*forests*

MDPI

*Article*

# Effect of Seasonal Rains and Floods on Seedling Recruitment and Compositional Similarity in Two Lowland Tropical Forests

**Brayan S. Polanía [1], Ana M. Aldana [2], Marius Bottin [1], Diana M. Cruz [3], Francisco Castro-Lima [4], Pablo R. Stevenson [3] and Adriana Sanchez [1,*]**

1. Programa de Biología, Facultad de Ciencias Naturales, Universidad del Rosario, Carrera 24 No. 63C-69, Bogotá 111221, Colombia; brayans.polania@urosario.edu.co (B.S.P.); m.bottin_pro@yahoo.com (M.B.)
2. Dirección de Investigación e Innovación, Universidad del Rosario, Bogotá 111711, Colombia; anama.aldana@urosario.edu.co
3. Laboratorio de Ecología de Bosques Tropicales y Primatología, Departamento de Ciencias Biológicas, Universidad de Los Andes, Carrera 1 No. 18A-12, Bogotá 111711, Colombia; dimacruzte@gmail.com (D.M.C.); pstevens@uniandes.edu.co (P.R.S.)
4. Independent Researcher, Bogotá 111711, Colombia; bojonawi@gmail.com

* Correspondence: adriana.sanchez@urosario.edu.co

Received: 24 October 2020; Accepted: 25 November 2020; Published: 2 December 2020

check for updates

**Abstract:** *Research Highlights*: Seasonally flooded and terra firme forests are characteristic ecosystems of the Colombian Orinoco Basin and of great importance in the maintenance of regional biodiversity and ecosystem function. These forests have a unimodal precipitation regime that can cause a temporal effect on the seedling regeneration niche. This could partly explain the high diversity and coexistence of plant species in these forests, as well as the similarity in composition of seedlings and trees. *Background and Objectives*: Seedlings are a key factor in the assembly of plant communities. We evaluated the effect of flooding and rains on the dissimilarity and compositional affinity between trees and seedlings of seasonally flooded and terra firme forests. *Materials and Methods*: the tree community of these forests in San Martín (Meta, Colombia) was characterized and compared with their respective seedling communities before (June) and after (December) rain and flooding (during the rainy season). We evaluated plant species diversity and abundance (Shannon diversity and Pielou eveness index), as well as the compositional dissimilarities of each tree community with their corresponding seedling community sampled at the beginning and end of rains and flooding (Bray–Curtis dissimilarity). We also compared sampling site composition using a NMDS analysis. *Results:* We found that the terra firme forest had higher diversity compared to the flooded forest. Seedling density in the seasonally flooded forest decreased significantly after the flood but not in the terra firme forest at the end of the rainy season. The compositional dissimilarity between trees and seedlings in the seasonally inundated forest also decreased after the flood. However, this pattern was not evident in the terra firme forest. *Conclusions:* These results indicate that seasonal flooding generates a strong ecological filter that affects the realized niche of plants in these forests. Our results can contribute valuable information for the effective development of assisted restoration and conservation programs.

**Keywords:** Bray–Curtis dissimilarity; community assembly; NMDS; regeneration niche; seasonally flooded forest; terra firme forest

## 1. Introduction

Lowland tropical forests are divided into several forest types. These types are characterized by complex ecological dynamics and multiple interactions between biotic and abiotic factors, such as temperature, drought, and flooding [1]. One of these types are the floodplain forests, which are classified according to their seasonality (i.e., season or permanent) and to the river type that floods them (e.g., white-water or várzea, black-water or igapó). The flooding regime and the nature of the river that floods them (nutrient-rich or nutrient-low) impose physiological limitations [1]. Seasonally flooded forests (SFF) perform key ecosystem functions such as water retention, cation exchange, the balance of nutrient cycle, and microclimate; these functions are associated with particular plant communities, which have a narrow regeneration niche [2]. Additionally, organic matter and sediments in the soil largely determine the ecological dynamics of their tree communities [1,3].

Other types of lowland tropical forests, such as terra firme forests (TFF), are also important in maintaining ecological stability and tree diversity in the Amazon and the Colombian Orinoco [4]. Studies have shown the importance of TFF for various primate species in Colombia, as well as the relationship between ecological integrity and the viability of associated primates [5–7]. Likewise, TFF of the Colombian Orinoco (especially in the Department of Meta), are considered key in the transition between the Andes and the Amazon [3,8]. Floristically, SFF are less diverse than TFF due to the ecophysiological challenges associated with floods [3,9,10]. Although nutrients and sediments seem to be important in the plant community assembly of TFF, the possible impact of changes in the seasonality of precipitation is not clearly understood [9–14].

SFF are characterized by higher monodominance and endemism of most plant species compared to TFF, which makes SFF a key system for ecological, conservation, and management studies [15]. Although the ecological and ecosystem importance of SFF is clearly documented, in Colombia, they have been poorly studied compared to Brazil, Venezuela, and Ecuador [16,17]. The few studies carried out in Colombia have focused on diversity analyzes, richness and abundance of tree species, leaving the ecological regeneration of seedlings, their recruitment and role in the diversity, composition, and functionality of the SFF and TFF barely explored (e.g., [6,18,19]).

Seedlings are an important stage in plant development and are key in the assembly of plant communities [6,20–23]. The successful establishment of seedlings recruited to mature individuals reinforces the identity of plant communities, and normally, adults in pristine forests have high compositional similarity or affinity with their seedlings [24–26]. For instance, community assembly in a tropical mixed forest of trees and palms is strongly influenced by successful recruitment and establishment of characteristic seedling species [23,24]. However, in other cases, seedlings are unable to establish, as may be the case with pioneer and long-lived pioneer species below closed canopies [27–29]. Although seedlings are essential for the assembly and affinity of communities, the ecological processes that allow their recruitment and establishment are not entirely clear and seem to be more complex than processes associated with environmental and geographical distances [30,31].

Thus, the regeneration niche indicates that seedling recruitment and establishment is influenced by heterogeneous microenvironmental conditions [30]. In addition, the temporal division in the regeneration niche allows the interspecific coexistence of seedlings and juveniles of highly diverse communities [6,21,32], more than at any other developmental stage [33–35]. In this sense, the temporal differentiation of the regeneration niche can increase the optimization of the available resources based on environmental changes, such as droughts, floods, and fires [21,36]. However, in tropical forests it is not clear when temporal niche differentiation is most effective during plant development [6]; this differentiation can also be altered by ecological factors such as the abundance of pollinators, seed dispersers, and fruiting seasons [5,6,37].

The temporal differentiation of the ecological niche could explain the high richness and coexistence of trees in tropical forests, facilitating the recruitment of seedlings of dominant and rare species, as well as the affinity between adults and seedlings within the community [6,25,32]. Although rare species are often remnants of attacks by natural enemies favored by dominant species [38], this does not fully explain the richness and coexistence patterns in various tropical areas [6,38]. Thus, SFF and TFF are excellent systems to assess the environmental effect of rain seasonality (on the TFF) and the effect of flooding (on the SFF), in the recruitment and seedling composition of each forest.

