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Effect of seasonal rains and floods in seedling recruitment and compositional affinity in two lowland tropical forests

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Abstract. Introduction: Seasonally flooded and terra firme forests are characteristic ecosystems of the colombian Orinoquia and of great importance in the maintenance of regional biodiversity and ecosystem functions. These forests have a unimodal precipitation regime that can cause a temporal division effect on the seedling regeneration niche. This could explain the high diversity and coexistence of plant species in these forests, as well as the compositional affinity between adults and seedlings, reinforcing the assembly of the community in mature forests. **Objective:** To evaluate the effect of flooding and rains on the dissimilarity and compositional affinity between adults and seedlings of a seasonally flooded and terra firme forests. **Methods:** We characterized the adult community of these forests in San Martín (Meta, Colombia) and compared it with their respective seedling communities before and after the flooding and rainy season, using Bray-Curtis dissimilarity and NMDS analysis. **Results:** We found that after flooding, compositional dissimilarity of the seasonally inundated forest decreased significantly between adults and seedlings, while their affinity increased significantly; however, this pattern was not as conclusive in the terra firme forest. **Conclusions:** These results indicate that seasonal flooding can cause temporary division in the seedling niche. However, it is important to consider the role of edaphic variables, which can be affected by floods and rains. Our results can contribute valuable information for the effective development of assisted restoration and conservation programs.

Key words: Bray-Curtis dissimilarity; community assembly; NMDS; regeneration niche; seasonal flood forest; terra firme forest

Total words:

Lowland tropical forests are divided into several forest types with complex ecological dynamics and multiple interactions between biotic and abiotic factors, such as temperatures, droughts, rains and floods (Guariguata & Kattán, 2002). Thus, flooded forests are ecosystems with ecological and physiological dynamics of great interest within tropical forests (Guariguata & Kattán, 2002), and can be classified according to their seasonality (as seasonal or permanent), if they are flooded by white or black waters (e.g., várzea and igapó, respectively), and flooded by rains or by rivers (Stevenson, Castellanos & Medina; 1999). Seasonal flood forests (SFF) perform key ecosystem functions such as water retention, cation exchange, balance of the nutrient cycle and microclimates; these functions maintain the potential for natural regeneration within the ecosystem (Ramos & García, 2016) and allow them to host a diverse fauna (Junk & Furch, 1993; Victorino, 2011). Additionally, organic matter and sediments in the soil largely determine the ecological dynamics of the tree communities in SFF (Guariguata & Kattán, 2002; Stevenson, Aldana, Cárdenas & Negret, 2018).

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 (Stevenson, Suescún, Aldana, Cano, Umaña et al., 2011). Extensive studies have shown the importance of TFF for various primate species in different departments of Colombia, as well as the relationship between ecological integrity and the viability of associated primates (Stevenson, Suescún & Quiñones, 2004; Norden, 2014; Norden & Stevenson, 2015). Likewise, TFF of the Colombian Orinoco are key in the transitional forest gradient between the Andes and the Colombian Amazon (Stevenson & Aldana, 2008; Stevenson et al., 2018). Regarding floristic diversity, SFF are less diverse than TFF due to the ecophysiological challenges associated with floods (Stevenson et al., 1999, 2018; Parolin, De Simone, Haase & Waldhoff, 2004). Although nutrients and sediments seem to be important in the plant community assembly of TFF, the possible impact of rains is not clearly understood (Gentry, 1982, 1988; Stevenson et al., 1999; Parolin et al., 2004; Wittmann, Householder, Piedade, de Assis, Schöngart, et al., 2013; Baez & Garate, 2017).

Therefore, 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 (Lopez & Kursar, 2007). Although the ecological and ecosystem importance of SFF is clearly documented, in Colombia they have been poorly studied compared to Brazil, Venezuela and Ecuador (Berry, 2002; Cano & Stevenson, 2009). The few studies carried out in Colombia have focused on diversity analyzes, richness and abundance of adult 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 (Norden, 2014; Stevenson, Ramírez, Casas & Henao, 2017).

Seedlings are a very relevant stage in the development of plants and a key factor in the assembly of plant communities (Forget, 1994; Schupp, 1995; Paine, Norden, Chave, Forget, Fortunel et al., 2011; Norden, 2014). Community assembly in tropical mixed forest of trees and palms is strongly influenced by successful recruitment and establishment of characteristic species seedlings (Norden, Chave, Belbenoit, Caubère, Châtele et al., 2008; Norden, Chazdon, Chao, Jiang & Vílchez, 2009). Additionally, the successful establishment of seedlings recruited to mature individuals reinforces the affinity of plant communities (Chao, Chazdon, Colwell & Shen, 2004; Chazdon, 2008). Likewise, adults in pristine forests have high compositional similarity or affinity with their seedlings (Chao et al., 2004; Chazdon, 2008; Norden et al., 2009). 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, as in the case of adult communities (Grubb, 1977; Coomes & Grubb, 2000).

