

Effect of *Acacia mangium* Willd plantations on the natural regeneration of a savanna

Efecto de las plantaciones de *Acacia mangium* Willd sobre la regeneración natural de una sabana

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ABSTRACT

Introducing alien species into natural ecosystems can generate important changes in water quality and supply level, ecosystem services, and biodiversity. Different results have been found with the appearance of alien species that contemplate both high invasion risks and opportunities to form new ecosystems that permit a new path toward restoration. This research aimed to analyze the contribution of *Acacia mangium* Willd. plantations for ecological restoration using both spectral instruments and conventional sampling to calculate the abundance or frequency of species appearances. Two analyses were conducted on four plant covers (an active plantation, a felled forest, and a gallery forest edge). The analysis was of a spectral type, evaluating two vegetation indices and their relationship with the Berger-Parker biotic dominance index (D); the vegetation indices were NDVI (the normalized difference vegetation index) and CVI (the chlorophyll vegetation index). The statistical methodologies involved spatial regression modeling to relate diversity and spectral indices and a permutational multivariate analysis of variance for the variables associated with regeneration. We found that felled plantations have a higher degree of

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similarity to gallery forests in terms of spectral indices and diversity when compared to active plantations. The composition and abundance of species of natural regeneration in plantations differ significantly from both regeneration in forests and regeneration in savannas.

Keywords: Berger-Parker index; ecosystem restoration; encroachment; gallery forest; permutational variant analysis; remote sensing.

RESUMEN

La introducción de especies exóticas en ecosistemas naturales puede generar cambios importantes a nivel de calidad y suministro de agua, servicios ecosistémicos y biodiversidad. Se han encontrado diferentes resultados con la aparición de especies exóticas que contemplan tanto altos riesgos de invasión como oportunidades para formar nuevos ecosistemas que permitan un nuevo camino hacia la restauración. El objetivo de esta investigación fue analizar la contribución de las plantaciones de Acacia mangium Willd. para la restauración ecológica, utilizando tanto instrumentos espectrales como muestreos convencionales para calcular la abundancia o frecuencia de aparición de especies. Se realizaron dos análisis en 4 cubiertas vegetales (plantación activa, bosque talado y un borde de bosque de galería). El análisis fue de tipo espectral evaluando 2 índices de vegetación y su relación con el índice de dominancia biótica (D) de Berger-Parker; los índices de vegetación fueron el NDVI (índice de vegetación de diferencia normalizada) y el CVI (índice de vegetación clorofílica). Las metodologías estadísticas incluyeron modelos de regresión espacial para relacionar los índices de diversidad y espectrales y un análisis multivariante permutacional de la varianza para las variables asociadas a la regeneración. Encontramos que las plantaciones taladas tienen un mayor grado de similitud con los bosques de galería en términos de índices espectrales y diversidad en comparación con las plantaciones activas. La composición y abundancia de especies de regeneración natural en las plantaciones difiere significativamente tanto de la regeneración en el bosque como en la sabana.

Palabras clave: análisis variante permutacional; bosque de galería; índice Berger-Parker; invasión; teledetección; restauración de ecosistemas.

INTRODUCTION

Global demand for wood goods is growing, and simultaneously, monospecific tree plantations (Fernandes *et al.*, 2016). They can increase environmental services (Searchinger, 2019) and reduce pressure on the extraction of wood from native natural forests (Arce-Baca, 2006). Indeed, the Colombian government recently promoted forest plantations as an alternative for both economic growth and ecological restoration (DNP, 2018) as a consequence of the incipient development of the forest sector at the national level and the environmental potential to support it (Santos *et al.*, 2018).

In contrast with the benefits of monospecific plantations, there is also large evidence of their negative effect on ecosystems. Planted species can become invasive (Richardson *et al.*, 2015) or can promote massive colonization of grassy ecosystems by woody vegetation, also known as encroachment (Wieczorkowski & Lehmann, 2022). In this case, there are reports of radical changes in the habitats of associated fauna (Sirami & Monadjem, 2012) and altered groundwater charging (Coetsee *et al.*, 2013) for a latitudinal range covering tropical and subtropical areas. Negative effects are linked not

only to changes induced by afforestation itself but also by soil tillage before planting that can destroy underground biomass of savanna species and by fire exclusion (Haddad *et al.*, 2021).