In this study we seek to: (i) compare the diversity and composition of SFF and TFF seedlings, before and after the rains and flooding; (ii) evaluate the effect of seasonal flooding on the dissimilarities and compositional affinity between the seedling and tree communities of an SFF; (iii) study the effect of the rainy season on seedlings of a TFF. Our first hypothesis is that the effect of seasonal precipitation is more pronounced on seedling species richness and abundance of SFF than TFF, due to the severe physiological limitations imposed by flooding [10]. As a second hypothesis, we propose that there is less compositional disparity and greater compositional affinity between SFF trees and seedlings will not differ the flood because the most abundant seedling species that survive the physiological challenges imposed by the flood [3,10,18,39] are more similar to the adult species [25,26,32,36]. Lastly, with respect to TFF, we hypothesize that there are no significant differences in dissimilarity and affinity between trees and seedlings sampled before and after the rains; although rain may be an important environmental factor for TFF, seedling dynamics in TFF are more strongly associated with different types of frugivores than with seasonal environmental conditions [5,34,37].

## 2. Materials and Methods

### *2.1. Study Area*

Our study was conducted in the Private Natural Reserve Rey Zamuro y Matarredonda, in the municipality of San Martín, Department of Meta, Colombia (Figure 1). The mean temperature in the Reserve is 27.5 °C, ranging from 19 to 35 °C [40–42]; seasonal annual rain is between 2600 and 3000 mm [42]. The dry season begins in early December and ends in late May, and the rainy season spans from June to the end of November [41,42]. The flora of the Reserve corresponds to the vegetation cover of the Serranía de Manacacías [44], which mainly consists of natural and artificial savannas, seasonally flooded forests (SFF), and terra firme forests (TFF). The SFF forest is inundated by Caño Cumaral (a small white-water river) during a five-month period (the rainy season), from June to November. Flood depth during the month of June was between 1 and 1.2 m. These forests have not been exposed to recent (at least in the last 50 years) anthropogenic disturbance (P.R. Stevenson and F. Castro-Lima, pers. obs.).

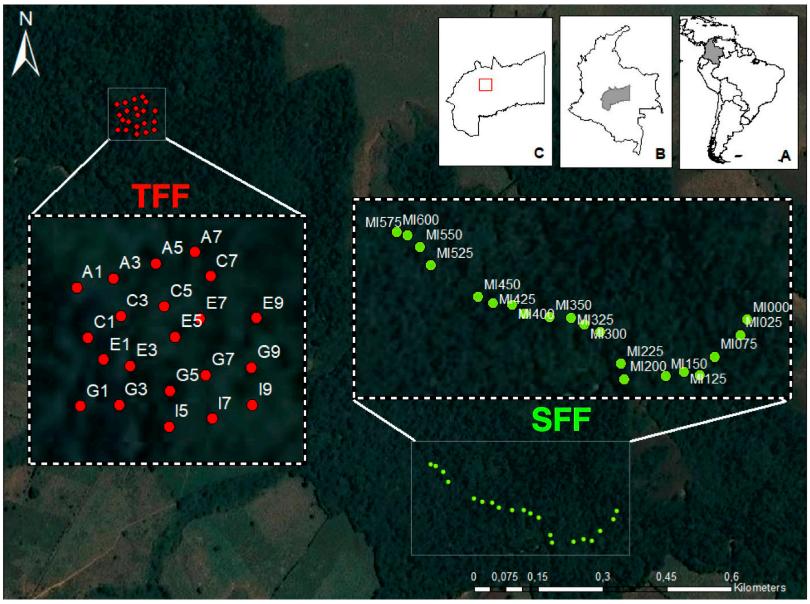


**Figure 1.** Study site and sampled areas within A. Colombia, B. Department of Meta, C. Municipality of San Martín. The dashed lines represent the sampled areas in a terra firme forest (TFF; red; 3°31′52.658″ N & 73°25′18.353″ W) and a seasonally flooded forest (SFF; green; 3°31′22.609″ N & 73°24′50.126″ W). Each area contains 10 × 10 m quadrats where all trees were sampled and labelled, and 2 × 2 m sub-quadrats where the seedling communities were sampled. Each point (21 in TFF and 20 in SFF) corresponds to the centroid of the seedling sub-quadrats and the tree quadrats.

## 2.2. Experimental Design

The sample areas were established in 2018 by Terrasos Habitat Bank (an organization specialized in structuring and operating environmental investments for the conservation of strategic ecosystems in Colombia) and Asociación de Becarios del Casanare, in the TFF and SFF, respectively (Figure 1). Within each of these areas, we used 10 × 10 m quadrats (TFF: n = 21, total area surveyed = 0.21 ha; SFF: n = 20, 0.20 ha), to sample the tree community. To sample the community of seedlings for woody plant species, we established sub-quadrats of 2 × 2 m at the centre of each of the 10 × 10 m tree quadrats, using the same centroid. The quadrats in SFF were established alongside the river (ca. 10–20 m from the river).

We considered trees as all plants with a diameter at breast height (DBH) ≥ 5 cm, and we considered all individuals < 1 m tall and < 1 cm basal diameter as seedlings [4]. Plants between 1–5 cm DBH were therefore not sampled either as trees or seedlings. We conducted sampling and labelling of all trees per quadrat in September 2018, and we sampled seedlings in both forests at the beginning of the rainy and flooding season in June 2019 and at the end, in December 2019.

Tree species were identified by P.R.S., D.M.C., and F.C., while seedling species were identified by B.S.P. with help of D.M.C. and F.C., and field guides from the Field Museum (fieldguides.fieldmuseum.org), filtered by the categories of "Tropical America", "Colombia or Peru or Brazil", "Plants" and "Seedlings" [44–47].

## 2.3. Data Analysis

Tree and seedling composition in the two forest types were characterized and compared in terms of abundance and richness for each quadrat. Families and woody species shared between the tree communities of SFF and TFF were determined, as well as the families and species with the highest abundance within each community. We also calculated the Shannon diversity and Pielou evenness index as descriptors of the tree and seedling community of both forests [48] with the Biodiversity R package version 3.5 [49,50]. It is important to clarify that the TFF is not flooded during the rainy season;

therefore, for this forest we compared the effect of before and after the rainy season, while in the SFF, we compared the effect of before and after flooding. Changes in the seedling species richness before and after the flooding and rains were statistically corroborated with a repeated-measures ANOVA using R [50].

The Bray-Curtis index of dissimilarity [51] was used for the analysis of beta diversity to compare and determine the compositional dissimilarities of each tree community with their corresponding seedling community, sampled at the beginning and end of the flooding and rains. This was done with the vegdist function of the Vegan R package [52] using species richness and abundance. Differences between trees and seedlings by forest type were statistically corroborated with a repeated-measures ANOVA [50].

