin, flooding – its frequency, duration, depth, and spatial variation – forms major gradients to which plants respond, explaining much of their distribution, composition, association, and abundance (Junk 1989, Lamotte 1990, Ferreira & Stohlgren 1999, Oliveira-Wittman *et al.* 2007, Parolin *et al.* 2004a, Parolin 2009, Wittmann *et al.* 2004a, Wittmann *et al.* 2006). Whereas at one end of the gradient, the unflooded *terra firme* forest may resemble rainforests elsewhere in the Neotropics (Kalliola *et al.* 1991, Lopez & Kursar 1999, Myster & Santacruz 2005), the forests that are spread out along the flooded gradient have a unique biology and ecology (Kalliola *et al.* 1991, Ferreira & Stohlgren 1999, Parolin *et al.* 2004a, Wittmann *et al.* 2004a, Wittmann *et al.* 2006, Oliveira-Wittman *et al.* 2007, Parolin 2009). Those plant adaptations include (1) seed structures to escape predation both from terrestrial mammals and from fish (Junk 1989) in order to germinate, (2) seedling strategies (Grubb 1977) either of growing fast in order to have their leaves above the next high water level or of being able to endure extended submersion, and (3) special

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root structures, such as aerenchyma tissue, to facilitate gas exchange under water (Junk 1989, Lopez & Kursar 1999, Parolin *et al.* 2004a, Parolin 2009) because of the reduction in oxygen solubility in water under high temperatures. The disturbances laid down on these gradients are, most often, natural treefalls because large parts of the Amazon have not been under extensive logging and agriculture (Myster 2007b, Myster 2009). The resulting gap dynamics is also expected to have its unusual aspects (Lamotte 1990, Wittmann *et al.* 2004a, Wittmann *et al.* 2006).

Therefore in order to better understand Amazonian rainforests, I first sampled five years of data from forest and gap plots in each of the three forest types found in northeastern Peru: dry forest that never floods, wet forest underwater from 1-5 months of the year, and very wet forest underwater for at least 6 months of the year. I then used those data to generate eight different structural parameters and to address the following questions: (1) How does gap creation affect the structure of the forest and which parameters are most affected?, (2) Which aspects of structure change as flooding increases in the forest, and do those patterns increase or decrease consistently?, and (3) Are there interactions in the way these two primary Amazon forest processes affect common structural parameters, that is does the action of one depend on the level of the other?

MATERIALS AND METHODS

Study site. The study site is the Tamshiyacu-Tahuayo Reserve (Reserva Comunal de Tamshiyacu-Tahuayo: www.perujungle.com, Myster 2007a, Myster 2009), located close to Iquitos, Peru (3°51'S, 73°13'W; elevation 106 m a.s.l) and named for two of the major whitewater rivers that run through it. The reserve is known for it's high biodiversity (Daly & Prance 1989, Daly & Mitchell 2000), particularly of primates (S. Leonard, unpub. data), and comprise low, seasonally inundated river basins of the upper Amazon. It is part of one of the largest (115,000 km²) protected areas in the Amazon with plant associations generally classified as wet lowland tropical rainforest (Ewel & Whitmore 1973, Lugo & Lowe 1995). Such rainforest can be more precisely divided into three types defined by the amount of flooding occuring during the rainy season in November to April (Kalliola *et al.* 1991): (1) *terra firme* forest (called dry here for ease of presentation) which is not flooded but may have depressions of clay soil called *aquajal*

that stay swampy throughout the year; (2) *restinga* forest (called wet) which is under water 1-5 months of the year with a maximum depth of 3 m, and (3) *tahuampa* forest (called very wet) which is under water at least 6 months of the year with a maximum depth of 6 m.