Encroachment has occurred at least during the last century worldwide, and its mechanisms are well documented (Wieczorkowski & Lehmann, 2022). However, encroachment under the above definition has not been addressed in Colombia, and instead, colonization by woody vegetation on grassy ecosystems has been viewed as a mean to avoid fire and thus to keep the productivity of plantations or to recover biodiversity (Fernández-Méndez *et al.*, 2012). Likely, this latter is related to old-growth savannas misrecognized as degraded forests, which in turn might be the result of misperceiving the role of fire (Veldman, 2016) and its interplay with climate and resource availability (De Dantas *et al.*, 2016).

Extension of agro-industrial crops, including plantation of nonnative trees for wood production, has increased during the last 25 years (from 112,000 to 169,000) in the Orinoco region in Colombia (Romero-Ruiz *et al.*, 2012; DNP, 2018; Vargas *et al.*, 2018). There is evidence of encroachment as a byproduct of these plantations in the savanna areas (Cortés-Pérez *et al.*, 2005; Fernández-Méndez *et al.*, 2012), and hence, further study is necessary considering the array of introduced species, ecological effects, and underlying mechanisms. With such knowledge, it would be possible to design sustainability and restoration strategies to address an alarming knowledge gap in the Orinoco region concerning the Andes and the Caribbean (Garibello *et al.*, 2021). In fact, many of the Australian acacias are linked to invasions of ecosystems; in recent years, twenty-three species have been recorded as invasive (Richardson & Rejmánek, 2011; Gibson *et al.*, 2011; Rejmánek & Richardson, 2013; Richardson *et al.*, 2015).

Acacia mangium Willd. is among the non-native tree species planted in the Orinoco region for wood production (Mercado Jr *et al.*, 2008). It has been reported as invasive (Richardson *et al.*, 2015), likely due to its life-history traits including high dispersal capacity, high growth rate, and competitive ability to modify soil and ecosystem conditions (Muñoz & Rodríguez González, 2024), as well as the extent and duration of its use. There is also evidence of its role in facilitating the growth of woody species in subtropical China (Yang *et al.*, 2009) and Southeast Asia (Norisada *et al.*, 2005). Its economic and ecological benefits relative to the enhancement of nutrient cycling and availability have raised conflicts of interest between foresters and conservationists (Haddad *et al.*, 2021), and thus sustainable management initiatives are needed.

Given the risks associated with the rapid expansion of areas occupied by tree plantations in the Orinoco region of Colombia, but also aware of the livelihoods of its inhabitants, affected by poverty and violence, the objective of this research was to analyze the contribution of *Acacia mangium* Willd. plantations to ecological restoration. Usingboth spectral instruments and conventional sampling, we assessed the abundance andfrequency of species appearances.

In this study, we compared the natural regeneration within *A. mangium* plantations to that of native vegetation. For this purpose, we sampled both active and felled plantations, along with the edge of a gallery forest and an unaltered savanna. We asked if the vegetation condition of plantations was similar to that of forest edges, if vegetation indexes are associated with plant diversity, and finally, if species assemblages differed between plantations and forest edges, and between plantations and natural savanna. This study aligns with the urgent need to integrate low-cost remote sensing methods with rapid field observations, addressing the challenge of studying and monitoring biodiversity under severe funding constraints.

MATERIALS AND METHODS

Study site. The study area is in the Colombian Orinoquia, situated in the department of Meta, municipality of Puerto Gaitán, town of Planas, specifically in a savanna, with a modified area in a forest agroecosystem of *A. mangium* with an extension of 2000 ha. Its coordinates are located between 3°05 'and 4°08' North latitude and between 71°05' and 72°30' West latitude. The climate is seasonal, with a dry season that goes from two to five months (between November and March-April) (Armenteras *et al.*, 2021) and an average annual temperature of 30°C (CONPES, 2018). The soils at the study site are associations of Oxisols and Ultisols (Gisbert Blanquer et al., 2010). The landscape includes forest ecosystems, savannas (composed mainly of species of grasses and dispersed woody plants), and modifications of these converted into agroecosystems for forestry and livestock production.