Finally, a non-metric multidimensional scaling analysis (NMDS) was used to compare the sampling sites according to their composition [52]. The calculations of the ordinations within each community matrix were run with different random starts until a stable solution was found (maximum random starts trymax = 50) in a two-dimensional system (k = 2); this was done with the metaMDS function of the Vegan R package. Once the ordinations were obtained for each community matrix, we compared trees and seedlings by forest type to assess the compositional affinity at the beginning and end of the rainy season and flooding. This affinity was statistically validated with the one-way ANOSIM nonparametric test (999 iterations) in the Past software (V3.25) [53]. In this test, there are two parameters to assess the comparisons: a $p$-value (statistical significance) and an R-value, which calculates the degree to which the ordinations are related to each other. R values between 0.75 and 1 indicate that ordinations are completely different, and values between 0 and 0.25 indicate that there is minimal difference [54]. This is a robust test for comparing and validating the affinity between ecological compositional arrangements [55,56].

## 3. Results

### 3.1. Forest Diversity and Composition

We sampled 748 individuals representing 44 families, 97 genera, and 143 species in the tree forest communities. Of these species, 36% were shared between SFF and TFF, 20% were exclusive to SFF and 44% to TFF. TFF had higher species, genera, and family diversity values than SFF (Table 1). Species richness in the seedling communities increased at the end of the rainy season in TFF ($p$ = 0.04), but not in SFF after flooding ($p$ = 0.38) (Table 1). The number of seedling individuals decreased in SFF ($p$ = 0.03) after the flood, compared with the end of the rainy season in TFF ($p$ = 0.61).

**Table 1.** Number of individuals (N), species richness (S), number (#) of genera and families, Shannon Wiener index (H′) and Pielou evenness index (J′) of trees and seedlings from the two forests analyzed. SFF = seasonally flooded forest; TFF = terra firme forest; Beginning of flooding = beg. flood (June); end of flooding = end flood (December); beginning of rains = beg. rain (June); end of rains = end rain (December).

| Forest Community | N | S | # Genera | # Families | H′ | J′ |
|---|---|---|---|---|---|---|
| Trees SFF | 331 | 80 | 59 | 36 | 3.58 | 0.87 |
| Trees TFF | 417 | 115 | 88 | 42 | 4.16 | 0.92 |
| SFF seedlings, beg. flood | 777 | 85 | 60 | 30 | 3.94 | 0.91 |
| SFF seedlings, end flood | 453 | 89 | 61 | 33 | 4.00 | 0.93 |
| TFF seedlings, beg. rain | 451 | 69 | 54 | 30 | 3.77 | 0.91 |
| TFF seedlings, end rain | 377 | 132 | 95 | 35 | 4.61 | 0.95 |

Regarding the shared species of tree communities, 36% of their abundance corresponded to *Combretum laxum* Jacq. (Combretaceae), *Crepidospermum rhoifolium* (Benth.) Triana & Planch. (Burseraceae), *Syagrus orinocensis* (Spruce) Burret, *Socratea exorrhiza* (Mart.) H. Wendl. and *Attalea insignis* (Mart. ex H. Wendl.) Drude (Arecaceae), *Pseudolmedia laevis* (Ruiz & Pav.) J.F. Macbr. and *Pseudolmedia hirsuta* Baill. (Moraceae). Tree dominance was stronger in SFF than TFF, as the ten most abundant species corresponded to 70% of the abundance in SFF compared with 42% in TFF (Table S1). In terms of composition, the families Arecaceae, Burseraceae, Combretaceae, Fabaceae, Lauraceae, Moraceae and Salicaceae represented 69% of the abundance of individuals in SFF, 59% of TFF, and 63% of the shared species. The palm family, Arecaceae, had the highest percentage of tree abundance in SFF, TFF and shared species, with 33%, 28% and 30%, respectively. This family was followed by Burseraceae (10%, 9% and 9%, respectively) and Moraceae (10%, 6% and 8%, respectively).

At the beginning of the rainy season, we found that TFF seedlings of *Iryanthera laevis* Markgr. and *Tococa guianensis* Aubl. contributed 20% of the relative abundance. At the end of the rains, this 20% relative abundance was contributed by these two along with eight additional species (Table S2). On the other hand, we found that at the beginning of the flood *Bactris brongniartii* Mart., *Miconia elata* (Sw.) DC., *Maquira coriacea* (H. Karst.) C.C. Berg and *Piper obliquum* (Ruiz & Pav.) Pers. contributed 20% of the relative abundance of seedlings in SFF; at the end of the flood, this percentage was contributed by *Bactris brongniartii*, *Lindackeria paludosa* (Benth.) Gilg, *Combretum laxum* and *Oenocarpus mapora* H. Karst. (Table S2). 15.6% of the abundance at the beginning of the flood and 20.1% at the end, corresponded to the palm family Arecaceae (which corresponded to 7.1% and 6.7% of the species richness, respectively.

### 3.2. Compositional Dissimilarity between Trees and Seedlings

The Bray–Curtis dissimilarity analysis (Figure 2) shows a different compositional pattern between trees and seedlings in each forest type. We found that trees of SFF had a higher compositional dissimilarity (ANOVA: $F = 23.03$, $p < 0.0001$, $df = 57$) with seedlings sampled at the beginning, than at the end of the flood (Figure 2A). The compositional dissimilarity between TFF trees and each of its seedling communities sampled at the beginning and end of the rains presented a marginal difference ($F = 0.65$, $p = 0.05$, $df = 60$) (Figure 2B).

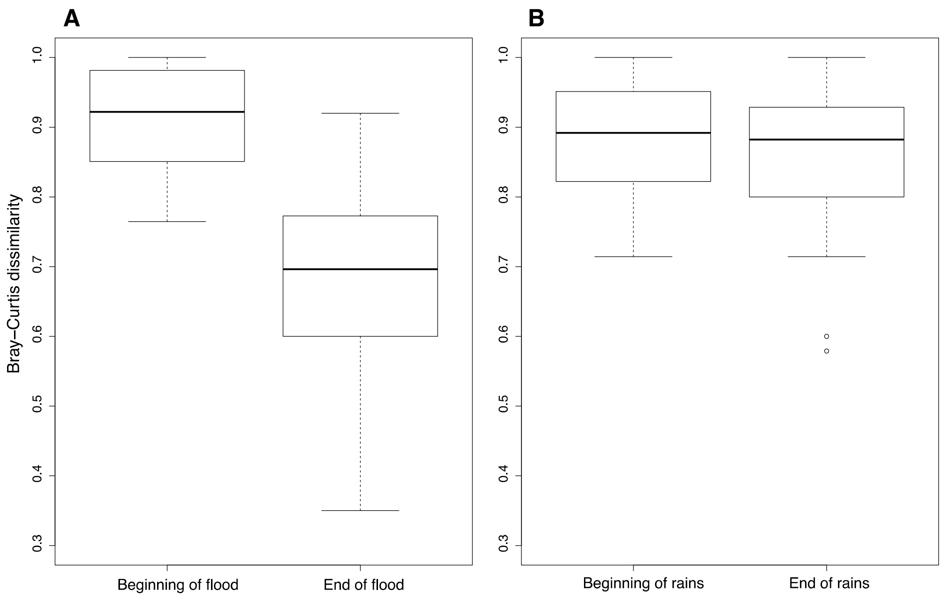


**Figure 2.** Bray-Curtis dissimilarities between tree and seedling compositions over time, for each forest type. (**A**) Dissimilarity between trees and seedlings in SFF at the beginning of the flooding and the end of the flooding. ($F = 23.03$, $P < 0.001$, $df = 57$). (**B**) Dissimilarity between trees and seedlings in TFF at the beginning and end of rains ($F = 0.65$, $P = 0.05$, $df = 60$). SFF = seasonally flooded forest; TFF = terra firme forest correspond to outliers.

