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Natural Sciences

Original article

Plant diversity of Neotropical dry forest fragments undergoing an ecological restoration process in the Colombian Caribbean

Diversidad vegetal en fragmentos de bosque estacionalmente secos sometidos a un proceso de restauración ecológica en el Caribe colombiano

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Abstract

Ecological restoration activities have been implemented in the tropical dry forest fragment of the Sanguaré Reserve, making it an ideal location for studying the effect of disturbances on the ecological structure of plant communities. Here, we analyze the impact of disturbance on alpha and beta diversity. Through Whittaker plots, we sampled weedy grassland, low shrub, tall shrub secondary forests, and mature forest vegetation covers. We calculated the effective number of species (alpha diversity) and communities (beta diversity), and performed cluster and detrended correspondence analyses (DCA). Sanguaré's diversity was lower than in other dry forests; besides containing the alien species *Morinda citrifolia*, its floristic composition also differed from other dry forest fragments, for example, in the absence of Capparaceae or Zygophyllaceae. The low shrub had the highest alpha diversity among the vegetation types. Beta diversity, cluster, and DCA analyses revealed three species assemblages. These results suggest that disturbance and restoration processes have allowed the formation of areas with different perturbation levels and species composition. The alpha diversity analysis suggested an intermediate disturbance hypothesis since tall shrubs had higher diversity values than the reference mature forest and the grassland. We found that biotic heterogenization had occurred in Sanguaré, showing that homogeneization does not always occur under disturbance. Our outcomes show that the structure of communities under restoration has composition and structure differences compared to undisturbed forests.

Keywords: Diversity; Plants; Ecological restoration; Sanguaré, Sucre.

Resumen

En la Reserva del Sanguaré se han venido realizando actividades de restauración ecológica en los fragmentos de bosque seco tropical, lo que la convierte en un lugar ideal para estudiar el efecto de la perturbación sobre la estructura ecológica de las comunidades vegetales. En este estudio analizamos el efecto de la perturbación en la diversidad alfa y beta. En parcelas de Whittaker se muestrearon praderas herbáceas, arbustos bajos, bosques secundarios altos y coberturas de vegetación forestal madura. Se calculó el número efectivo de especies (diversidad alfa) y comunidades (diversidad beta), y se hizo un análisis de correspondencia corregido (DCA). Sanguaré tiene una diversidad más baja que otros bosques secos: además de contener la especie exótica *Moringa citrifolia*, la composición florística difiere de otros fragmentos forestales secos, por ejemplo en la ausencia de Capparaceae o Zygophyllaceae. Entre los tipos de vegetación, las coberturas de arbustales bajos presentaron la mayor diversidad alfa. Los análisis de diversidad beta, así como los de clúster y DCA, revelaron tres conjuntos de especies. Estos resultados sugieren que los procesos de perturbación y restauración han permitido la formación de áreas con diferentes niveles de perturbación y de composición de especies. Los resultados de la diversidad alfa sugieren que la hipótesis de perturbación intermedia ocurre en el área, ya que los arbustales altos tenían valores de diversidad más altos con respecto al bosque maduro de referencia y al

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pastizal. En la diversidad beta se halló un proceso de heterogeneización biótica, lo que demuestra que la homogenización no siempre ocurre bajo perturbación. Los resultados de nuestro estudio muestran que la estructura de las comunidades en proceso de restauración o restauradas presentan diferencias en cuanto a su composición y estructura en comparación con bosques no perturbados.

Palabras claves: Diversidad; Plantas; Restauración ecológica; Sanguaré, Sucre.

Introduction

Disturbance is defined in ecology as an event that physically inhibits, injures, or kills some individuals in a community, creating opportunities for other individuals to grow or reproduce (**Baumgartner**, 2020). Despite being generally deemed the main factor influencing species diversity and ecosystem structure, variation in disturbance is poorly understood in areas undergoing ecological restoration (**Mackey & Currie**, 2001). Although species composition has been extensively studied to analyze the effect of disturbance on vegetation in dry forest fragments (**Calbi *et al.***, 2020), relatively few studies have attempted to integrate the changes in species assemblages expressed in alpha and beta diversity indices and ecological succession in areas undergoing ecological restoration.

Disturbance affects primarily the temporal and spatial variability of community structure, thus influencing alpha diversity and altering plant community assembly. Diversity is higher during early succession as new species arrive, but through later succession stages, richness may also decline and increase the dominance of some taxa (**Dantas de Miranda *et al.***, 2019; **Olascuaga *et al.***, 2016). There is a relationship between species richness and diversity resulting in a hump-shaped disturbance, where plant and animal communities' diversity peaks at intermediate levels of disturbance (**Catford *et al.***, 2012). This relationship is proposed as the result of trade-offs between species' ability to compete, colonize ecological niches, and tolerate disturbance (**Connell**, 1978).