The substrate of these forests is composed of alluvial and fluvial Holocene sediments from the eastern slopes of the Andes. In particular, the *terra firme* forest is located on a Pleistocene river terrace and has a high decree of marine sediments that can be rich in calcium, phosphorus, and magnesium (Pitman *et al.* 1999). Annual precipitation ranges from 2.4 to 3 m per year, while the average temperature is relatively steady at 26°C. Due to the flooding, soil fertility is high contributing to the complex vertical structure of the forest (Myster 2007a). A separate analysis of the same plots used in this study showed that the most numerous species in dry forest was *Dendropanax querectorum*, in dry gaps *Licania* sp., in wet forests *Couratari guianensis*, *Mouriri* sp. and *Genipa* sp., in wet gaps *Genipa* sp. and *Mouriri* sp., in very wet forests *Hevea brasiliensis* and *Couratari guianensis*, and in very wet gaps *Genipa* sp., *Alchornea* sp. and *Virola peruviana* (Myster 2007a). In addition, *terra firme* forest contains the tree genera *Chorisia*, *Eschweilera*, *Hura*, *Spondias*, and *Virola* while the two flooded forests contain trees such as *Calycophyllum spruceanum*, *Ceiba samauma*, *Inga* spp., *Cedrela odorata*, *Copaifera reticulata*, *Phytelephas macrocarpa* with under-story palms such as *Scheelea* spp., *Guazuma rosea*, and *Piptadenia pteroclada* (see Prance 1979, Puhakka *et al.* 1992, Daly & Mitchell 2000 and Myster 2007a for details on the vegetation). Common successional woody plants found in treefall gaps include *Adenaria floribunda*, *Alchornea castaneifolia*, *Salix martiana*, *Annona hypoglauca*, and *Cecropia latiloba*.

Experimental design. Within each of the three forest types, five microsites were selected in June of 1997. Although some logging for mahogany (*Swietenia macrophylla*) has occurred in the past in all three forests, using information gathered at the reserve from past scientific research and from local people working at the reserve very effort was made to select individual study areas that resembled primary forest as much as possible. At each microsite a fresh average-sized (100-300 m²: Brokaw 1982) gaps was chosen, in the center of which a 5 m x 5 m (25 m²) plot was established (suggested for sampling gaps of this size: Thompson *et al.* 1998). For comparative and statis-

tical purposes, an equivalent plot was also established in the forest adjacent to each gap.

Each of these 30 plots was sampled during May of 1998 through 2002 for a total of five years of regrowth. At every sampling each tree stem at least 50cm tall was measured for height (using a tangent height gauge for tall trees), measured for basal diameter, and identified for species (see Myster 2007a for the complete species list). Taxonomic references included Gentry (1993), Vasquez-Martinez (1997), and Ruokolainen & Tuomisto (1998). In addition, the web sites for the Missouri Botanical Garden (www.mobot.org) and for specific surveys done in the Peruvian Amazon (www.iiap.org.pe) were also used as taxonomic sources. Finally, in a few instances when plants could not be identified to species, common morphospecies were collected and deposited in the Iquitos herbarium. This data is stored in the archives of the Luquillo Experimental Forest LTER site in Puerto Rico USA as LTERDBAS#150 and their web site may be visited (luq.lternet.edu) for further details.

Statistical analysis. After allowing for significant successional and structural development, the 2002 data were used to generate eight parameters of structure and growth: species richness, generic richness, average height, maximum height, basal area, density, above-ground biomass (derived from the Amazon tree allometric equations found in Nascimento & Laurance [2001], which use both basal diameter and height of all trees in a plot), and turnover (turnover at year 2002 = [species present at year 2001 but not present at year 2002 + species present at year 2002 but not present at year 2001] / [richness at year 2001 + richness at year 2002]; Diamond 1969, Myster &

Pickett 1994). As the closest year to 2002, data from 2001 were used to compute turnover. Because richness trends could have been undermined by similar densities (i.e., some plots could have had more species solely due to the larger number of stems sampled there), Fisher's alpha (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 in Rosenzweig (1995).

Analysis of variance (split-plot design) and the means testing procedure Ryan-Einot-Gabriel-Welsch (SAS 1985) were used to investigate the main effects of openness (forest vs. gap; one degree of freedom) and forest type (dry vs. wet vs. very wet; two degrees of freedom) along with the interactive effect between the two main effects (two degrees of freedom) on these parameters. Main effects are given in the text. When there are only two means given they were significantly different and when there are three means given, the mean which was significantly different is in bold. Means ± standard deviation are given for all results. Significant interaction effects are also graphed for clarity of presentation. Variance assumptions were tested and found to be well justified. Finally, the sequential Bonferroni test was employed (Rice 1989) but did not suggest that any significant results were unreliable.

RESULTS

There were seven structural parameters that differed significantly between forest plots and gap plots (main effect of openness: Table 1). Trees were significantly smaller in gaps compared with the forest, both in

TABLE 1. F statistic and significant p-value summary table for all main and interactive effects. A p-value between 0.05 and 0.01 is indicated by *, a p-value between 0.01 and 0.001 is indicated by **, and a p-value that is less than 0.001 is indicated by ***.