### 3.3. Affinity between Trees and Seedlings

The NMDS analysis ordered the composition of the quadrats sampled in the different communities analyzed. Paired comparisons were reliable according to the range of stress values found (0.18–0.21). There was a clear separation between the compositional ordination of trees and seedlings at the beginning of the flood, which was significant ($p < 0.001$, R = 0.45). The comparison between SFF trees and seedling arrangements at the end of the flood (Figure 3B) was also significant ($p < 0.001$), although the R-value was much lower (R = 0.13). Both comparisons between trees and seedlings in TFF were significant ($p < 0.001$; Figure 4), but a higher affinity of trees and seedlings was found at the end of the rainy season (R = 0.35; Figure 4B), than at the beginning (R = 0.40; Figure 4A). The affinity between palms (the most abundant and diverse family) and seedlings was higher after the flood ($p < 0.001$, R = 0.10), compared to the beginning ($p < 0.05$, R = 0.40) (Figure S1). In the TFF, a slightly higher affinity was found before the rains ($p < 0.05$, R = 0.22), than at the end of the season ($p < 0.05$, R = 0.24) (Figure S2).

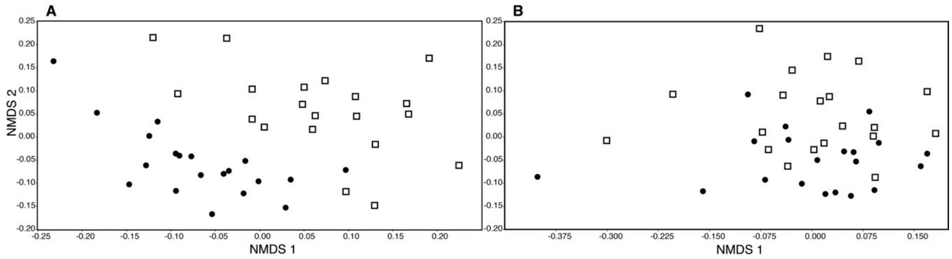


**Figure 3.** Comparison between ordinations (**A**) SFF trees-seedlings at the beginning of the flood (R = 0.45; $p < 0.001$; stress = 0.19); (**B**) SFF trees-seedlings at the end of the flood (R = 0.13; $p < 0.001$; stress = 0.20) by means of Non-Metric Dimensional Scaling (NMDS) analysis. The empty squares (□) correspond to the composition of seedlings per sampling quadrat and the solid circles (•) to trees. SFF = seasonal flooded forest.

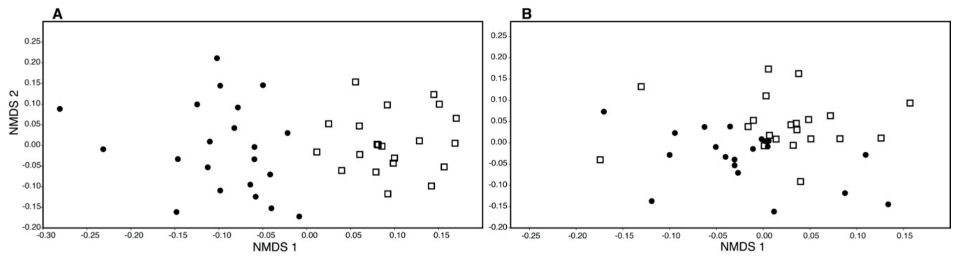


**Figure 4.** Comparison between ordinations (**A**) TFF trees-seedlings at the beginning of the rains (R = 0.40; $p < 0.001$; stress = 0.21), (**B**) TFF trees-seedlings at the end of the rains (R = 0.35; $p < 0.001$; stress = 0.18) by means of Non-Metric Dimensional Scaling (NMDS) analysis. The empty squares (□) correspond to the composition of seedlings per sampling quadrat and the solid circles (•) to trees. TFF = terra firme forest.

## 4. Discussion

In our first hypothesis we proposed that the effect of seasonal rains and floods would be more pronounced on seedling species richness and abundance of seasonally flooded forest (SFF) than terra firme forest (TFF). In fact, the seedling communities of TFF had an increase in species richness at the end of the rainy season, while in SFF there was no significant change. The abundance was lower in TFF after the rainy season. The dissimilarity between seedling and tree compositions in SFF decreased significantly and compositional affinity increased significantly post-flooding, as we had hypothesized (Hypothesis 2). For trees and seedlings in TFF, we found that the rainy season marginally affected the dissimilarities, while the affinity increased slightly after the rainy season; this is contrary to our hypothesis (Hypothesis 3).

### *4.1. Forest Diversity and Composition*

For the tree community we found greater diversity, equitability, and specific richness in TFF compared to SFF (Table 1). Our specific richness result is similar to the specific richness in TFF compared to SFF in the Amazon region of Caquetá [57]. Baez and Garate [14] found a greater number of families, genera and species in TFF compared to SFF in northern Peru, consistent with our results. Regarding $\alpha$ diversity and equitability, they also found the highest Shannon and Pielou evenness index in TFF [14]. The same pattern of diversity was reported for forests in the Colombian Chocó, where greater species diversity was found in TFF compared to flooded forests [58]. This pattern of higher species richness in TFF versus SFF seems to extend to the Neotropics in general [11,12,57]. The higher diversity values and tree richness of TFF compared to SFF may be mainly due to the hostile environmental conditions that characterize the latter [14,37]. Although Gentry (1988) showed that there is a strong positive relationship between periodic precipitation and diversity in lowland tropical forests at large scales, at local scales it appears that periodic flooding exerts more pressure on diversity differences between flooded and terra firme forests [10,17,59].

Several of the tree species with the highest relative abundance for TTF (Table S1) have also been reported as important in La Macarena (Meta), while *Combretum laxum* was the only species of importance in SFF [5]. Stevenson et al. [5] only reported two tree shared species between TTF and SFF, while we report three (*Attalea insignis*, *Crepidospermum rhoifolium* and *Oenocarpus mapora*). This pattern is in agreement with the niche assembly, given the effect that seasonal floods have on the soil and plants [5,10,60,61]. Furthermore, environmental distances have been the main deterministic factors explaining the compositional differences among lowland forests in Colombia compared to neutral factors such as dispersal limitation [3]. The tree composition of SFF was strongly influenced by the high relative abundance of two palm species *Oenocarpus mapora* (21.5%) and *Attalea insignis* (11.2%), while for TFF the contribution of these palms was lower (Table 1). This pattern of higher density of few palm species is characteristic of SFF, as well as their greater richness and lower abundance in TFF [14]. In this sense, TFF and SFF can be considered as mixed forests and these forests are characteristic of La Serranía de Manacacías, which extends throughout San Martín and surrounding municipalities [44].