Positive and negative responses of beta diversity to disturbance have been documented depending on processes acting at different scales (**Filgueiras *et al.***, 2016; **Rito *et al.***, 2021; **Socolar *et al.***, 2016). Low or reduced levels of disturbance will lead to decreasing diversity through competitive exclusion and the dominance of long-lived species, while high or increased levels of disturbance will eliminate species that are unable of rapid recolonization and growth. As a result, community diversity shows two behaviors (**Huston**, 1979). On the one hand, disturbance can lead to low beta diversity because increasing niche selection of disturbance-tolerant species homogenizes the community composition (**Vellend *et al.***, 2007). On the other hand, disturbance can increase beta diversity by causing divergence in community composition by increasing habitat filtering across environmental gradients, known as biotic heterogenization (**Myers *et al.***, 2015). However, the effect of human disturbance remains poorly understood in Neotropical seasonally dry forests' beta diversity (**Rito *et al.***, 2021).

Neotropical dry forests (NSDFs) occur in areas with rainfall less than 1800 mm per year and a period of 3 to 6 months of negative hydrological balance (<100 mm precipitation per month), resulting in mostly deciduous vegetation (**Banda *et al.***, 2016). NSDF has a limited and disjointed geographic distribution from México to Argentina, including the Antilles (**Pennington *et al.***, 2009). Seasonality makes NSDF forests particularly interesting ecosystems in the Neotropics (**De-Nova *et al.***, 2012). Also, human settlements are commonly found in NSDF because of the favorable climatic conditions and easy-to-clear lands (**Murphy & Lugo**, 1995; **Sánchez-Azofeifa *et al.***, 2005). NSDFs have been preferred for agriculture and human settlement in Mesoamerica, the Caribbean, and South America (**Banda *et al.***, 2016; **Murphy & Lugo**, 1995; **Sánchez-Azofeifa *et al.***, 2005). This chronic anthropogenic pressure (**Miles *et al.***, 2006) has resulted in NSDF ranking third in terms of loss of forest cover, after boreal forests and humid tropical forests (**Chaturvedi *et al.***, 2017). However, research in this ecosystem is underrepresented, generating a lag in our understanding of the effects of anthropogenic disturbance in NSDFs.

In Colombia, NSDF is mainly distributed in the Magdalena and Cauca valleys and the Caribbean plains (**Pizano *et al.***, 2014), where they have been severely fragmented, degraded, and cleared, to the point that they are currently considered among the most threatened ecosystems (**Olascuaga *et al.***, 2016). More than 90% of NSDF has been degraded, while only 11% of the original coverage remains (**Pizano *et al.***, 2014) in protected areas, including civil society reserves (CSR). The Sanguaré CSR, located in the Caribbean plains in the department of Sucre, was strongly degraded; however, its biodiversity has improved after 20 years of ecological and reforestation projects (**Angarita-Hernández *et al.***, 2014; **Sanmartín-Sierra *et al.***, 2016). Nevertheless, areas in Sanguaré remain in various successional stages and, therefore, they are a good model for better understanding the effects of human disturbance on alpha and beta diversity, and hence, plant ecological community structure. Here, we analyzed the community structure of disturbed NSDF fragments within the CRS Sanguaré (Sucre, Colombia) to explore how ecological disturbance impacts the ecological structure (alpha and beta diversity) of plant communities. We aimed to answer the following questions: How do alpha and beta diversity change across different types of disturbed vegetation? Moreover, are species assemblages related to disturbed vegetation types, with the most disturbed communities showing homogenization (*e.g.,* low beta diversity)?

Materials and methods

Study area

The Sanguaré Natural Reserve is located at the northern tip of the Gulf of Morrosquillo (San Onofre, Sucre) (**Figure 1**). The annual mean temperature ranges between 24°C and 38°C. Mean annual rainfall is 800–1,000 mm with peaks in September–November and May–June, and dry periods during the rest of the year. Vegetation is represented mainly by the families Fabaceae, Malvaceae, Meliaceae, Rubiaceae, and Sapindaceae in tropical dry forest remnants, however, anthropogenic savannahs and mangroves also occur in this area (**Sanmartín-Sierra *et al.***, 2016).