Response variable	Main effect (openness)	Main effect (forest type)	Interaction effect
Species richness	3.66	8.21**	5.64**
Genera richness	2.62	7.84**	5.57**
Average height	30.21***	3.20	1.22
Maximum height	17.25**	0.62	0.09
Basal area	6.89*	0.20	0.10
Density	4.84*	13.68***	2.93
Above-ground biomass	21.26**	1.98	2.34
Turnover	7.02*	5.02*	3.02
Fisher's alpha diversity	4.98*	5.12*	6.43*

average height (480 ± 54 cm vs. 1050 ± 75 cm) and maximum height (2100 ± 126 cm vs. 4500 ± 988 cm). Trees were also thinner in gaps (400 ± 56 cm^2 mean basal area vs. 2300 ± 123 cm^2), had lower stem density (22 ± 5 stems/plot on average vs. 27 ± 9 stems/plot), and had less above-ground biomass (11 ± 3 kg/m^2 vs. 38 ± 12 kg/m^2). Finally, trees turned over more in the gaps than in the forest (20 ± 4 % vs. 15 ± 2 %), but gaps showed less alpha diversity (70 ± 12 vs. 80 ± 9).

There were five structural parameters that differed significantly between dry forest plots, wet forest plots, and very wet forest plots (main effect of forest type: Table 1). There were significantly fewer species in the very wet forest compared with the other forests (21 ± 6 species/plot on average in dry forest vs. 18 ± 4 in wet forest vs. **11** ± 2 in very wet forest) and fewer genera (20 ± 4 vs. 16 ± 3 vs. **10** ± 1). There were also significantly fewer trees in the wet and very wet forests (**31** ± 7 vs. 29 ± 5 vs. 18 ± 8). In addition, tree species turned over more in the wet and very wet forests (**8** ± 1 % vs. 21 ± 3 % vs. 22 ± 5 %) but the very wet forest had less alpha diversity (70 ± 7 vs. 72 ± 10 vs. **60** ± 4). Whereas more prolonged flooding led to less complexity in species, genera, and density, increased flooding meant more complexity in turnover and alpha diversity.

Three of the structural parameters showed significant interaction effects (Table 1). The plots with the most species were in the dry forest and in the wet gaps (Figure 1A), and those same plots had the most genera (Figure 1B). However, the plots with the greatest alpha diversity were in the wet forest and wet gaps (Figure 1C).

DISCUSSION

Richness of both species and genera was greatest in the dry forest compared with the wet and very wet forest (Parolin *et al.* 2004a), which may be due in part to root burial by sedimentation in flooded forests (Junk 1989, Lopez & Kursar 1999). However, alpha diversity was highest in the wet forest and wet gaps, followed by the dry forest (see Valencia *et al.* 2004) and very wet forest. Forest plots contained more trees that were also taller and larger with more above-ground biomass compared with gap plots, regardless of where the plots were located. For those parameters that allowed comparison between main effects, stems were densest in dry forest plots compared with the other forest plots, though to a lesser degree in forest plots compared with gap plots, while turnover was greater in gap plots compared with forest plots as well as in very wet and wet forest plots compared with those in dry forest. Both the density and turnover effects might best be explained either by the loss of small stems, by the action of moving water, or by the physical damage due to the weight of debris. Finally interaction effects may allow us to look at flooding as a disturbance (Salo & Kalliola 1990) because it also removes plant biomass (Myster 2003), facilitating comparison with gap formation.

Richness did not correspond well with the other parameters, suggesting that by itself it is not a significant mechanism affecting other parameters (Tilman *et al.* 1997). However, there was an inverse relationship between above-ground biomass and turnover, suggesting that plots get more individuals or growth from resident species rather than from invasion by new, more productive species over time. This is expected because low-production successional environments, with low rates of competitive displacement and high diversity, should have high turnover while productive mature environments should have low turnover because their species are longer-lived and difficult to invade given their high rates of competitive displacement leading to dominance by only a few species and low diversity (Huston 1994).

The study plots had significantly higher richness, greater density, more basal area, and biomass compared to western Brazil forests (Ferreira & Prance 1998, Thompson *et al.* 1998) but similar densities to another Peruvian Amazon rainforest (Pitman *et al.* 1999). Also, alpha diversity was similar to forest in the Ecuadorean Amazon (Valencia *et al.* 1994). Turnover computed in other years showed a decrease with time, just as Myster & Pickett (1994) showed after agriculture in the temperate zone (New Jersey USA), as pioneer species are replaced faster than late-successional species.