Spectral indices. The indices involved that showed spatial data were the NDVI and the CVI. NDVI is an index used in remote sensing to assess the presence and condition of vegetation on the earth's surface and is calculated between reflectances in the near infrared (NIR) and visible red (RED) spectra (Tucker, 1979). The CVI (Canopy Vegetation Index) is an index used to measure the density and activity of vegetation on a land surface, particularly in areas where the vegetation canopy is predominant (Pettorelli et al., 2005). For the estimation of the evaluated spectral indices, the Google Earth Engine (GEE) platform (Gorelick et al., 2017) was used, using the collection of high-resolution multispectral images of the COPERNICUS-Sentinel 2 constellation (COPERNICUS / S2_ SR) with Level 2A processing, where the spectral response at ground surface level was already obtained. A search range for S2_SR images was generated between 2020-10-01 and 2021-03-25 using a 50% cloudiness filter, so only satellite images that met this condition were used. After obtaining the satellite images, an orthophotomosaic was generated using as a criterion the median of each of the digital levels of the image.

Once the indices were calculated, an estimated area was applied around the proposed sampling points (12 points per treatment), thus constructing sample units of 10 m in diameter, adjusted to the maximum spectral resolution of the images for the bands used. **Biodiversity Index**. The Berger Parker index (D) was used as the biodiversity index;

this establishes the measure of the numerical importance of the most abundant species, thus calculating the dominance of vegetation whose range varies between 0 and 1. The index establishes that the closer the score is to 1, the greater the vegetation dominance and the lower the diversity (Caruso *et al.*, 2007).

Measurement of plant diversity through conventional sampling. An initial review of the three ecosystems analyzed was carried out to get a close appreciation of the state of the vegetation and the possible introduction of *A. mangium* as an invasive species. For the measurement of plant diversity in the different ecosystem scenarios, a sampling adaptation of Campbell *et al.* (2003) was used, where the individuals were counted, and the DBH (diameter of breast height) and DAB (days after bud break) were determined. Natural regeneration was evaluated by the identification of morphospecies and the assessment of their frequency of appearance. The abundance measure was the number of 1 m² subplots in which a species appeared in a sampling unit (i.e. "frequency of appearance"). This assessment included the quantification of the abundance of seedlings of woody species, herbs, and grasses. To explore possible differences in the assemblage of species in the different covers, we used the natural regeneration data of the herbaceous stratum Up to 1.3 m.

Based on this information, quantifiers (measurements, observations, and records) were obtained that allowed a comparison between scenarios such as stem density, basal area at plot scale, species richness, and the balance between their abundances (fairness).

The frequency for each type of vegetation is the number of subplots in which a species appears divided by the total number of subplots (= 400) expressed as a percentage. "Active" refers to a four-year-standing *A. mangium* plantation. "Felled" refers to a 12-year-old plantation of the same species sampled 1.5 years after logging.

Statistical analysis. Following the standard approach in most spatial analyses of starting with a non-spatial linear regression model and then testing, if this so-called reference model is not capable of generating a positive effect, then the reference model should be extended with spatial interaction effects. It is precisely the way it is used in this research because, when testing various ecological indices associated with richness, abundance, or diversity as response variables and another group of spectral indices as explanatory variables, spatial dependence was found. Therefore, it was necessary to expand the models that considered this possibility. By having information on ecological and spectral indices, different tests were carried out with different models, starting with pure autoregressive models and moving up to autoregressive models with explanatory variables. However, the assumptions of normality in the residuals and final independence of residuals, as well as the possibility of finding models that showed goodness of fit, only allowed us to find a pair of spectral indices. These spectral indices were the CVI (an estimated index of chlorophyll in the plant that varies between -1 and 1) and the NDVI (as explanatory). The D or Berger index-Parker dominance index (that varies between 0

and 1) was a response for which a SARAR autoregressive model was finally fitted, using the connections at all distances as a weight matrix, that is, for all neighbors. The model finally used was written as:

$$y = \lambda Wy + \alpha \iota_n + X\beta + u$$
$$u = \rho Wu + \varepsilon$$

where the vector of the respons e variable represented by the spectral index was associated, λ represents the autoregressive coefficient, W is the matrix of spatial weights, α represents the coefficient associated with the intercept, and ι_n represents a vector of ones of length n, X represents the matrix of the explanatory variables associated with the spectral indices, β represents the vector of parameters for the explanatory variables, and u represents the spatially dependent residuals. In the second part of the equation, a dependency structure is proposed for the residuals u, whereby ρ represents the spatial autocorrelation coefficient and ϵ the final residuals, for which the assumptions of independence and normality are expected to be fulfilled, with zero mean and variance (Elhorst, 2014).