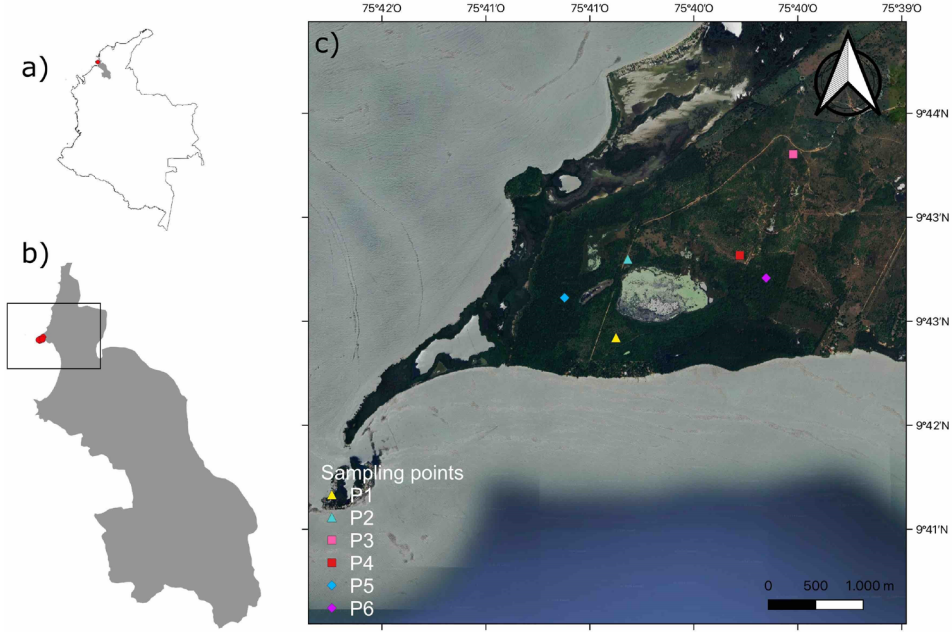

Figure 1. Geographic distribution of sampling sites in **(a)** Colombia, **(b)** the department of Sucre, and **(c)** Sanguaré, showing details of sampling units

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Plant survey and taxonomic identification

To evaluate the impact of disturbance on the ecological structure of vegetation, we surveyed five types of vegetation: (P1-P2) weedy grassland, (P3) low shrub, (P4) tall shrub, (P5) secondary forest, and (P6) reference or mature forest. These vegetation types belong to different stages of ecological succession and were defined based on the diameter at breast height (DBH). Weedy grassland and low and tall shrubs were associated with current disturbance events, while secondary forest and reference or mature forest vegetation types were not undergoing current disturbance. In each vegetation type, we used Whittaker plots to perform multiscale sampling of vegetation (**Whittaker**, 1977). Each multiscale sampling plot (50×20 m) included the following subplots: 10 subplots of 2×0.5 m, where all herbaceous individuals (DBH) <1 cm were surveyed. Additionally, we measured all trees and shrubs with DBH 1–4.99 in two 5×2 m subplots. A central subplot of 20×5 m was included where we measured all trees with DBH 5–9.99 cm. Finally, all trees with DBH ≥ 10 cm were measured in the 50×20 m plot. This method provides better comparisons of community richness than single-scale measurements, allows the evaluation of the influence of spatial scale on local species richness patterns, and facilitates the development of the relationship between species, abundance, and the area to estimate larger-scale richness patterns (**Stohlgren *et al.***, 1995).

We used taxonomic keys (**Barajas *et al.***, 2005; **Fernández-Alonso**, 2003; **Fernández-Alonso & Xhonneux**, 2002; **Gentry**, 1993; **Mendoza *et al.***, 2004) and comparisons with herbarium specimens at the HEUS herbarium to perform taxonomic identification. Acronyms followed **Holmgren *et al.*** (1990), updated based on **Thiers** (2018). Specimens were deposited at the HEUS herbarium.

Survey completeness

The expected number of species per cover type (forest and disturbed areas) was calculated using rarefaction and extrapolation–interpolation curves to establish whether the samples were representative of each transect (**Chao *et al.***, 2014). This method, described by **Chao *et al.*** (2014), uses the sample and a completeness curve drawn with twice the size of the smallest reference sample to be compared, with a 95% confidence interval obtained by resampling 100 bootstrap pseudoreplicates. This analysis was implemented with the R package (**Hsieh *et al.***, 2016) according to the parameters used by **Chao *et al.*** (2014) and **Colwell** (2012).

Alpha and beta diversity analyses

To compare species richness among locations, we used the effective numbers of species (**Jost**, 2007). Effective numbers of species (also known as equivalent numbers) can be analyzed using several levels or orders that allow the comparison of the magnitude of the differences in diversity between localities, quantifying how much diversity is lost or gained among localities (**Moreno *et al.***, 2011). We calculated the zero-order diversity (${}^0D_\alpha$) or species richness, first-order diversity (${}^1D_\alpha$) or exponential of the Shannon index, which weights diversity by the relative abundance of species, and second-order diversity (${}^2D_\alpha$), or the inverse of the Simpson index. All indices were based on the statistical estimation of the true effective number of any order $D \geq 0$, estimating diversity profiles via discovery rates of new species (**Chao & Jost**, 2015). We calculated these effective numbers of species with a 95% confidence interval obtained by resampling 100 bootstrap pseudo-replicates. The bootstrap method allowed us to obtain unconditional variances and confidence intervals for all rarefied and extrapolated estimators. The results of the diversity analyses were used to plot a diversity profile. In addition to extrapolation-interpolation curves, we used the R iNEXT package (**Hsieh *et al.***, 2016), with the parameters used by **Chao *et al.*** (2014) and **Colwell** (2012), to calculate the effective number of species.