In the seedling communities, the observed changes in the presence and relative abundance of the ten most important species at the beginning and at the end of the rains and floods (Table S2), may be subjected to environmental changes associated with the temporal differentiation of the species regeneration niche [21,26,30,32,62,63]. Environmental heterogeneity exerts a greater filter in seedling communities of tropical forests than in any subsequent ontogenetic phase [5,10,35]. As a consequence, populations are composed of species with diverse adaptations in order to face the environmental challenges [36]. A fundamental environmental factor that shapes the geographic distribution of forest species and communities, especially in TFF, is drought stress [64]. In the Amazon basin, drought has been associated with large-scale mortality of plants [65–67]. Seedlings with high growth rates during the wet season, as well as seedlings adapted to cope with drought, have been shown to have higher probability of survival [67,68]. Although we did not measure the effect of drought, the species richness and Shannon index in the seedling community was lower at the beginning of the rainy season (June 2019, which marks the end of the dry season). This pattern could be related to the effects of the dry season in seedling establishment. In addition to the environmental filter, the changes observed here may be due to temporal divisions in seedling recruitment, decreasing competition and seed bank availability, which could maintain the coexistence of multiple species and high plant diversity [5,32,69–71].

In the SFF of the Central Amazon, richness and abundance patterns of várzea (white-water flooded forest) seedlings differs depending on the successional age of the forest. In early-age forests, the abundance of seedlings is almost ten times higher than that reported in older floodplain forests [72]. Likewise, it was reported that within the same plot (early or late succession) there are changes in abundance and species richness, mainly associated with different levels of flooding or its duration. The greatest changes within-forest were found in early-age várzea. It has also been found that in this forest type seedling richness increases after flooding but the abundance tends to decrease [73]. In contrast, seedling richness in igapó (black-water flood forest) decreases as flooding increases [73]. Our results are congruent with what has been reported for várzea, since Caño Cumaral is a small white-water river flooding the SFF. An additional factor that can influence richness and abundance patterns in SFF is high anthropic intervention, where species dominance is low, compared to areas with low intervention [74].

### 4.2. Compositional Difference and Affinity between Trees and Seedlings

The Bray–Curtis analysis showed that the dissimilarity between the SFF seedling community and trees decreased at the end of the flood (Figure 2), with respect to the dissimilarity at the beginning of the flood. This indicates that after the seasonal flooding, the seedling community is more similar to the trees of the sampling sites. Likewise, the greater proportion of shared tree and seedling species at the end of the flood corroborates these results (Table S2). The NMDS analysis (Figure 3B), also showed that after the flooding the affinity between seedlings and trees is significantly stronger. Seasonal flooding is considered to have a relevant deterministic effect on plant communities [11,12]. This could be due to the fact that seedlings that physiologically tolerate flooding, oxygen deficiency and differential nutrient availability [3,10,32,57], are more likely to establish their regeneration niche and advance to adult stages, maintaining the compositional identity of the community [23,30]. In the particular case of palms of the Amazon floodplain, they have been shown to accumulate carbohydrates during the flooding [75], to the extent that reserves in the roots are not exhausted even after 300 days of submersion [76]. Given that many palm species have diverse adaptations to flooding (e.g., [77]), this could explain the higher affinity between seedlings and trees after this period (Figure S1). The niche temporal division [34] may also explain the changes in compositional dissimilarity and affinity maintaining the assembly of the plant community throughout the different stages of plant development [25,26].

Regarding the compositional affinity between the tree and seedling communities in TFF, marginal differences were found between the dissimilarities of trees with the seedling community (Figure 2B). The NMDS analysis showed a slight increase in compositional affinity (R = 0.35) just after the rainy season, but this affinity was not very different to what was observed at the beginning of the rains (R = 0.40). Even though TFF is not under the effect of seasonal floods, it can be susceptible to intense rains for a period of almost six months, which can decrease the nutrient availability of the soil [3,10]. However, drought and its duration may be the decisive factor affecting the plant composition of TFF [64–66]. This could explain the higher dissimilarity (Figure 2B) and lower affinity (Figure 4A) at the end of the dry season (May) and beginning of the rainy season (June), since seedlings of the TFF may be more sensitive to the effects of drying [67,68].

## 5. Conclusions

In this study we found that seasonal flooding is an important filter on the temporal regeneration niche of SFF seedlings. Likewise, we found that at the end of the flood, the compositional affinity between seedlings and trees of the SFF increased with respect to the beginning of the flood. This indicates that before the flood many seedlings are established, but at the end of the flood, only seedlings able to withstand the extreme conditions survive. Regarding the TFF, we found that the compositional affinity between seedlings and trees increased slightly at the end of the seasonal rains, possibly reflecting the effects of the dry season on the seedling community. Our results provide valuable information on the role of a regular environmental event (unimodal precipitation and flooding) on the assembly of seedlings and their temporal affinity with trees in two types of tropical forests of great importance for the Colombian Amazon and Orinoco. Additionally, our findings could be useful for restoration and conservation programs aimed at maintaining community identity in these forest types, especially in SFF, which is one of the less studied ecosystems in Colombia and one of the most threatened by anthropogenic factors [3,9].

**Supplementary Materials:** The following are available online at http://www.mdpi.com/1999-4907/11/12/1297/s1: Table S1: Ten most important species according to their relative abundance (%) in the tree community per sampled forest; Table S2: Ten most important seedling species sampled according to their relative abundance (%) per forest. Figure S1: Comparison between ordinations (A) SFF palm trees-seedlings at the beginning of the flood (R = 0.40; $p < 0.05$; stress = 0.12); (B) SFF trees-seedlings at the end of the flood (R = 0.10; $p < 0.001$; stress = 0.17) by means of Non-Metric Dimensional Scaling (NMDS) analysis. The empty squares correspond to the composition of seedlings per sampling quadrat and the solid circles to trees. SFF = seasonal flooded forest. Figure S2: Comparison between ordinations (A) TFF palm trees-seedlings at the beginning of the rains (R = 0.22; $p < 0.05$; stress = 0.18), (B) TFF trees-seedlings at the end of the rains (stress = 0.16; $p < 0.05$; R = 0.24) by means of Non-Metric Dimensional Scaling (NMDS) analysis. The empty squares correspond to the composition of seedlings per sampling quadrat and the solid circles to trees. TFF = terra firme forest.

**Author Contributions:** Conceptualization, B.S.P., A.M.A., and A.S.; methodology, B.S.P., A.M.A., and A.S.; formal analysis, B.S.P. and M.B.; investigation, B.S.P.; data curation, B.S.P., M.B., D.M.C., P.R.S., and F.C.-L.; writing—original draft preparation, B.S.P., A.M.A., M.B., and A.S.; writing—review and editing, A.M.A., P.R.S., and A.S.; visualization, B.S.P. and A.S.; supervision, A.M.A. and A.S.; project administration, B.S.P. and A.S.; funding acquisition, A.M.A. and A.S. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research was funded with funds from the Universidad del Rosario awarded to Adriana Sánchez and the L'Oréal Colombia Prize for Women in Science awarded to Ana M. Aldana (2014).