Due to the structure of the vegetation of S, it was excluded in the initial stage, leaving the structures with greater similarity: Active, Felled, and Gallery. It is underlined that the landscape was not introduced as a factor in the spatial model since the main idea was to generate the model, predict the response, which in this case was the BP index that had the best statistical behavior, and, with these predictions, characterize each of the landscapes with the spectral indices and show the ability of the model to discriminate between each of these three landscapes. The last analysis involved a Permanova (Permutational Analysis of Variance) to compare three ecosystems in terms of ecological indices for a clearer perception of their statistical differences.

In the spatial regression modeling, the Berger-Parker index (D) was used as the answer and as an explanatory variable for the measurements of the spectral indices CVI, NDVI, and the 60 available coordinates of the three types of plantations (G, T, and A). Although 34 additional indices were tested, only the CVI and NDVI fulfilled the assumptions necessary for their adjustment to normality and independence of the residuals.

Likewise, a hierarchical cluster analysis dendrogram was performed using Ward's method to quantify the correct ecosystem classifications. The cluster was carried out to create a confusion matrix looking for whether the spatial modeling explained the correlations of the studied plant covers. We found that such a correlation did exist.

For the final analysis, the variation in the structure of the assemblages of the different ecosystem scenarios was visually represented by an nMDS (non-metric multidimensional scaling) arrangement based on a Bray-Curtis dissimilarity matrix. The matrix was generated from the square root of the frequency of appearance for each

species in each survey. Possible associations between the abundance of the species and the management axes were identified from a Spearman correlation that used as input a standardization by totals applied to the transformed data of frequency of appearance in each plot. A "permutational multivariate analysis of variance" (PERMANOVA) was used as an inferential analysis to test the null hypothesis of no differences in the structure of assemblages when comparing the coverages studied. Both the ordering and the PERMANOVAs were done with the "Vegan" package (Oksanen *et al.*, 2019).

RESULTS AND DISCUSSION

Differences were found among the three ecosystems studied, where, particularly in the gallery forest, a lower dominance was found.

Vegetation indices. A spatial statistical relationship was found between the explanatory variables associated with the NVDI and CVI spectral indices and the response variable associated with the Berger-Parker diversity index D. (Table 1.)

Estimate	Value	Standard error	Value Z	p value
Intercept	0.688	0.297	2.315	0.0206
NDVI	-0.369	0.177	-2.086	0.037
CVI	-0.093	0.047	-2.001	0.045

Table 1. Coefficients associated with the explanatory variables and intercept(adjustment of the SARAR autoregressive spatial model).

(Figure 1) was used to characterize the estimate of the D index by ecosystem. This index had the highest value in Active. Likewise, a relative percentage difference between the ecosystem scenarios Active and Gallery of 22.2% was higher in Active, indicating a greater dominance of some plant species in this ecosystem, which then represents a greater plant diversity in Gallery. On the other hand, in the comparison of Active and Felled, a relative percentage difference of 14.2% was found in favor of the active one, finding a lower dominance in the Felled scenario, which is represented by greater diversity at this stage (Table 2). Concerning the comparison of the other scenarios about this index, a lower percentage (6.9%) was found in the comparison of the scenarios of Gallery about Felled, which may suggest quite similar behavior between these two ecosystems (Figure 1).