To determine whether beta diversity homogenization had occurred in the most disturbed communities, we measured variation among the samples using the **Whittaker** (1952) beta diversity index (β_W) (software Past 3.2) (**Hammer *et al.***, 2001) and calculated

the effective number of communities (β_T) using the gamma multiplicative partition $D_\beta = D_\Upsilon/D_\alpha$ (Jost, 2007). We decomposed diversity and computed the confidence interval for α, β, and ϒ with Monte-Carlo simulations, assuming the species distribution and resampling them (**Marcon *et al.***, 2012) with the R Entropart package (**Marcon & Hérault**, 2015). Beta diversity corresponds to the effective number of different communities in the landscape. It has a minimum value of one (no difference between sample units) and a maximum value equivalent to the number of sampling units, when these do not share any species (**Halffter & Ros**, 2013). We assumed that each type of vegetation represented one virtual community when each sampling unit differed from the others, assuming here a total of six virtual communities without differences.

To establish whether dissimilarity among the communities in the study area was shaped by spatial turnover or nestedness, and, therefore, test whether plant assemblages conformed to the nested subset pattern, we used the function 'beta.multi.abund' in the R package Betapart (**Baselga & Orme**, 2012). This function separates the Bray-Curtis (β_{BC}) dissimilarity index into a balanced variation component ($\beta_{BC.BAL}$), i.e., turnover, and an abundance gradient component ($\beta_{BC.GRA}$), i.e., nestedness (**Baselga**, 2017). Similarly, we used the 'beta-pair.abund' function to compute three distance matrices using pairwise dissimilarities ($\beta_{BC.BAL}$, $\beta_{BC.GRA}$, and β_{BC}). To visualize the similarity between species assemblages, we used the overall dissimilarity matrix, measured as Bray-Curtis (β_{BC}) multiple-site dissimilarity, to carry out a cluster analysis in the R package Vegan (**Fisher-Reid *et al.***, 2012). Further, to establish if there were species assemblages related to disturbed types of vegetation, we carried out a non-metric multidimensional scaling analysis (MNS) to explore associations between species and types of vegetation. These analyses were performed in PAST 4.11 (**Hammer *et al.***, 2001).

Results

Species composition

A total of 73 species distributed among 36 families (**Table 1**) were found in Sanguaré. Overall, Fabaceae (12 species), Rubiaceae (7), Bignoniaceae (5), and Poaceae (4) were the richest families, while the richest genera were *Machaerium* (43 species), *Psidium* (36), *Stylogyne* (34), and *Hiraea* (33). The species with the largest numbers of individuals were *Machaerium arboreum,* followed by *Psidium guineense*, *Stylogyne turbacensis, Mascagnia ovatifolia,* and *Ouratea nitida*.

The species composition of each vegetation cover was different, *e.g* in P1 we found 17 species distributed among 17 genera and 17 families. We don't find a dominant family or genus. In addition, *Cnidoscolus, Commelina,* and *Hymenaea* were exclusive to this vegetation cover (**Table 1**). P2 have the poor species diversity with 15 species distributed in 15 genera and seven families. However, P2 is different to P1, because of species mainly belong to Bignoniaceae, Fabaceae, Rubiaceae, and Malpighiaceae. As well as P2, in P3 Bignoniaceae and Fabaceae are the richest families, but we also found a lot of species of Dilleniaceae. A total of 12 species, 10 genera, and 10 families were found in P3. P4 is composed of 20 species that belong to 18 genera and 18 families, being also Fabaceae and Bignoniaceae the richest families. In P5, we found the highest values of richest with 35 species distributed in 31 genera and 23 families. In addition, Fabaceae and Rubiaceae are the richest families. P6 is composed of 16 species that belong to15 genera and 10 families. As well as P5 Fabaceae and Rubiaceae are the richest families.

Survey completeness

The species completeness for the whole study area was 100%, suggesting that the sampling was representative reaching 90% for P1, 95% for P2 and P5, 94% for P3, 98% for P4, and 93.7% for P6. For each type of cover, sampling completeness estimates slightly differed by increasing the size of the reference sample in terms of individuals to double (from 72 to 144 in P1, 121 to 242 in P2, 175 to 350 in P3, 137 to 274 in P4, 46 to 92 in P5, and

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Table 1. Checklist of species found in the Sanguaré tropical dry forest, Sucre, Colombia. Lowercase letters *a-h* indicate species with restricted occurrence in the sampling units: species that mainly occur in: a) P3; b) P4 and P3; c) P4; d) P1; e) P2; f) P5; g) P6 and other sampling units, and h) species that mainly occur in P6.