In answer to the first question in the introduction – How does gap creation affect the structure of the forest and which parameters are most affected? – these aspects of canopy structure were determined by tree-fall gap dynamics: forest plots had more stems, and taller trees compared with gap plots. Consequently, gap dynamics includes phases of canopy structural development such as ground coverage, organized vertical growth, and surface arrangement at multiple levels as well as crown differentiation with the death of over-story trees. In answer to the second question – Which aspects of structure change as flooding increases in the forest, and do they increase
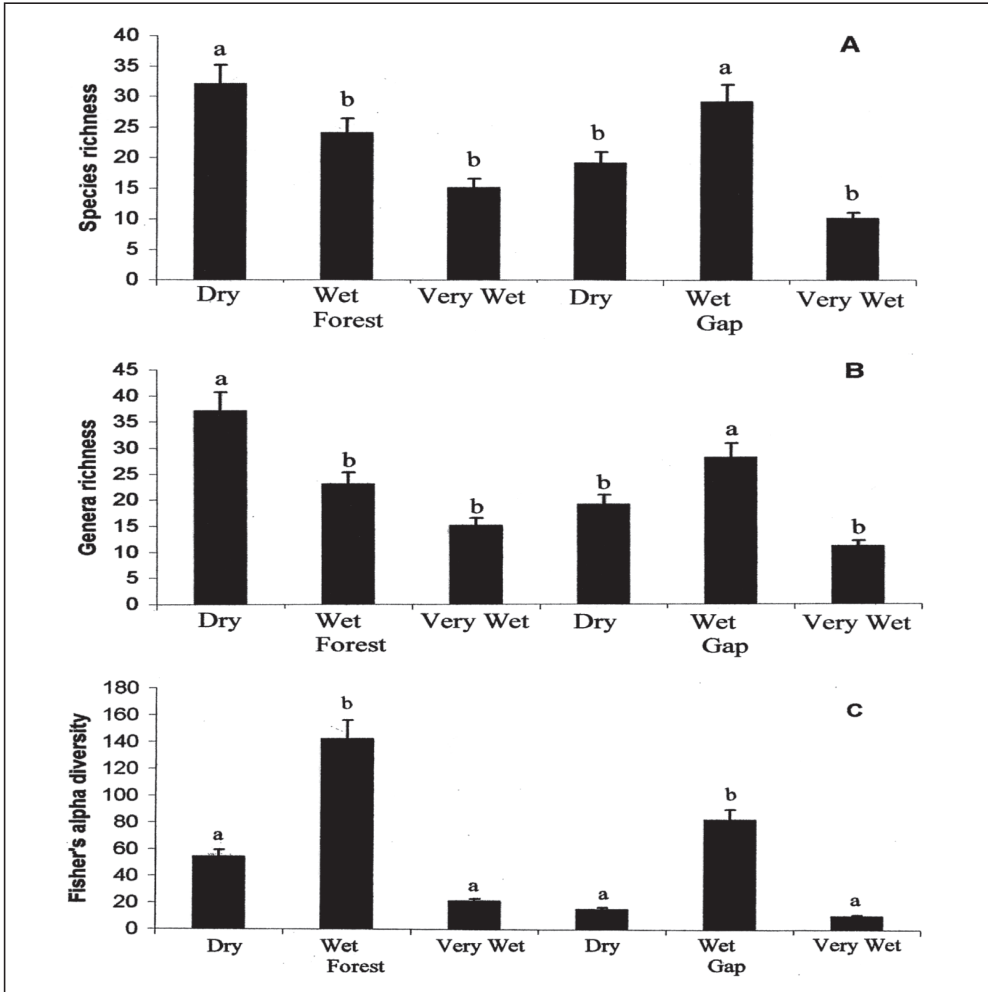
FIG. 1. Means and standard errors of (A) species richness in all plots grouped by the significant interaction effect between openness x forest type, (B) genera richness in all plots grouped by the significant interaction effect of openness x forest type, and (C) Fisher's alpha diversity in all plots grouped by the significant interaction effect of openness x forest type. Means testing results are indicated by lowercase letters. If groups were significantly different, as given in Table 1, then letters are different.

or decrease in complexity? – the structural composition of the canopy did differ among the forest types where the dry forest had more species, more genera, and more stems than the flooded forests. Finally to answer the third question – Are there interactions in the way these two primary Amazon forest processes affect common structural parameters, that is does the action of one depend on the level of the other? – the significant interaction effects showed a sharp increase

in species and genera richness in both dry forest and wet gaps, with Fisher's diversity at its highest in forest and gap plots of moderate flooding (cf Ferreira & Stohlgren 1999).