Thus, the regeneration niche indicates that seedling recruitment and establishment is influenced by heterogeneous microenvironmental conditions (Grubb, 1977). In addition, the temporal division in the regeneration niche allows the interspecific coexistence of seedlings and juveniles of highly diverse communities (Schupp, 1995; Chesson, 2000; Norden, 2014), more than at any other developmental stage (Webb & Peart, 2000; Norden, Chave, Caubère, Châtelet, Ferroni et al., 2007; Metz, Comita, Chen, Norden, Condit et al., 2008). Stevenson et al. (2017) found that the mortality of almost 50% of dominant seedlings of a TFF in Vichada (Colombia) was associated with dry soil and strong exposure to the sun after seasonal rains, while non-dominant seedlings were established with greater success. In this sense, the temporal differentiation of the regeneration niche can increase the optimization of the available resources based on regular seasonality such as droughts, floods and fires (Chesson & Warner, 1981; Schupp, 1995). However, in tropical forests

it is not clear at what moment of the natural regeneration niche, temporal differentiation is most effective (Norden, 2014); this differentiation can be altered by ecological factors such as the abundance of pollinators, seed dispersers and fruiting seasons (Stevenson, 2004; Norden, Chave, Belbenoit, Caubère, Châtelet et al., 2007a; Norden, 2014).

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 (Chao et al., 2004; Chesson, 2000; Norden, 2014). Rare species are often remnants of attacks by natural enemies favored by dominant species (Connell & Green, 2000), however this does not fully explain the richness and coexistence patterns in various tropical areas (Norden, 2014). Thus, SFF and TFF are an excellent system to assess the effect of seasonality of rains on the TFF and the effect of flooding on the SFF, in the recruitment of seedlings. Furthermore, it is possible to determine the environmental filters associated with microclimates (Grubb, 1977) before and after rains and floods and their effect on seedling composition in SFF and TFF. In this way, the temporal differentiation in the recruitment niche proposed by Chesson & Warner (1981) and modeled by Chesson (2000) could be evaluated in ecosystems.

In this study we therefore seek to: 1. evaluate the effect of seasonal flooding on the dissimilarities and compositional affinity between the seedling and adult communities of an SFF; 2. study the effect of the rainy season on seedlings of a TFF and 3. compare the results obtained for the SFF and the TFF, before and after the rains/flooding. In SFF we expect to find less compositional disparity and greater compositional affinity between adults and seedlings after the flood, because the most abundant seedling species that survive the physiological challenges imposed by the flood (Parolin et al., 2004; Stevenson et al., 2017, 2018; Soong, Janssens, Grau, Margalef, Stahl et al., 2020) should be more similar to adult species (Chesson & Warner, 1981; Chesson, 2000; Chao et al., 2004; Chazdon, 2008). In TFF we expect no significant differences in the dissimilarity and affinity between adults and seedlings sampled before and after the rains; although rain is an important environmental factor for TFF, it may not impose severe limitations such as the ones experienced by the SFF (Parolin et al., 2004). Furthermore, seedling dynamics in TFF are more strongly associated with the seed bank and different types of frugivores than with temporary environmental conditions (Stevenson et al., 2004; Norden et al., 2007, 2007a).