Helicteres guazumifolia Kunth [a]	*Lecythis minor* Jacq. [c]
Bactris guineensis (L.) H.E. Moore [a]	*Davilla nitida* (Vahl) Kubitzki [c]
Chomelia spinosa Jacq. [a]	*Erythroxylum carthagenense* Jacq. [d]
Coccoloba coronata Jacq. [a]	*Axonopus compressus* (Sw.) P. Beauv. [d]
Coutoubea spicata Aubl. [a]	*Bidens riparia* Kunth [d]
Hexasepalum teres (Walter) J.H.Kirkbr[a]	*Cnidoscolus urens* (L.) Janti [d]
Handroanthus coralibe (Standl.) S.O. Grose [a]	*Securidaca diversifolia* (L.) S.F. Blake [d]
Hyptis suaveolens (L.) Poit. [a]	*Calliandra pittieri* Standl. [d]
Ipomoea trifida (Kunth) G. Don [a]	*Ouratea nitida* (Sw.) Engl. [d]
Macroptilium lathyroides (L.) Urb. [a]	*Hymenaea courbaril* L. [e]
Mimosa pigra L. [a]	*Rosenbergiodendron formosum* (Jacq.) Fagerl. [e]
Mimosa pudica L. [a]	*Hybanthus calceolaria* (L.) Oken [e]
Prosopis juliflora (Sw.) DC. [a]	*Tabebuia ochracea* (Cham.) Standl. [e]
Rauvolfia viridis Willd. ex Roem. & Schult. [a]	*Morinda citrifolia* L. [e]
Sida linifolia Juss. ex Cav. [a]	*Fridericia chica* (Bonpl.) L.G. Lohmann [e]
Sida urens L. [a]	*Senna mutisiana* (Kunth) H.S. Irwin & Barneby [e]
Spermacoce verticillata L. [a]	*Hiraea reclinata* Jacq. [e]
Stachytarpheta orubica Vahl [a]	*Doliocarpus dentatus* (Aubl.) Standl. [f]
Varronia curassavica Jacq. [a]	*Cecropia peltata* L. [f]
Waltheria indica L. [a]	*Coursetia ferruginea* (Kunth) Lavin [f]
Xylosma intermedia (Seem.) Triana & Planch. [a]	*Myrospermum frutescens* Jacq. [f]
Merremia umbellata (L.) Hallier f. [b]	*Piper aduncum* L. [f]
Rottboellia cochinchinensis (Lour.) Clayton [b]	*Stylogyne turbacensis* (Kunth) Mez [g]
Turnera subulata Sm. [b]	*Bursera simaruba* (L.) Sarg. [g]
Megathyrsus maximus (Jacq.) B.K.Simon & S.W.L.Jacobs [b]	*Copaifera canime* Harms [g]
Cyperus compressus Jacq. [b]	*Crescentia cujete* L. [g]
Eleusine indica (L.) Gaertn. [b]	*Cupania latifolia* Kunth [g]
Psidium guineense Sm. [b]	*Ficus nymphaeifolia* Mill. [g]
Cyperus odoratus L. [b]	*Hamelia axillaris* Sw. [g]
Spermacoce alata Aubl. [b]	*Spondias mombin* L. [g]
Commelina diffusa Burm. f. [b]	*Sterculia apetala* (Jacq.) H. Karst. [g]
Bauhinia ungulata L. [c]	*Allophylus racemosus* Sw. [h]
Curatella americana L. [c]	*Attalea butyracea* (Mutis ex L. f.) Wess. Boer [h]
Erythrina fusca Lour. [c]	*Tabernaemontana cymosa* Jacq. [h]
Machaerium arboreum (Jacq.) Benth. [c]	*Bignonia corymbosa* Vent. Bureau ex K. Schum. [h]
Byrsonima crassifolia (L.) Kunth [c]	*Nectandra membranacea* (Sw.) Griseb. [h]

81 to 162 in P6). This means that, even if more individuals were collected in the study area, the sampling would continue to represent the five types of vegetation: (P1-P2) weedy grassland, (P3) low shrub, (P4) tall shrub, (P5) secondary forest, and (P6) reference or mature forest (**Figure 2a-2b**). Furthermore, when richness was compared between the five types of vegetation, we found with 95% confidence that the expected richness would continue to be higher in P3, even if all the existing species were recorded.

Alpha and beta diversity analyses

Comparing the effective number of species across vegetation types showed that P3 was the richest and most diverse (**Figure 3**). P5 had the lowest value of richness (^{0}D) but a similar effective number of species (^{1}D) and effective number of dominant species (^{2}D) to

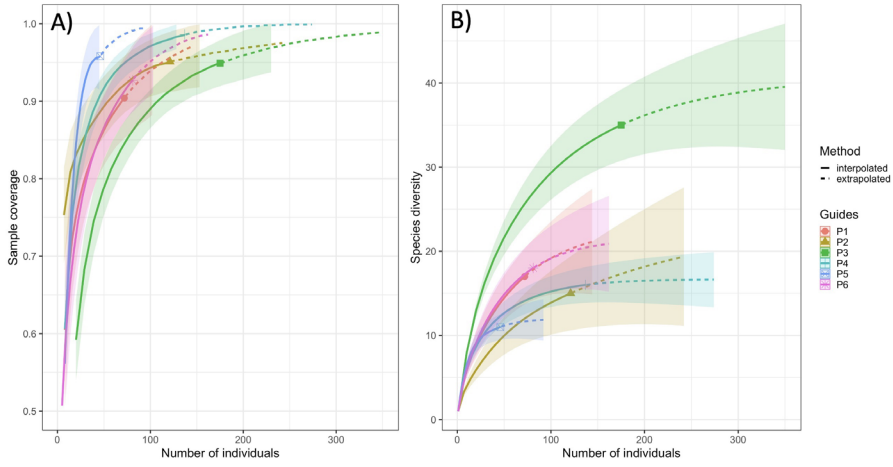

Figure 2. (a) Sample completeness curves using rarefaction and interpolation-extrapolation based on woody plant abundance. Solid lines represent sample coverage (interpolation), while broken lines show extrapolation from the samples. **(b)** Rarefaction, interpolation-extrapolation curves based on woody plant abundance. Solid lines represent the species richness sampled (interpolation) and broken lines show the species richness extrapolation.