This last result may suggest an "intermediate gradient" hypothesis (similar to the intermediate disturbance hypothesis of Connell [1978]) where species from both the dry and very wet forest can exist in the wet forest and add to its diversity. How-

ever, a "mass effects" hypothesis (Stevens, 1992) is more likely, where species from dry and very wet forest and their gaps have overlapping ranges in the wet forest and wet gaps (Wittmann *et al.* 2004a), causing continuous immigration into the wet areas even though these new species are easily out-competed there. In fact high flood tolerance and the ability of their seeds to survive submersion for months have been observed in several tree species of the *terra firme* forest (Lopez & Kursar 1999). If true this mass effects hypothesis may help explain the maintenance of high diversity, not just in Peru, but throughout the Amazon. However, confirmation of this pattern must await further sampling in order to address alternative explanations (e.g. succession: Whittmann & Junk 2003, Wittmann *et al.* 2004b).

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REFERENCES

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

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. Science, 199: 1302–1309.

Daly, D.G., & G.T. Prance. 1989. Brazillian Amazon. Pp. 401–426 in Campbell, D.G., & H. Hammond (eds). Floristic inventory of tropical countries. New York Botanical Garden, New York.

Daly, D.G., & J.D. Mitchell. 2000. Lowland vegetation of tropical South America. Pp. 391–453 in Lentz, D.L. (ed). Imperfect balance: landscape transformation in the Pre-Columbian Americas. Columbia University Press, New York.

Diamond, J.M. 1969. Avifaunal equilibria and species turnover rates on the Channel Islands of California. Proc. Nat. Acad. Sci. 64: 57–63.

Ewel, J.J., & J.L. Whitmore. 1973. The ecological life zones of Puerto Rico and the Virgin Islands. U.S. Forest Service Research Paper ITF-18. Institute of Tropical Forestry, Rio Piedras, Puerto Rico.

Ferreira, L.V., & G.T. Prance. 1998. Species richness and floristic composition in four hectares in the Jau National Park in upland forests in Central Amazonia. Bio. Cons. 7: 1349–1364.

Ferreira, L.V., & T.J. Stohlgren. 1999. Effects of river fluctuation on plant species richness, diversity, and distribution in a floodplain forest in Central Amazonia. Oecologia 120: 582–587.

Fisher, R.A., Corbet, A.S., & C.B. Williams. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. J. Anim. Ecol. 12: 42–58.

Gentry, A. 1993. A field guide to woody plants of northwest South America (Colombia, Ecuador, Peru). Conservation International, Washington, D.C.

Gleason, H.A. 1926. The individualistic concept of the plant association. Bull. Torrey Bot. Club 53: 1–20.

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

Huston, M.A. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, Cambridge.

Junk, W.J. 1989. Flood tolerance and tree distribution in central Amazonian floodplains. Pp. 47–64 in Holm-Nielsen, L.B., Nielsen, I.C., & H. Balslev (eds). Tropical forests: Botanical dynamics, speciation and diversity. Academic Press, New York.

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

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

Lopez, O.R., & T.A. Kursar. 1999. Flood tolerance of four tropical tree species. Tree Phys. 19: 925–932.

Lugo, A.E. & C. Lowe. 1995. Tropical Forests: management and ecology. Springer-Verlag, New York.

Myster, R.W. 2001. Mechanisms of plant response to gradients and after disturbances. Bot. Rev. 67: 441–452.

Myster, R.W. 2003. Using biomass to model disturbance. Comm. Ecol. 4: 101–105.

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., & S.T.A. Pickett. 1994. A comparison of rate of succession over 18 yr in 10 contrasting old fields. Ecology 75: 387–392.

Myster, R.W., Thomlinson, J.R., & M.C. Larsen. 1997. Predicting landslide vegetation in patches on landscape gradients in Puerto Rico. Land. Ecol. 12: 299–307.