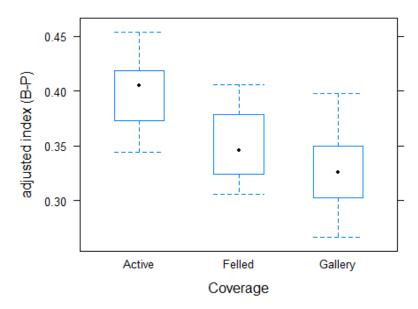


Figure 1. Distribution by type of coverage of the Berger-Parker index (Biodiversity) adjusted by spatial regression.

For the NVDI index in Gallery, a greater relative percentage difference (27.9%) was obtained for A and F (29.9%). On the other hand, in the analysis of the same index between the scenarios Active and Felled, a difference in the percentage of 1.58% was found in favor of Active (Table 2). These results were in favor of the DBH found, namely: 17.3 for G, 8.5 for A, and 7.6 for Felled. (Table 3). Regarding the CVI index, relative percentage differences were found for F of 2.47% and 12.31% for Active and Gallery, respectively. Likewise, a percentage difference of 9.6% was found in this index in comparison to Active and Gallery (Table 2). F is the ecosystem with greater variability for NVDI, while Gallery had more heterogeneous values for CVI.

	NVDI			CVI		
Treatments	Count	Average	SD	Count	Average	SD
(A)Active	20	0,638	0,031	20	3,822	0,365
(F)Felled	20	0,628	0,092	20	3,917	0,426
(G)Gallery	20	0,816	0,034	20	3,487	0,473

Table 2. Distribution of the measurements of the NDVI and CVI indices by ecosystem

The confusion matrix (Table 3) and the ordering of the sites according to the spectral indices show that there is an appreciable degree of similarity between the felled plantations with the other two scenarios. The confusion matrix suggests that there is no similarity between active plantations and gallery forests (there were no cases of active planting that were classified as from gallery or gallery to active plantin), despite tree dominance in both cases.

	(A)	(G)	(F)	Total
(Felled)	4	3	10	17
	6,67%	5,00%	16,67%	28,33%
(Gallery)	0	17	7	24
	0,00%	28,33%	11,67%	40,00%
(Active)	16	0	3	19
	26,67%	0,00%	5,00%	31,67%
Column Total	20	20	20	60
	33,33%	33,33%	33,33%	100,00%

Table 3. Matrix of correct classifications (data collected in the field and classification according to spatial modeling)

The best percentages of correct classifications were found within the same ecosystem, indicating a good level of accuracy when comparing real and fitted data (Table 3).

Values of remote sensing indexes related to vegetation structure and functioning suggest that vegetation of active and felled plantations of A. *mangium* is comparable to that of gallery forest. In the first case, the similarity is related to the canopy of the standing plantation, but in regards to felled plantations, without a canopy of A. *mangium*, there is evidence of encroachment verifiable by sight and a species assemblage dominated by shrubs and trees (Table 5).

A. mangium can induce changes in natural ecosystems due to its traits, such as a rapid growth rate and a high capacity to compete with native autochthonous plants (Morris *et al.*, 2011). In the initial evaluation stage of our research, we did not find this type of behavior in *A. mangium*, with a tendency for F to be similar ecosystems to G (in the analysis involving the spectral indices and the biodiversity) that could mean a transition from the felled crop to a gallery forest rather than to another type of ecosystem (i.e., savanna). This was also corroborated by the permutational analysis (including an S of diversity carried out). Likewise, in the analysis of the D index (understood as a dominance index), similar scenarios were felled and Gallery in terms of less dominance or greater diversity.

It should be taken into account that, due to the few long-term studies carried out in terms of the increase in native biodiversity after the introduction of *A. mangium*, it is advisable to establish precautionary principles as established in the Rio Declaration of 1992 (Raffensberger & Tickner, 1999). One of the possible long-term consequences of the large-scale establishment of *A. mangium* plantations is that the accumulation of massive reserves of long-lived seeds in the soil with high reproductive capacity can ensure the persistence of this species, resulting in a prolonged invasion with frequent and severe disturbances (Gaertner *et al.*, 2014). In particular, the seeds of acacias may have seeds

protected by a thick coating that can harden and, in fire situations, may break, allowing the seeds to germinate when conditions are favorable (Enright & Lamont, 2001).