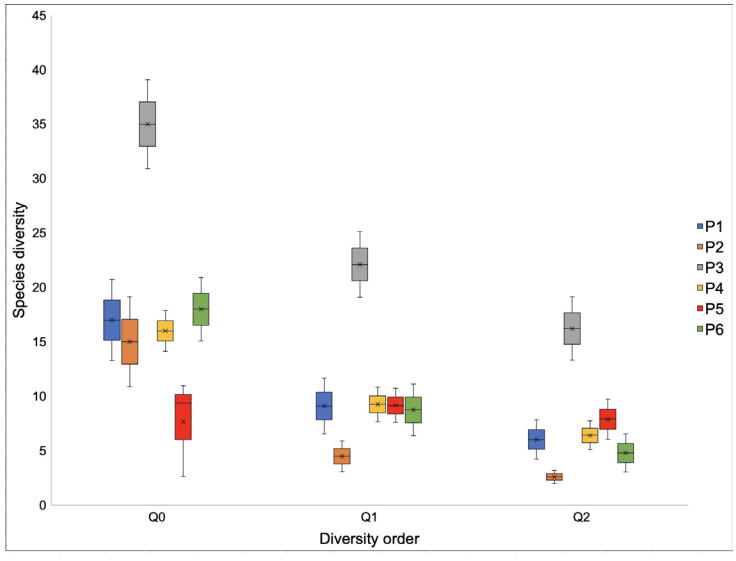

Figure 3. Alpha diversity profiles as a function of q order for ordinary Hill numbers q D (^{0}D, ^{1}D and ^{2}D) of the localities sampled in Sanguaré, Colombia

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P1, P4, and P6 (**Figure 3**). P2 had similar richness (^{0}D) to P1, P4, and P6 but lower ^{1}D and ^{2}D values than P1, P4, and P6 (**Figure 3**). According to the Whittaker beta diversity index (βw = 2.9) and the effective number of communities ($^0D_\beta$ = 3.4), the six types of vegetation cover formed three distinct species assemblages. The Bray-Curtis-based cluster analysis also found three groups, although dissimilarity was high: Group 1 contained P1 and P2 with 63% dissimilarity, Group 2 contained P3 and P4 with 76% dissimilarity, and Group 3 contained P5 and P6 with 88% dissimilarity (**Figure 4**).

The DCA-based vegetation covers and species composition returned two axes that together explained 94% of the variation (88% and 6%) (**Figure 5**). Axis 1 of the DCA grouped species abundance and occurrence of different vegetation covers. We found eight

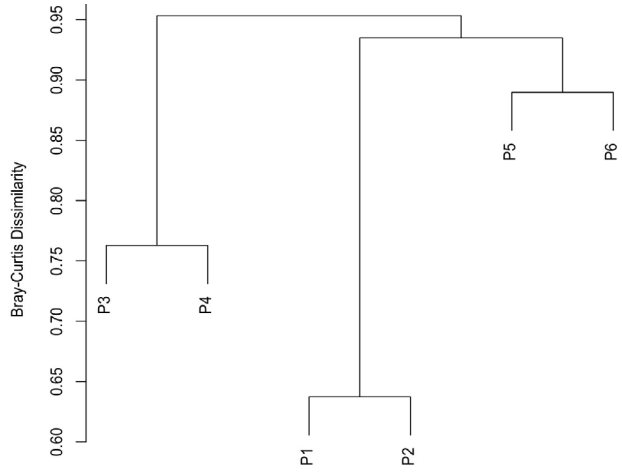

Figure 4. Cluster analysis based on Bray-Curtis dissimilarity (beta diversity) of vegetation covers in the study area