MATERIALS AND METHODS

Study site: Our study was conducted in the Private Natural Reserve Rey Zamuro y Matarredonda, 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 (Stevenson, 2011; Aldana & Stevenson, 2016); seasonal annual rain is usually between 600 and 3000 mm (Aldana & Stevenson, 2016). The dry season begins in early December and ends in late May, and the rainy season from early June to the end of November (IDEAM, 2011; Stevenson, 2011). The flora of the Reserve corresponds to the main vegetation cover of the Serranía de Manacacías (Minorta, Rangel, Castro & Aymar, 2019), which mainly consists of natural and artificial savannas, seasonal flood forests (SFF) and terra firme forests (TFF).
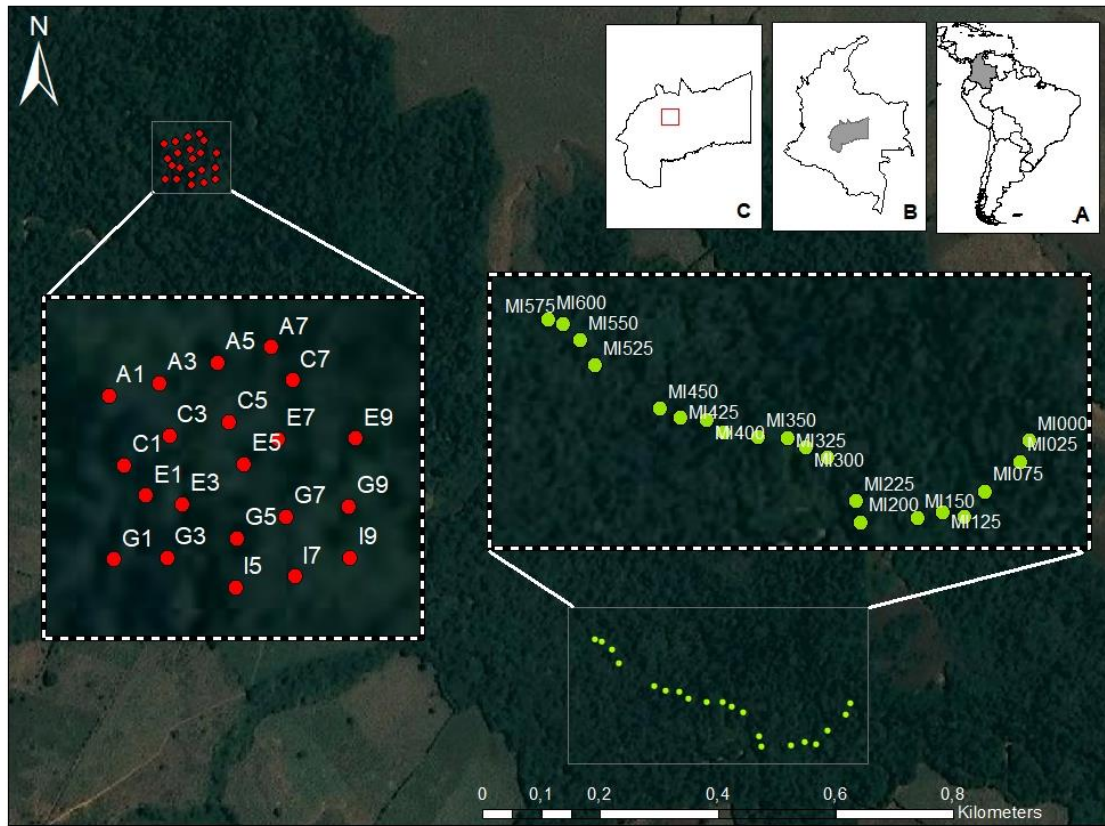
Fig. 1. Study site and sampled plots; A. Colombia, B. Department of Meta, C. Municipality of San Martín. Sampled plots in a TFF (red; 3°31'52.658" N & 73°25'18.353" W) and a SFF (green; 3°31'22.609" N & 73°24'50.126" W).

Experimental design: two plots 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), in the SFF and TFF (Fig. 1). These plots correspond to 1 ha in each forest type. The community of adult woody species (DBH > 5 cm) of SFF and TFF (ADSFF and ADTFF, respectively) were sampled in 10 x 10 m quadrats within each plot and these quadrats were established around the plot center, shown in Fig. 1. ADSFF and ADTFF were sampled in September 2018 and all trees were labeled with DBH > 5 cm.

To sample the community of seedlings of woody species, sub-quadrats of 2 x 2 m were established within the adult quadrats; all individuals with a maximum height of 1 m and a diameter of 1 cm at the base of the soil were considered seedlings (Stevenson et al., 2017). These seedlings were sampled in both forests at the beginning of the rainy and flooding season in June and at the end, in December 2019. In total, 20 quadrats were sampled in the SFF and 21 in the TFF (Fig. 1). We did not sample the 25 quadrats due to inaccessibility (i.e. downed trees) and missing information (i.e. four plot labels were missing in the SFF and five in the TFF). Therefore, our analyzes were performed for the quadrats where we had paired information for adults and seedlings. The quadrats in SFF were established alongside the river. It is important to mention that the TFF are 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.

Adult species were identified by experts from the Terrasos Habitat Bank, while seedling species were identified based on the "Catálogo de pastos y plántulas del Banco de Hábitat Terrasos-Meta" and field guides from the Field Museum (fieldguides.fieldmuseum.org), filtered in the categories of "Tropical America", "Colombia or Peru or Brazil", "Plants" and "Seedlings" (Betancur & Fernández, 2001; Gil & Vallejo, 2005; Álvarez & Paine, 2015; Baez, Garate, Dueñas & Zevallos, 2019).