**Acknowledgments:** We would like to thank Cesar Barrera for supporting our work in the Private Natural Reserve Rey Zamuro y Matarredonda, as well as Andrea Barrera, Alfredo Navas, Laura Ramos, and all the people who contributed to our work in the Habitat Bank. We would also like to thank Terrasos and Asociación de Becarios del Casanare for access to plot information from the Habitat Bank, Liz Tatiana Velasco for her help during fieldwork and plant identification, and Carolina Alvarez for her help with literature references. The authors also wish to thank two anonymous reviewers and the Academic Editor who helped improve the quality of the manuscript and James Richardson for his help with English editing.

**Conflicts of Interest:** The authors declare no conflict of interest.

## References

1. Guariguata, M.R.; Kattán, G. *Ecología y Conservación de Bosques Neotropicales*; Libro Universitario Regional: Cartago, Costa Rica, 2002; pp. 15–98.
2. Ramos-Montaño, C.; García-Cond, M.R. Características Ecosistémicas asociadas a la actividad ganadera en Arauca (Colombia): Desafíos frente al cambio climático. *Orinoquia* **2016**, *1*, 28. [CrossRef]
3. Diaz, P.R.S.; Aldana, A.; Cárdenas, S.; Negret, P.J. Flooding and soil composition determine beta diversity of lowland forests in Northern South America. *Biotropica* **2018**, *50*, 568–577. [CrossRef]
4. Stevenson, P.R.; Suescún, M.; Aldana, A.M.; Cano, A.; Umaña, M.N.; Correa, D.; Casas, L.F.; Villanueva, B. Diversidad arbórea en bosques de40 tierras bajas en Colombia: Efectos del ambiente, las perturbaciones y la geografía. *Hipótesis* **2011**, *12*, 29–35.
5. Stevenson, P.R.; Suescún, M.; Quiñones, M.J. Characterization of forest types at the CIEM, Tinigua Park, Colombia. *Field Stud. Fauna Flora Macarena Colomb.* **2004**, *14*, 1–20.
6. Norden, N. De Porqué la Regeneración Natural es Tan Importante Para la Coexistencia de Especies en los Bosques Tropicales. *Colomb. For.* **2014**, *17*, 247–261. [CrossRef]
7. Norden, N.; Stevenson, P.R. Influence of frugivore activity on the species abundance of seedlings and saplings in a lowland tropical forest in Colombia. *J. Trop. Ecol.* **2015**, *31*, 291–303. [CrossRef]
8. Stevenson, P.R.; Aldana, A.M. Efectos potenciales de la extinción de la atelina y la fragmentación de los bosques sobre la diversidad y composición de las plantas en la cuenca occidental del Orinoco, Colombia. *Rev. Int. Primatol.* **2008**, *29*, 365–377. [CrossRef]
9. Stevenson, P.; Castellanos, M.; Medina, A. Elementos arbóreos de los bosques de un plano inundable en el Parque Natural Tinigua, Colombia. *Caldasia* **1999**, *21*, 38–49.
10. Parolin, P.; De Simone, O.; Haase, K.; Waldhoff, D.; Rottenberger, S.; Kuhn, U.; Kesselmeier, J.; Kleiss, B.; Schmidt, W.; Pledade, M.T.F.; et al. Central Amazonian Floodplain Forests: Tree Adaptations in a Pulsing System. *Bot. Rev.* **2004**, *70*, 357–380. [CrossRef]
11. Gentry, A.H. Patterns of Neotropical Plant Species Diversity. In *Evolutionary Biology*, 2nd ed.; Hecht, M.K., Wallace, B., Prance, G.T., Eds.; Springer: Boston, MA, USA, 1982; Volume 15, pp. 1–84.
12. Gentry, A.H. Changes in Plant Community Diversity and Floristic Composition on Environmental and Geographical Gradients. *Ann. Mo. Bot. Gard.* **1988**, *75*, 1–34. [CrossRef]
13. Wittmann, F.; Householder, E.; Piedade, M.T.F.; De Assis, R.L.; Schöngart, J.; Parolin, P.; Junk, W.J. Habitat specifity, endemism and the neotropical distribution of Amazonian white-water floodplain trees. *Ecography* **2012**, *36*, 690–707. [CrossRef]
14. Baez, S.; Garate, J.S. Estructura y composición florística arbórea en dos tipos de bosque en la Zona de Amortiguamiento, Reserva Nacional de Tambopata. *Q'EUÑA* **2017**, *8*, 39–50.