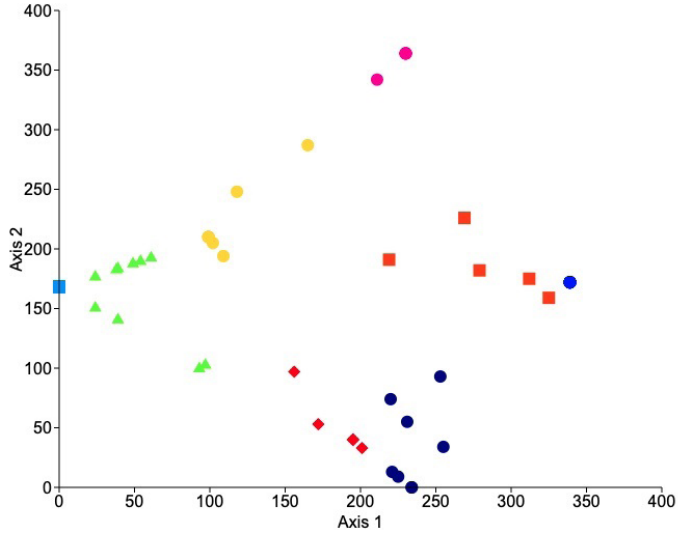

Figure 5. DCA analysis of 184 woody plant taxa in communities from six vegetation cover types in Sanguaré: Species that only occur in P3 (blue square); species that mainly occur in P4 and P3 (green triangle); species that only occur in P4 (yellow dot); species that only occur in P1 (red diamond); species that mainly occur in P1 and P2 (orange dot); species that mainly occur in P5 (pink dot); species that mainly occur in P6 but are also present at low abundance in other vegetation covers (blue dot), and species that mainly occur in P6 (light blue dot)

groups: (a) species that only occurred in P3; (b) species that mainly occurred in P3, and P4; (c) species that only occurred in P4; (d) species that only occurred in P1; (e) species that mainly occurred in P1 and P2; (f) species that mainly occurred in P5; (g) species occurring mostly in P6 but also in other vegetation covers at lower abundance, and (h) species that mainly occurred in P6 (**Tabla 1**).

Discussion

Species composition

The floristic diversity of Sanguaré is similar to other dry forest fragments where Fabaceae is the richest and most abundant family (**Carrillo-Fajardo *et al.***, 2007; **Gentry**, 1995; **Mendoza**, 1999; **Olascuaga *et al.***, 2016). While Fabaceae is the richest family in dry forests overall (**Banda *et al.***, 2016; **Mercado-Gómez *et al.***, 2021), this outcome also suggests that the study area has responded positively to the restoration process in Sanguaré (**Pizano *et al.***, 2014; **Vargas Figueroa *et al.***, 2016; **Vargas**, 2012). This family has several adaptations that make it successful in dry forests, including easy propagation, high growth rates, low water loss due to compound leaves, and defensive structures (spines) (**Ceroni-Stuva**, 2003; **Gei *et al.***, 2018). Furthermore, Fabaceae species are nitrogen-fixers (**Bhaskar *et al.***, 2016; **Vargas *et al.***, 2015), which makes them important in early regeneration areas and promotes resilience and shifts in succession in a forest type with almost no pioneer species, and an important taxon for ecological restoration (**Avendaño-Yáñez *et al.***, 2018). This result also suggests that most of the forest fragments in Sanguaré are in the secondary succession stage, as high Fabaceae richness has been found in secondary dry forest fragments in the Caribbean, Valle del Cauca, and Magdalena regions of Colombia (**Mendoza**, 1999).

Besides Fabaceae, we found a high richness and abundance of Rubiaceae. Different floristics studies of dry forests have reported Rubiaceae as one of the four richest families in dry forests (**Herazo-Vitola *et al.***, 2017; **Luna-Blanco *et al.***, 2022; **Mercado-Gómez *et al.***, 2021). However, in Sanguaré, the species compositions are typical of forests undergoing regeneration (**Mendoza *et al.***, 2004). **Tobgay *et al.*** (2021) have found that Rubiaceae species have a wide adaptability range, making them relatively resilient to anthropogenic effects. On the other hand, although floristic composition studies in dry forests have found high diversity of Capparaceae, Malvaceae, and Euphorbiaceae, this was not the case in Sanguaré; in fact, we did not record Capparaceae species, which are normally found in dry forests (**Mercado-Gómez & Escalante**, 2020; **Mercado-Gómez *et al.***, 2019). Plant cover loss, microclimate changes, and competition for resources may have influenced the failure of the establishment and development of native plant species in Sanguaré, including species from Capparaceae and Malvaceae (**Carbonó-Delahoz & García**, 2010).

Alpha and beta diversity analyses

Diversity analysis revealed that disturbances can promote alpha diversity under certain conditions, creating opportunities for new species to colonize or for existing species to expand and occupy new ecological areas. We found that ^{1}D and ^{2}D values were lower in weedy grassland (P1 and P2). These areas are mainly composed of grasses and lianas, but also contain *Morinda citrifolia*, an exotic species that typically occurs in disturbed forests, exotic grasslands, open areas near the shoreline and around villages, littoral forest understory, and fallow areas and waste dumps (**Heryanto *et al.***, 2009). Usually, *M. citrifolia* is found in disturbed forests at early stages of ecological succession, suggesting that this species can rapidly colonize areas that have been altered by human activities like logging or agriculture (**Olascuaga *et al.***, 2016). We also found *Hiraea reclinate* in weedy grassland (P1 and P2). This woody vine is distributed in wet or dry primary and secondary forests (**Anderson**, 2016). **Schnitzer *et al.*** (2021) demonstrate that liana abundance within tropical forests is increasing rapidly because of forest gaps; thus, the disturbance has emerged as one of the leading hypotheses to explain increasing liana and vine abundance in Sanguaré. Ecological processes such as environmental filtering may have also mediated grassland community assembly following restoration; however, a phylogenetic community structure analysis is necessary to test this hypothesis (**Mudrák *et al.***, 2023).