Data analysis: adults 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 ADSFF and ADTFF communities were determined, as well as the families and species with the highest abundance within each community. We also calculated the Shannon diversity and the J de Pielou index as descriptors of the adult and seedling community of both forests (Carmona & Carmona, 2013) with the Biodiversity R package (Kindt & Coe, 2005), version 3.5 (R Core Team, 2019). Changes in the seedling species richness before and after the flooding and rains were statistically corroborated with a repeated measures ANOVA using R (R Core Team, 2019).

The Bray-Curtis multivariate analysis of dissimilarity (Domínguez, Hernández, González, Cantú, Alanís et al., 2018) was used for the analysis of beta diversity to compare and determine the compositional dissimilarities of each adult 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 (Oksanen, Blanchet, Friendly, Kindt, Legendre et al., 2019) using species richness and abundance. Differences between adults and seedlings by forest type were statistically corroborated with a repeated measures ANOVA.

Finally, a non-metric multidimensional scaling analysis (NMDS) was used to compare the sampling sites according to their composition; we used the stress values as reported in the literature (Maza, Macedo, Rodríguez, Oyama & Martínez, 2014). 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 adults 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) (Clarke, 1993). 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 (Gómez, Castaño & Livia, 2010). This is a robust test for comparing and validating the affinity between ecological compositional arrangements (Barrios, Trujillo & Sánchez, 2011).

RESULTS

Forest diversity and composition: 748 individuals represented in 44 families, 97 genera and 143 species were sampled in the adult forest communities. Of these species, 36 % were shared between SFF and TFF, 20 % were exclusive to SFF and 44 % to TFF. Likewise, TFF had higher species, genera and family diversity and richness (Table 1). In the seedling communities, species richness increased significantly (P = 0.04) at the end of the rainy season in TFF, while in SFF it increased (albeit not significantly) after flooding (P = 0.38) (Table 1). The number of seedling individuals

decreased significantly in SFF (P = 0.03) after the flood, in contrast to the non-significant decrease at the end of the rainy season in TFF (P = 0.61).

Regarding the shared species of adult communities, 36% of their abundance corresponded to *Combretum laxum* (Combretaceae), *Crepidospermum rhoifolium* (Burseraceae), *Syagrus orinocensis, Socratea exorrhiza* and *Attalea insignis* (Arecaceae), *Pseudolmedia laevis* and *Pseudolmedia obliqua* (Moraceae). The ten most abundant species corresponded to 70 % of the abundance in ADSFF and 42 % in ADTFF (Table S1). The families Arecaceae, Burseraceae, Combretaceae, Fabaceae, Lauraceae, Moraceae and Salicaceae represented 69 % of the abundance of individuals in ADSFF, 59 % of ADTFF, and 63 % of the shared species. Arecaceae was the family with the highest percentage of abundance in ADSFF, ADTFF 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* and *Tococa guianensis* contributed 20 % of the relative abundance. At the end of the rains, this 20 % relative abundance was contributed by these two and eight additional species (Table S2). On the other hand, we found that at the beginning of the flood *Bactris brongniartii, Miconia elata, Maquira coriacea* and *Piper obliquum* contributed 20 % of the relative abundance of seedlings in SFF, while at the end of the flood, this percentage was contributed by *Bactris brongniartii, Lindackeria paludosa, Combretum laxum* and *Oenocarpus minor* (Table S2).

TABLE 1

Number of individuals (N), species richness (S), number (#) of genera and families, Shannon Wiener index (H ') and Pielou equitability index (J') of adult tree and seedlings from the two forests analyzed. SFF = seasonal flooded forest; TFF = terra firme forest; ADSFF = adults of seasonal flooded forest; ADTFF = adults of 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'
ADSFF	331	80	59	36	3.58	0.87
ADTFF	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

Compositional dissimilarity between adults and seedlings: The Bray-Curtis dissimilarity analysis (Fig. 2) shows a different compositional pattern between comparisons of adults and seedlings in each forest type. We found that ADSFF had a greater and significantly different (P < 0.0001) compositional dissimilarity with seedlings sampled at the beginning than at the end of the flood (Fig. 2A). The compositional dissimilarity between ADTFF and each of its seedling