15. Lopez, O.R.; Kursar, T.A. Interannual variation in rainfall, drought stress and seedling mortality may mediate monodominance in tropical flooded forests. *Oecologia* **2007**, *154*, 35–43. [CrossRef] [PubMed]
16. Berry, P.E. Diversidad y endemismo en los bosques neotropicales de bajura. In *Ecología y Conservación de Bosques Neotropicales*, 1st ed.; Guariguata, M., Kattan, G., Eds.; Libro Universitario Regional: Cartago, Costa Rica, 2002; pp. 83–96.
17. Cano, A.; Stevenson, P.R. Diversidad Y Composición Florística de Tres Tipos de Bosque en la Estación Biológica Caparú, Vaupés. *Colomb. For.* **2008**, *12*, 63–80. [CrossRef]
18. Stevenson, P.R.; Ramírez, M.A.; Casas, L.F.; Díaz, L.F.H. Forestación de bosques en sabanas de la altillanura colombiana: Relevancia de las condiciones ambientales para el establecimiento de plántulas. *Biota Colomb.* **2017**, *18*, 99–109. [CrossRef]
19. Duivenvoorden, J.F.; Svenning, J.-C.; Wright, S.J. Ecology: Beta Diversity in Tropical Forests. *Science* **2002**, *295*, 636–637. [CrossRef]
20. Forget, P.-M. Recruitment Pattern of Vouacapoua americana (Caesalpiniaceae), a Rodent-Dispersed Tree Species in French Guiana. *Biotropica* **1994**, *26*, 408–419. [CrossRef]
21. Schupp, E.W. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. *Am. J. Bot.* **1995**, *82*, 399–409. [CrossRef]
22. Paine, C.E.T.; Norden, N.; Chave, J.; Forget, P.-M.; Fortunel, C.; Dexter, K.G.; Baraloto, C. Phylogenetic density dependence and environmental filtering predict seedling mortality in a tropical forest. *Ecol. Lett.* **2011**, *15*, 34–41. [CrossRef]
23. Norden, N.; Chave, J.; Belbenoit, P.; Caubère, A.; Châtelet, P.; Forget, P.; Riéra, B.; Viers, J.; Thébaud, C. Interspecific variation in seedling responses to seed limitation and habitat conditions for 14 Neotropical woody species. *J. Ecol.* **2009**, *97*, 186–197. [CrossRef]
24. Norden, N.; Chazdon, R.L.; Chao, A.; Jiang, Y.-H.; Vílchez-Alvarado, B. Resilience of tropical rain forests: Tree community reassembly in secondary forests. *Ecol. Lett.* **2009**, *12*, 385–394. [CrossRef] [PubMed]
25. Chao, A.; Chazdon, R.L.; Colwell, R.K.; Shen, T.-J. A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecol. Lett.* **2004**, *8*, 148–159. [CrossRef]
26. Chazdon, R.L. Chance and determinism in tropical forest succession. In *Tropical Forest Community Ecology*, 1st ed.; Carson, W.P., Schnitzer, S.A., Eds.; Wiley Blackwell: Hoboken, NJ, USA, 2008; pp. 384–408.
27. Hubbell, S.P.; Foster, R.B. Diversity of canopy trees in a neotropical forest and implications for conservation. In *Tropical Rain Forest: Ecology and Management*, 1st ed.; Sutton, S.L., Whitmore, T.C., Chadwick, A.C., Eds.; Blackwell Science Inc: Oxfordshire, England, 1983; Volume 36, pp. 25–41.
28. Hubbell, S.P.; Foster, R.B. The spatial context of regeneration in a neotropical forest. In *Colonization, Succession and Stability*, 1st ed.; Gray, A.J., Crawley, M.J., Edwards, P.J., Eds.; Blackwell Science Inc: Oxfordshire, UK, 1987; Volume 26, pp. 395–412.
29. Castellanos, M.C.; Stevenson, P.R. Phenology, seed dispersal and difficulties in natural recruitment of the canopy tree Pachira quinata (Malvaceae). *Rev. Biol. Trop.* **2011**, *59*, 921–933. [CrossRef] [PubMed]
30. Grubb, P.J. The Maintenance of Species-Richness in Plant Communities: The Importance of the Regeneration Niche. *Biol. Rev.* **1977**, *52*, 107–145. [CrossRef]
31. Coomes, D.A.; Grubb, P.J. Impacts of root competition in forests and woodlands: A theoretical framework and review of experiments. *Ecol. Monogr.* **2000**, *70*, 171–207. [CrossRef]
32. Chesson, P. General Theory of Competitive Coexistence in Spatially-Varying Environments. *Theor. Popul. Biol.* **2000**, *58*, 211–237. [CrossRef]
33. Webb, C.O.; Peart, D.R. Habitat associations of trees and seedlings in a Bornean rain forest. *J. Ecol.* **2000**, *88*, 464–478. [CrossRef]
34. Norden, N.; Chave, J.; Caubère, A.; Châtelet, P.; Ferroni, N.; Forget, P.-M.; Thébaud, C. Is temporal variation of seedling communities determined by environment or by seed arrival? A test in a neotropical forest. *J. Ecol.* **2007**, *95*, 507–516. [CrossRef]
35. Metz, M.R.; Comita, L.S.; Chen, Y.-Y.; Norden, N.; Condit, R.; Hubbell, S.P.; Sun, I.-F.; Noor, N.S.B.M.; Wright, S.J. Temporal and spatial variability in seedling dynamics: A cross-site comparison in four lowland tropical forests. *J. Trop. Ecol.* **2008**, *24*, 9–18. [CrossRef]
36. Chesson, P.L.; Warner, R.R. Environmental Variability Promotes Coexistence in Lottery Competitive Systems. *Am. Nat.* **1981**, *117*, 923–943. [CrossRef]

37. Norden, N.; Chave, J.; Belbenoit, P.; Caubère, A.; Châtelet, P.; Forget, P.-M.; Thébaud, C. Mast Fruiting is a Frequent Strategy in Woody Species of Eastern South America. *PLoS ONE* **2007**, *2*, e1079. [CrossRef] [PubMed]
38. Connell, J.H.; Green, P.T. Seedling dynamics over thirty-two years in a tropical rain forest tree. *Ecology* **2000**, *81*, 568–584. [CrossRef]
39. Soong, J.L.; Janssens, I.A.; Grau, O.; Margalef, O.; Stahl, C.; Van Langenhove, L.; Urbina, I.; Chave, J.; Dourdain, A.; Ferry, B.; et al. Soil properties explain tree growth and mortality, but not biomass, across phosphorus-depleted tropical forests. *Sci. Rep.* **2020**, *10*, 1–13. [CrossRef]
40. Stevenson, P.R. The Abundance of Large Ateline Monkeys is Positively Associated with the Diversity of Plants Regenerating in Neotropical Forests. *Biotropica* **2011**, *43*, 512–519. [CrossRef]
41. Aldana, A.; Stevenson, P.R. Forest fragments of the Andean piedmont as carbon sinks. *Trop. Conserv. Sci.* **2016**, *9*. [CrossRef]
42. Minorta, V.; Rangel, J.O.; Castro, F.; Aymar, G. La vegetación de la Serranía de Manacacías (Meta) Orinoquía colombiana. In *Diversidad Biótica*, 1st ed.; Rangel, J.O., Ed.; Colombia Diversidad Biótica XVII: Bogotá, Colombia, 2019; Volume 8, pp. 155–234.
43. Pronósticos y Alertas: Indicadores Climatológicos. Available online: http://www.pronosticosyalertas.gov.co/mapas-graficos-tiempo-clima/indicadores-climatologicos (accessed on 7 September 2019).
44. Árboles y Arbustos de la Parcela Permanente de 25 ha- Reserva Natural La Planada, Nariño, Colombia. Available online: https://fieldguides.fieldmuseum.org/es/gu%C3%ADas/gu%C3%ADa/183 (accessed on 19 October 2019).
45. Nariño-Hojas de la Reserva Ñambí: Guía para Principiantes. Available online: https://fieldguides.fieldmuseum.org/es/guías/guía/11 (accessed on 19 October 2019).
46. Plántulas de Cocha Cashu-Madre de Dios, Perú. Available online: https://fieldguides.fieldmuseum.org/es/guías/guía/243 (accessed on 19 October 2019).
47. Plantas Leñosas de Madre de Dios. Available online: https://fieldguides.fieldmuseum.org/guides/guide/1159 (accessed on 19 October 2019).
48. Carmona, V.; Carmona, T. La diversidad de los análisis de diversidad. *Bioma* **2013**, *14*, 20–28.
49. Kindt, R.; Coe, R. *Tree Diversity Analysis: A Manual and Software for Common Statistical Methods for Ecological and Biodiversity Studies*, 1st ed.; World Agroforestry Centre: Nairobi, Kenia, 2005; pp. 19–150.
50. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria; Available online: http://www.R-project.org/ (accessed on 15 July 2020).
51. Gómez, T.G.D.; González, B.N.H.; Rodríguez, H.G.; Silva, I.C.; Rodríguez, E.A.; Alvarado, M.D.S. Estructura y composición de la vegetación en cuatro sitios de la Sierra Madre Occidental. *Rev. Mex. Cienc. For.* **2018**, *9*, 9–34. [CrossRef]
52. Oksanen, J.; Guillaume Blanchert, F.; Kindt, R.; Legendre, P.; O'Hara, B.; Simpson, G.L.; Solymos, P.; Stevens, M.H.H.; Wagner, H. Vegan: Community Ecology Package. R Packag. Version. Available online: http://CRAN.R-project.org/package=vegan (accessed on 1 September 2019).
53. Maza-Villalobos, S.; Macedo-Santana, F.; Rodríguez-Velázquez, J.; Oyama, K.; Martinez-Ramos, M. Variación de la estructura y composición de comunidades de árboles y arbustos entre tipos de vegetación en la Cuenca de Cuitzeo, Michoacán. *Bot. Sci.* **2014**, *92*, 243–258. [CrossRef]
54. Clarke, K.R. Non-parametric multivariate analyses of changes in community structure. *Austral Ecol.* **1993**, *18*, 117–143. [CrossRef]
55. Lemos, L.G.; Castaño, N.C.; Nivia, G.D. Composición y Estructura del Ensamblaje de Crustáceos Brachyura de la Plataforma Continental de la Guajira Colombiana y su Relación con la Profundidad y las Características del Sedimento. *Bull. Mar. Coast. Res.* **2016**, *39*, 359–379. [CrossRef]
56. Barrios, E.; Trujillo, C.; Sánchez, T. Macroinfauna asociada a fondos blandos en el costado sur de la bahía de Taganga, Caribe colombiano durante la época de lluvias. *Intropica* **2011**, *6*, 71–88.
57. Londoño, A.C.; Alvarez, E. Composición florística de dos bosques (tierra firme y várzea) en la región de Araracuara, Amazonia Colombiana. *Caldasia* **1997**, *19*, 431–463.
58. Herrera, L.F.; Flórez, D.M.; Segura, B.; Mena, R.A.; Alvarez, E. Diversidad y estructura de bosques contrastantes en la región del Chocó-Darién, Colombia. *Rev. Investig. Agrar. Ambient.* **2018**, *9*, 17–28.
59. Jones, M.M.; Tuomisto, H.; Clark, D.B.; Olivas, P. Effects of mesoscale environmental heterogeneity and dispersal limitation on floristic variation in rain forest ferns. *J. Ecol.* **2006**, *94*, 181–195. [CrossRef]