Structure of the assemblages of natural regeneration. The PERMANOVAs suggest that the assemblages of plantation types differed from each other and also differed from the assemblages of the savanna and the gallery forest. The largest divergences occurred between the felled plantation and the savanna, while the smallest divergences occurred between the plantations and the gallery forest (Table 4). NMDS ordination (Stress=0.16) confirms such differences and their magnitude according to the grouping of sampling units. Additionally, the dominant life forms in each scenario suggested that the differences not only occurred at the floristic level and relative abundance but also at the level of life forms (Table 4). No shoots of *A. mangium* were found in any of the vegetation types. This could indicate that the seeds should have a stimulus, such as changes in temperature or humidity deltas, for germination.

Table 4. Summary of results of permutational multivariate analyses of variance (PERMANOVA) assessing differences in assemblage structure of natural regeneration between four types of vegetation in the Colombian Llanos

General Comparisons	Source of variation	df	Mean Squares	R ²	F	Р
	Stage	2	6.758	0.803	116.45	0.001
Types of plantations and savanna	Residual	57	0.058	0.196		
anu savanna	Total	59		1.000		
	Stage	2	6.662	0.727	76.128	0.001
Types of plantations and gallery forest	Residual	57	0.087	0.271		
and ganery lorest	Total	59		1.000		
Pairwise comparisons				R ²	F	Р
Savanna vs Active				0.736	106.26	0.003
Savanna vs Felled				0.788	141.11	0.003
Active vs felled				0.734	104.68	0.003
Gallery vs Active				0.625	63.40	0.003
Gallery vs Felled				0.649	70.34	0.003
Active vs Felled				0.733	104.68	0.003

Stage	Species	Abundance (%)	Life form	Spearman coefficient with nMDS axis 1	Spearman coefficient with nMDS axis 2
Active	Bromeliaceae sp.	82.3	Rosette	0.10	-0.65
	Curatella americana	56.3	Shrub	0.45	-0.76
	Clidemia rubra	37.3	Shrub	0.06	-0.66
	Poaceae sp.2	13.5	Grass	0.10	-0.59
	Schyzaryum semiberbe	8.3	Grass	0.01	0.59
Felled	Sipanea pratensis	43.8	Forb	-0.03	0.65
	Miconia rufescens	42.5	Shrub	-0.06	0.70
	Schyzaryum semiberbe	41.7	Grass	0.01	0.59
	Protium guianense	39.7	Tree	-0.05	0.69
	Quiina macrophylla	38.0	Tree	-0.12	0.72
Gallery forest	Eucharis sp.	46.7	Forb	-0.64	0.06
	Caladium macrotites	41.7	Forb	-0.68	-0.20
	Eugenia sp.	34.5	Treelet	-0.64	-0.04
	Guarea sp.	34.0	Tree	-0.65	-0.03
	Blechnum sp.	20.0	Fern	-0.55	-0.11
Savanna	Andropogon leucostachyus	86.5	Grass	0.74	-0.07
	Hyptis conferta	42.0	Forb	0.70	-0.12
	Aristida capillacea	35.0	Grass	0.63	-0.10
	Curatella americana	22.8	shrub	0.45	-0.76
	Bulbostylis junciformis	19.3	tussock grass	0.60	-0.09

Table 5. Frequency, life form, and Spearman's correlation coefficients of dominant
species in four types of vegetation at the Colombian Llanos.

*Frequency for each type of vegetation is the number of subplots in which a species appears divided by the total number of subplots (= 400) expressed as a percentage. "Active" refers to a four-year-standing *A. mangium* plantation. "Felled" refers to a 12-year-old plantation of the same species sampled 1.5 years after logging.

The structure of the assemblage of natural regeneration differs significantly among the types of vegetation studied. The greatest divergences occurred between savanna and felled plantations, while the smallest differences occurred between plantation types and gallery forests (Table 5). Our results therefore suggested that *A. mangium* plantations inhibit the establishment of grasses and yet facilitate the establishment of woody vegetation. In the felled plantations, we even found as co-dominant two species of trees typical of mature forests: the large tree *Protium guianense* (Gutierrez-Rodríguez *et al.*, 2015) and *Quiina macrophylla* from the understory (Gentry & Vásquez, 1993).