communities sampled at the beginning and end of the rains presented a marginally significant difference (P = 0.05) (Fig. 2B).
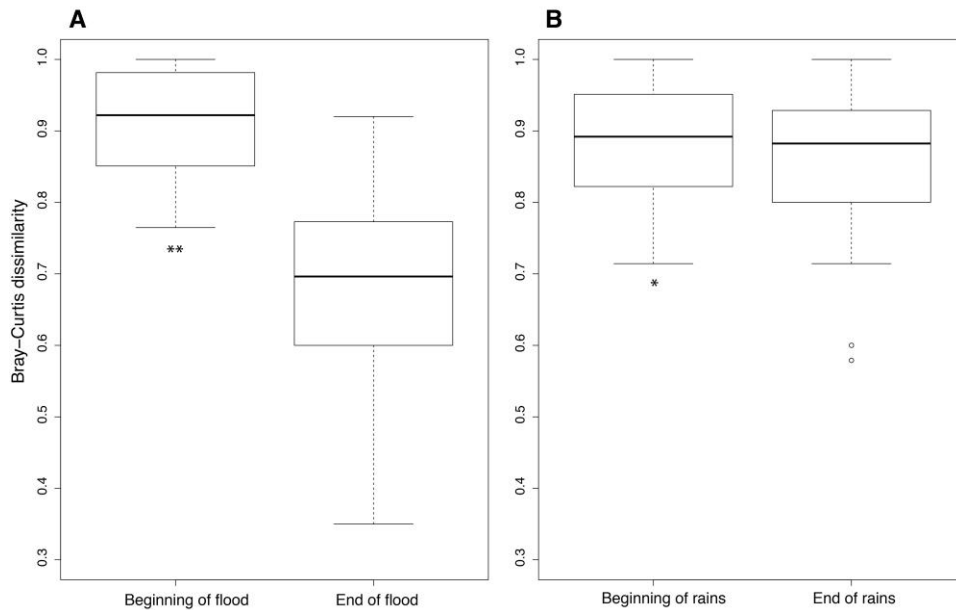

Fig. 2. Bray-Curtis dissimilarities between adult and seedling compositions over time, for each forest type. A) Dissimilarity between ADSFF and SFF seedlings at the beginning of the flooding and the end of the flooding. B) Dissimilarity between ADTFF and TFF seedlings at the beginning and end of rains. ** (P < 0.0001), * (P = 0.05).

Affinity between adults 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). Figure 3A shows a clear separation between the compositional ordination of ADBIE and seedlings at the beginning of the flood in SFF, which was significant (P < 0.001, R = 0.45). The comparison between ADSFF and seedling arrangements at the end of the flood (Fig. 3B) was also significant (P < 0.001), although the R value was much lower (R = 0.13) indicating greater compositional affinity between the ordinations. Both comparisons between adults and seedlings in TFF were significant (P < 0.001; Fig. 4), but a higher affinity of ADTFF and seedlings was found at the end of the rainy season (R = 0.35; Fig. 4B) than at the beginning (R = 0.40; Fig. 4A).
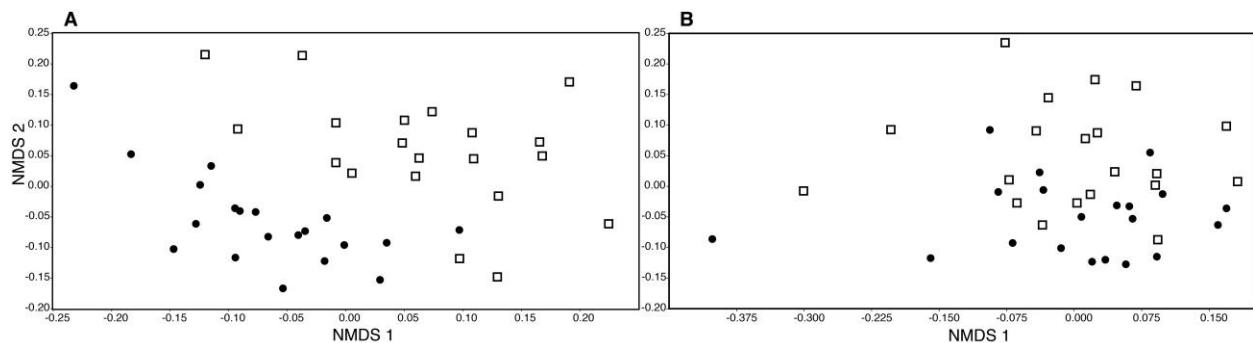

Fig. 3. Comparison between ordinations A) ADSFF - seedlings at the beginning of the flood (stress = 0.19; P < 0.001; R = 0.45); B) ADSFF - seedlings at the end of the flood (stress = 0.20; P < 0.001; R=0.13) by means of Non-Metric Dimensional Scaling (NMDS) analysis. The empty