60. Trujillo, W.C.; Henao, M.M. Plant species richness and turnover in the orinoco slope of the andes in Colombia. *Colomb. For.* **2018**, *21*, 18–33. [CrossRef]
61. Correa, D.F.; Stevenson, P.R. Estructura y diversidad de bosques de galería en una sabana estacional de los Llanos Orientales colombianos (Reserva Tomo Grande, Vichada). *Orinoquia* **2010**, *14*, 31–48.
62. Fenner, M. *Seeds—The Ecology of Regeneration in Plant Communities*, 2nd ed.; CABI: New York, NY, USA, 2000; pp. 76–134.
63. Forget, P.M.; Lambert, J.E.; Hulme, P.E.; Vander Wall, S.B. *Seed Fate: Predation, Dispersal, and Seedling Establishment*, 1st ed.; CABI Publishing: Panamá, Panamá, 2005; pp. 24–78.
64. Choat, B.; Jansen, S.; Brodribb, T.J.; Cochard, H.; Delzon, S.; Bhaskar, R.; Bucci, S.J.; Feild, T.S.; Gleason, S.M.; Hacke, U.G.; et al. Global convergence in the vulnerability of forests to drought. *Nat. Cell Biol.* **2012**, *491*, 752–755. [CrossRef]
65. Nepstad, D.C.; Tohver, I.M.; Ray, D.; Moutinho, P.; Cardinot, G. Mortality of Large Trees and Lianas Following Experimental Drought in an Amazon Forest. *Ecology* **2007**, *88*, 2259–2269. [CrossRef]
66. Feldpausch, T.R.; Phillips, O.L.; Brienen, R.J.W.; Gloor, E.; Lloyd, J.; Lopez-Gonzalez, G.; Monteagudo-Mendoza, A.; Malhi, Y.; Alarcón, A.; Álvarez Dávila, E.; et al. Amazon forest response to repeated droughts. *Glob. Biogeochem. Cycles* **2016**, *30*, 964–982. [CrossRef]
67. Marimon, B.S.; Oliveira-Santos, C.; Marimon-Junior, B.H.; Elias, F.; De Oliveira, E.A.; Morandi, P.S.; Prestes, N.C.C.D.S.; Mariano, L.H.; Pereira, O.R.; Feldpausch, T.R.; et al. Drought generates large, long-term changes in tree and liana regeneration in a monodominant Amazon forest. *Plant Ecol.* **2020**, *221*, 733–747. [CrossRef]
68. Poorter, L.; Hayashida-Oliver, Y. Effects of seasonal drought on gap and understorey seedlings in a Bolivian moist forest. *J. Trop. Ecol.* **2000**, *16*, 481–498. [CrossRef]
69. Ibanez, T.; Hart, P.J. Spatial patterns of tree recruitment in a montane Hawaiian wet forest after cattle removal and pig population control. *Appl. Veg. Sci.* **2020**, *23*, 197–209. [CrossRef]
70. Muledi, J.; Bauman, D.; Jacobs, A.; Meerts, P.; Shutcha, M.; Drouet, T. Tree growth, recruitment, and survival in a tropical dry woodland: The importance of soil and functional identity of the neighbourhood. *For. Ecol. Manag.* **2020**, *460*, 117894. [CrossRef]
71. Bautista, S. Patrones de Productividad de Frutos y Dispersión de Semillas en Diferentes Bosques de Colombia, y su Relación con la Biomasa de Primates. Masters' Thesis, Universidad de los Andes, Bogotá, Colombia, 2019.
72. Shoengart, J.; de Oliveira-Wittmann, A.; Wittmann, F.; Parolin, P.; Piedade, M.T.F. Patterns of structure and seedling diversity along a flooding and sucessional gradient in Amazonian floodplain forests. *Pesqui. Bot.* **2007**, *58*, 119–138.
73. Kotowski, W.; Beauchard, O.; Opdekamp, W.; Meire, P.; Van Diggelen, R. Waterlogging and canopy interact to control species recruitment in floodplains. *Funct. Ecol.* **2010**, *24*, 918–926. [CrossRef]
74. Da Rocha, M.; Feitosa, Y.O.; Wittmann, F.; Piedade, M.T.F.; Resende, A.F.; De Assis, R.L. River damming affects seedling communities of a floodplain forest in the Central Amazon. *Acta Bot. Bras.* **2020**, *34*, 192–203. [CrossRef]
75. Scarano, F.R.; Cattânio, J.H.; Crawford, R.M.M. Root carbohydrate storage in young saplings of an Amazonian tidal várzea forest before the onset of the wet season. *Acta Bot. Bras.* **1994**, *8*, 129–139. [CrossRef]
76. Schluter, U.B.; Furch, B.; Joly, C.A. Physiological and Anatomical Adaptations by Young Astrocaryum jauari Mart. (Arecaceae) in Periodically Inundated Biotopes of Central Amazonia. *Biotropica* **1993**, *25*, 384–396. [CrossRef]
77. Parolin, P. Submerged in darkness: Adaptations to prolonged submergence by woody species of the Amazonian floodplains. *Ann. Bot.* **2008**, *103*, 359–376. [CrossRef] [PubMed]