The facilitating role of adult *A. mangium* individuals has been previously reported concerning the growth of subtropical forest species in China (Yang *et al.*, 2009) as well as the growth of dipterocarp species from the humid forest in Southeast Asia (Norisada

et al., 2005). Monocultures of other non-native tree species have also been reported as facilitators of the establishment of native woody vegetation, particularly in the highlands and floodplains of the orinoquía, in the departments of Arauca, Vichada, and Meta. (Mora-Fernández, 2015). *Pinus caribaea* plantations aged between 10 and 15 years led to the establishment of a continuous shrub layer dominated by pioneers, but in which mature gallery forest species also appear (Cortés-Pérez *et al.*, 2005).

The mechanisms by which *A. mangium* plantations benefit the establishment of wood vegetation in our study may correspond to changes in the soil. This assertion is because both the vegetation structure comparable to that of forest edge and active plantations, along with species assemblages co-dominated by tree saplings, arose after logging when there was no chance of microclimate amelioration resulting from a standing canopy. Specifically, *A. mangium* might have increased Nitrogen status and soil Carbon accretion (Koutika & Richardson, 2019), as previously reported by Yang et al. (2005) and by Yang et al. (2009). For this latter, a facilitating effect on native tree species was also reported for their basal diameter and chlorophyll fluorescence, although such an outcome was the result of both soil and microclimate amelioration.

The implications of the colonization of woody vegetation as a consequence of the planting of A. mangium in the well-drained plains of Colombia are uncertain. Increased woody cover in a tropical savanna can negatively affect soil carbon (Berthrong et al., 2012), groundwater recharge (Coetsee et al., 2013), and diversity (Ratajczak et al., 2012). In this context, the recommendations of the recent study by Haddad et al. (2021) in the Brazilian Cerrado are pertinent. After characterizing the vegetation at a site where a pine plantation had been felled fifteen years ago, the authors suggest that the restoration of tropical savannas could occur through three strategies: logging as such, control of woody colonization, and the introduction of species from the herbaceous stratum of well-conserved savannas. Taking into account these recommendations but also considering that the information to restore the savannas of eastern Colombia is almost non-existent (Garibello *et al.*, 2021), we propose that in the felled areas (1) the supply of propagules of the herbaceous species of well-conserved savannas be characterized in detail; (2) the interaction between these species and the woody vegetation be established; (3) the changes in the cover of the woody vegetation are monitored; and (4) establish the effect of the possible novel nutrient status on the performance of a wide array of herbaceous species. This information is important in deciding whether or not to bear the costs of controlling woody vegetation and propagating well-preserved savanna grasses. Likewise, this is consistent with the recommendations of Fernandes et *al.* (2016) to evaluate the consequences of afforestation in savannas.

The invasive nature of *A. mangium* also makes it necessary to monitor the abundance of its shoots, particularly after the occurrence of possible fires. The fact that we did not find outbreaks of *A. mangium* in any of the four covers that we characterized suggests that the risk of invasion is low for now. However, caution must be given as invasion takes several

decades to manifest, particularly at large-scale plantings (Richardson & Rejmánek, 2011; Richardson *et al.*, 2015). Indeed, a possible invasion has already been reported in the well-drained plains of the Orinoco region, as a growing population with individuals capable of reproducing was found more than 100 m from a plantation (Quevedo-Padilla, 2018). The main mechanism of invasion of *A. mangium* is the accumulation of huge quantities of seeds, and hence, this metric, along with seed viability and shoot abundance, should be estimated within plantations and their vicinity.

CONCLUSIONS

We found a negative association between spectral indices and the dominance of a few species when comparing *A. mangium* plantations with gallery forests in a natural savanna in Colombia. Less species dominance with less species regeneration was found in gallery and logging ecosystems. Regarding these variables, felled plantations showed a greater similarity to forests compared to active plantations. On the other hand, when evaluating natural regeneration, we did not find shoots of *A. mangium*. We also established that the composition of the natural regeneration of plantations differs significantly from the composition of the regeneration of natural grasslands and the composition of the regeneration. Further studies should evaluate the effects of plantations in the longer term, particularly about the establishment of typical species of well-conserved savannas.

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