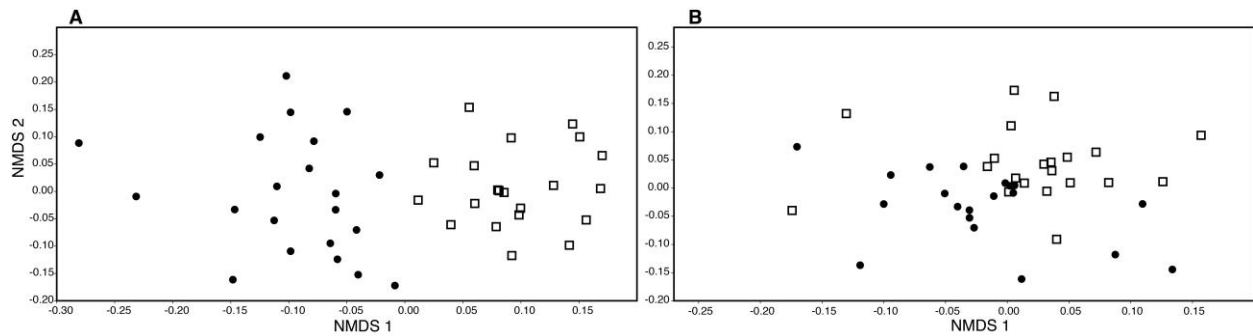squares correspond to the composition of seedlings per sampling quadrat and the solid circles to adults.

Fig. 4. Comparison between ordinations A) ADTFF - TFF seedlings at the beginning of the rains (stress = 0.21; P < 0.001; R = 0.40), B) ADTFF - TFF seedlings at the end of the rains (stress = 0.18; P < 0.001; R = 0.35) by means of Non-Metric Dimensional analysis Scaling (NMDS). The empty squares correspond to the composition of seedlings per sampling quadrat and the solid circles to adults.

DISCUSSION

We found that post-flood, the dissimilarity between seedling and adult compositions in SFF decreased significantly and compositional affinity increased significantly, as we had hypothesized. For adults and TFF seedlings we found that the rainy season marginally affected the dissimilarities, while the affinity increased slightly after the rainy season; this is different from what we had hypothesized.

Diversity: For the adult community we found greater diversity, equitability, and specific richness in ADTFF compared to ADSFF (Table 1). Our specific richness result is similar to that reported by Londoño and Alvarez (1997), who found a higher specific richness in TFF compared to SFF in the Amazon region of Caquetá. Baez and Garate (2017) found a greater number of families, genera and specific richness in TFF compared to SFF in northern Peru, consistent with our results. Regarding alpha diversity and equitability, Baez & Garate (2017) found the highest Shannon and Pielou index in TFF, as reported here. This pattern of diversity was also reported for forests in the Colombian Chocó, where greater species diversity was found in TFF compared to flood forests (Herrera, Flórez, Segura, Mena & Alvarez, 2018). This pattern of higher species richness in TTF versus SFF seems to extend to the Neotropics in general (Gentry, 1982; Gentry, 1988; Gentry, 1990, Londoño & Alvarez, 1997).

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 (Stevenson, 2004; Baez & Garate, 2017). 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 (Parolin et al., 2004; Cano & Stevenson, 2009). The lower oxygen availability and nutrient leaching, as a consequence of seasonal flooding, exert an abiotic filter of great relevance in SFF tree establishment (Parolin et al., 2004). Jones, Tuomisto, Clark and Olivas (2006) reported that soil drainage capacity, nutrient availability, and canopy opening were correlated with differences in tree diversity in some TFF of Costa Rica.

Tree composition: Several of the species with the highest relative abundance for ADTTF (Table S1) have also been reported as important in the TFF of La Macarena (Meta), while *Combretum laxum* was the only species of importance in ADSFF coinciding with those found by Stevenson et al. (2004). However, they only reported two adult shared species between TTF and SFF, while we report four. This pattern could indicate some degree of similarity between these adult forests, although this is contradictory with the niche assembly, which establishes that the composition and structure of plant communities is determined by the environmental conditions of the sites (Jones et al., 2006; Trujillo & Henao, 2018). In this sense, the two adult communities studied here should be markedly different since ADSFF presents seasonal floods that should cause greater compositional changes in the soil (Stevenson et al., 2004; Correa & Stevenson, 2010). 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 (Stevenson et al., 2018). However, Stevenson et al. (2018) highlighted the importance of analyzing the composition of these forests based on determined environmental conditions such as the duration and frequency of flooding, as well as the composition of the soil of these forests.

On the other hand, the tree composition of ADSFF was strongly influenced by the high relative abundance of *Oenocarpus minor* (21.5%) and *Attalea insignis* (11.2%), while for ADTFF 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 (Baez & Garate, 2017). In this sense, ADTFF and ADSFF can be considered as mixed forests and these forests are characteristic of La Serranía de Manacacías, which extends throughout San Martín and surrounding municipalities (Minorta et al., 2019).