Myster, R.W., & P.G. Santacruz. 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. Revista de la Pontificia Universidad Católica der Ecuador. 76: 111–124.

Nascimento, H.E.M., & W.F. Laurance. 2001. Total above-ground biomass in central Amazonian rainforests: a landscape-scale study. For. Ecol. Manag. 157: 1–11.

Oliveira-Wittmann, A., Wittman, F., Schongart, J., Parolin, P., & M.T.F. Piedade. 2007. Patterns of structure and species diversity along a flooding and successional gradient in Amazonian floodplain forests. Pesquisas Botanica 58: 119–138.

Parolin, P. 2009. Submerged in darkness: adaptations to prolonged submergence by woody species of the Amazonian floodplains. Ann. Bot. 103: 359–376.

Parolin, P, De Simone, O., Haase, K., Waldhoff, D., Rottenberger, S., Kuhn, U., Kesselmeier, J. Schmidt, W., Piedade, M.T.F., & W.J. Junk. 2004a. Central Amazon floodplain forests: tree survival in a pulsing system. Bot. Rev. 70: 357–380.

Pickett, S.T.A., & P.S. White. 1985. The ecology of natural disturbance and patch dynamics. Academic press, Orlando.

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

Prance, G.T. 1979. Notes on the vegetation of Amazonia III. The terminology of Amazonian forest types subject to inundation. Brittonia 31: 26–38.

Puhakka, M.E., Kalliola, R., Rajasita, M., & J. Salo. 1992. River types, site evolution and successional vegetation patterns in Peruvian Amazonia. J. Biogeog. 19: 651–665.

Rice, W.R. 1989. Analyzing tables of statistical tests. Evolution 43: 223–225.

Risser, R.G. 1987. Landscape ecology: state of the art. Pp. 123–145 in Turner, M.G. (ed.). Landscape heterogeneity and disturbance. Ecological studies 64. Springer-Verlag, New York.

Rosenzweig, M.L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge UK.

Ruokolainen, H., & H. Tuomisto. 1998. Vegetacion natural de la zona de Iquitos. Pp. 253–365 in Kalliola, R., & F. Flores (eds.). Geoecologia y desarrollo amazonico: Estudio integrado en la zona de Iquitos, Peru. S. Ann. Univ. Turkuensis, Ser. A II, Turku, Finland.

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

Salo, J.S., & R.J. Kalliola. 1990. River dynamics and natural forest regeneration in the Peruvian Amazon. Pp. 245–256 in Gentry, A.H. (ed.). Four Neotropical rainforests. Yale University Press, New Haven.

Stevens, G.C. 1992. The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. Am. Nat. 140: 893–911.

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

Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, N.J.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., & E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. Science 277: 1300–1302.

Turner, M.G., & V.H. Dale. 1991. Modeling landscape disturbance. Pp. 134–146 in Turner, M.G., & R.H. Gardner (eds). Quantitative methods in landscape ecology: the analysis and interpretation of landscape heterogeneity. Ecological studies 82. Springer-Verlag, New York.

Valencia, R., Balslev, H., Guillermo, P., & C. Mino. 1994. High tree alpha-diversity in Amazonian Ecuador. Biol. Cons. 3: 21–28.

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

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. 1973. Vegetation of the earth and the ecological systems of the geo-biosphere. Springer-Verlag. New York.

Watt, A.S. 1947. Pattern and processes in the plant community. J. Ecol. 35: 1–22.

Whittaker, R.H. 1975. Communities and ecosystems. MacMillian, New York.

Wittmann, F., & W.J. Junk. 2003. Sapling communities in Amazonian white-water forests. J. Biogeog. 30: 1533–1544.

Wittmann, F., Anhuf, D., & W.J. Junk. 2004a. Tree species distribution and community structure of central Amazonian várzea forests by remote-sensing techniques. J. Trop. Ecol. 18: 805–820.

Wittmann, F., Junk, W.J., & M.T.F. Piedade. 2004b. The várzea forests in Amazonia: flooding and the highly dynamic geomorphology interact with natural forest succession. For. Ecol. Manag. 196: 199–212.

Wittmann, F. Schongart, J., Montero, J.C., Motzer, T., Junk, W.J., Piedade, M.T.F., Queiroz, H.L., & M. Worber. 2006. Tree species composition and diversity gradients in white-water forests across the Amazon Basin. J. Biogeog. 33: 1334–1347.