Compositional difference and affinity between adults and seedlings: The changes that we observe in presence and relative abundance of the ten most important seedlings species in the two forests 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 (Grubb, 1977; Schupp, 1995; Chesson, 2000; Fenner, 2000; Forget, Lambert, Hulme & Vander Wall, 2005; Chazdon, 2008). In tropical forests, environmental heterogeneity exerts a greater filter in seedling communities than in any subsequent ontogenetic phase (Warner & Chesson, 1981; Parolin et al., 2004; Norden et al., 2007), causing populations to be composed of species with adaptations to face the environmental challenges (Metz et al., 2008). In addition to the environmental filter, the changes observed here may be due to temporal divisions in seedling recruitment, decreasing competition and promoting the effect of temporary environmental filtering, which could maintain the coexistence of high plants diversity (Chesson & Warner, 1981; Schupp, 1995; Ibañez & Hart, 2020; Muledi, Bauman, Jacobs, Meerts, Shutcha et al., 2020).

The Bray-Curtis analysis showed that the dissimilarity between the SFF seedling community and adults decreased significantly at the end of the flood (Fig. 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 adults of the sampling sites. Likewise, this is corroborated by the greater proportion of shared adult and seedling species at the end of the flood (Table S2) and by the NMDS analysis (Fig. 3B), where after flooding the affinity between seedlings and adults is significantly stronger. Seasonal flooding is considered to be a relevant deterministic effect on plant communities (Gentry, 1982, 1988); this could be due to the fact that seedlings that physiologically tolerate flooding, oxygen deficiency and differential nutrient availability (Schupp, 1995; Londoño & Alvarez, 1997; Parolin et al., 2004; Stevenson et al., 2018) will be more likely to establish their regeneration niche and advance to adult stages, maintaining the compositional identity of the

community (Grubb, 1977; Norden et al., 2008). Furthermore, the niche temporal division (Chesson & Warner, 1981) may also explain the changes in compositional dissimilarity and affinity maintaining the assembly of the plant community throughout the different stages of plant development (Chao et al., 2004; Chazdon, 2008).

Regarding the compositional affinity between the adult and seedling communities in TFF, marginally significant differences were found between the dissimilarities of ADTFF with the seedling community (Figure 2B). Likewise, the NMDS analysis showed a slight increase in the compositional affinity (R = 0.35) just after the rainy season, but this affinity was not very different to that 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 and they could decrease the nutrient availability from the soil (Parolin et al., 2004; Stevenson et al., 2018) or cause their loss due to landslides (Killeen, Siles, Soria & Correa, 2005; Lozano, Busmann, Kupers & Lozano, 2008). Therefore, high seasonal precipitation could be considered an environmental filter but more studies are necessary to corroborate the relationship between rains and nutrient loss.

Additionally, after seasonal rains, the availability of light could be higher in addition to lower nutrient and sediment leaching (Parolin et al., 2004). This could explain the significant increase in species richness in the seedling community at the end of the rains. Also, this could be due to opportunistic sun seeds (Schupp, 1995) that germinate and grow quickly with few days of sun at the end of the rains. However, Stevenson et al. (2017) discovered that by transplanting native and foreign seedlings from one type of terra firme forest to another (in Vichada), the mortality of almost half of the natives was associated with dry land and strong exposure to the sun after the rains. For this reason, it is unclear whether seasonal rains or severe droughts are most decisive in these forests with respect to the temporal regeneration niche associated with the assembly of plant communities throughout their life history.

CONCLUSIONS AND IMPLICATIONS FOR CONSERVATION

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 adults of the SFF increased with respect to the beginning of the flood. This indicates that just before the flood many seedlings are established and at the end of the flood only the seedlings of certain adult species survive, maintaining the forest assembly. Regarding the TFF, we found that the compositional affinity between seedlings and adults increased slightly at the end of the seasonal rains, however, this pattern was not as evident as in the case of the flood in SFF. Our results provide valuable information on the role of two regular environmental events on the assembly of seedlings and their temporal affinity with adults of two types of tropical forests of great importance for the piedmont, and their connectivity with the Colombian Amazon and Orinoquia. Based on this, our findings could be useful for restoration and conservation programs aimed at maintaining community identity in these forest types. Based on our results, we could provide clues for the seasonality that favors active restoration processes in SFF (eg, planting seedling species that resist the flood), as well as the most relevant species within the community. Finally, our results contribute to increasing our knowledge of the SFF, which is one of the ecosystems less studied in Colombia and one of the most threatened by anthropogenic factors (Stevenson et al., 1999, 2018).

RESUMEN

Efecto de las lluvias e inundaciones estacionales en el reclutamiento de plántulas y la afinidad composicional en dos bosques tropicales de tierras bajas. **Introducción:** Los bosques inundables estacionales y de tierra firme son ecosistemas característicos de la Orinoquia colombiana y de gran importancia en el mantenimiento de biodiversidad y funciones ecosistémicas regionales. Estos bosques están bajo un pulso de precipitación unimodal que puede ejercer un efecto de división temporal sobre el nicho de regeneración de plántulas. Esto podría explicar la alta diversidad y coexistencia de especies vegetales en estos bosques, así como la afinidad composicional entre adultos y plántulas que refuerza el ensamblaje de la comunidad en bosques maduro. **Objetivo:** Nuestro objetivo fue evaluar el efecto de la inundación estacional y de las lluvias de temporada sobre la disimilitud y afinidad composicional entre adultos y plántulas de un bosque inundable y de tierra firme. **Métodos**: Para esto, caracterizamos la comunidad de adultos de estos bosques en San Martín (Meta) y la comparamos con sus respectivas comunidades de plántulas antes y después de la temporada de inundación y lluvias usando análisis de disimilitud de Bray-Curtis y NMDS. **Resultados:** Encontramos que posterior a las inundaciones disminuyó significativamente la disimilitud florística entre adultos y plántulas del bosque inundable y aumentó significativamente la afinidad entre estos; sin embargo, este patrón no fue tan concluyente en el bosque de tierra firme. **Conclusiones:** Estos resultados podrían indicar que las inundaciones estacionales pueden causar división temporal sobre el nicho de las plántulas. Sin embargo es importante profundizar en el rol de variables edáficas posiblemente afectadas por la inundación y las lluvias. Nuestros resultados pueden aportar información para el desarrollo efectivo de programas de restauración asistida y conservación.

PALABRAS CLAVE: bosque inundable estacional; bosque de tierra firme, disimilitud de Bray-Curtis; ensamblaje de comunidades; nicho de regeneración; NMDS

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SUPPLEMENTARY MATERIAL

Table S1. Ten most important species according to their relative abundance (%) in the adult community per sampled forest.

Seasonal flood forest adults		Terra firme forest adults	
Species	Relative abundance (%)	Species	Relative abundance (%)
Oenocarpus minor	21.5	*Astrocaryum gynacanthum*	7.0
Attalea insignis	11.2	*Attalea insignis*	5.7
Combretum laxum	7.7	*Geonoma deversa*	5.1
Dichapetalum spruceanum	7.3	*Syagrus orinocensis*	4.6
Pseudolmedia obliqua	5.0	*Oenocarpus minor*	4.5
Protium glabrescens	4.6	*Oenocarpus bataua*	3.5
Crepidospermum rhoifolium	4.2	*Protium guianense*	3.3
Pseudolmedia laevis	3.1	*Eschweilera bracteosa*	3.3
Casearia javitensis	2.7	*Ryania speciosa*	2.7
Matayba sp.	2.7	*Crepidospermum rhoifolium*	2.7

Table S2. Ten most important seedling species sampled according to their relative abundance (%) per forest.

	Relative abundance (%)	
Seasonal flood forest seedlings	**Beginning of flood**	**End of flood**
Bactris brongniartii	6.7	5.4
Lindackeria paludosa	-	5.1
Miconia elata	5.7	4.1
Maquira coriacea	5.3	-
Combretum laxum	-	4.6
Oenocarpus minor	-	4.3
Piper obliquum	4.0	3.1
Inga thibaudiana	3.9	-
Attalea insignis	-	3.6

Socratea exorrhiza	-	3.6
Xylopia sericea	3.2	2.8
Crepidospermum rhoifolium	3.1	4.3
Pseudolmedia laevis	2.8	-
Geonoma deversa	2.7	-
Syagrus orinocensis	2.6	-
Terra firme forest seedlings	**Beginning of rains**	**End of rains**
Iryanthera laevis	12.4	2.1
Tococa guianensis	8.2	2.4
Dialium guianense	-	4.2
Neea amplifolia	3.5	-
Licania kunthiana	3.1	-
Maripa sp.	3.1	-
Oenocarpus bataua	3.1	1.6
Pseudolmedia laevis	3.1	-
Licania subarachnophylla	2.9	-
Cordia nodosa	2.7	-
Schnella outimouta	2.4	-
Brosimum lactescens	-	1.9
Oenocarpus minor	-	1.9
Virola sebifera	-	1.9
Paullinia pachycarpa	-	1.6
Inga villosissima	-	1.6
Inga brachyrhachis	-	1.6