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Although we sampled forest fragments composed of broadleaf or leafy trees, they had low diversity values (^1D and ^2D) (**Figure 3**), showing that tall shrubs, secondary forests, and mature forests are not necessarily the richest vegetation cover. These areas are composed of species that are typical of more advanced states of succession; for example, secondary forest (P5) had a high abundance of *Cecropia peltata,* a fast-growing pioneer typical of larger disturbed patches in Neotropical forest (**Fleming & Williams**, 1990). **McKey** (1988) pointed out that this species allows the arrival of other taxa and, therefore, facilitates the colonization of disturbed areas by lianas and small trees. *Machaerium arboreum* Vogel also occurs in these vegetation covers; this species is wind-dispersed, facilitating its propagation in dry environments. It plays an important role in the restoration process in Sanguaré because it contributes to the recovery and enrichment of impoverished soils (**Meléndez González**, 2009). *Stylogyne turbacensis* also had a high abundance and, likewise, has been associated with disturbed forests (**Luna-Blanco *et al.***, 2022). These species limit the development of herbaceous plants, lianas, and shrubs, leading to the local extinction of shade-intolerant or early succession species, which tend to have a short life cycle (**Luna-Blanco *et al.***, 2022).

The Low shrub vegetation type (P3) had higher values of ^0D, ^1D, and ^2D. Low shrubs present high environmental variability and, therefore, a wide range of microhabitats that can be colonized by different species, including grasses, vines, lianas, and trees with the capacity to compete and tolerate disturbance in both disturbed and undisturbed forests (**Chambers *et al.***, 2014). Our findings revealed that diversity is low in the early stages of succession when several pioneer species are introduced, reaches its maximum during the mid-succession period when mid-succession and climax species co-occur, and, finally, declines due to competitive exclusion among climax species (**Nakadai & Suzuki**, 2022). This outcome of diversity can be explained by the intermediate disturbance hypothesis of **Connell** (1978) predicts higher diversity in areas with an intermediate degree of disturbance. Besides, the IDH suggests that sufficient disturbance facilitates the establishment of early-stage (disturbance-dependent) species in late-stage formations and, thus, can increase diversity, whereas excessive disturbance is intolerable for some species and, so, will reduce diversity even in early-stage communities (**Connell**, 1978; **Sheil & Burslem**, 2013). This pattern of diversity has also been found in different ecosystems where diversity values are higher in an area with intermediate disturbance than in undisturbed forests (**Addo-Fordjour *et al.***, 2015; **Ghazoul**, 2002; **Swart *et al.***, 2019).

Although we found that the beta diversity index suggests approximately three species assemblages and the Bray-Curtis dissimilarity showed shared species among P1-P2, P3-P4, and P5-6, cluster analysis indicated that each vegetation cover was distinct due to the high dissimilarity among the groups. Although P2 and P1, or weedy grassland, shared more species than other vegetation covers, this similarity was relatively low, only 35%. Low and tall shrub plots also shared species, but they had a 75% dissimilarity among them, while between secondary forest and mature forest the dissimilarity was even higher (90%). DCA outcomes support the idea that each vegetation cover is different because we found eight groups, only three of which represent species turnover: P4-P3, P1-P2, and P6, with the other sampling units supporting the βw and $^0D_\beta$ outcomes. The dissimilarity index allowed us to interpret the amount of variation in species composition between sampling units. In this sense, we found a high variation, which is explained as a high beta diversity index because of the low level of similarity between the species composition of the weedy grassland, low shrub, tall shrub, secondary forest, and reference or mature forest (**Whittaker**, 1960).

Forest fragments in Sanguaré were cleared for cattle grazing or crop cultivation, leaving these areas devoid of vegetation. High or increased levels of disturbance in Sanguaré eliminated native species that are incapable of rapid recolonization and growth, and, hence, they facilitated biological invasion by species from nearby fragments or nonnative taxa that grow rapidly (**Catford *et al.***, 2012). Disturbance causes divergence in plant community composition (high beta diversity) between different sites by

increasing habitat filtering across environmental gradients and forming dissimilar species assemblages (**Socolar *et al.***, 2016). In Sanguaré, disturbance altered beta diversity by changing the relative importance of community assembly mechanisms that influence spatial aggregation of species across landscapes.

The higher observed beta diversity in Sanguaré indicated an overall biotic heterogenization process consistent with the idea that the originally diverse vegetation is now reduced to small and isolated patches, with unique disturbance histories and impoverished communities derived from a larger regional species pool (**Vidal *et al.***, 2019). To explain post-disturbance increases in beta diversity or heterogenization, **Tatsumi *et al.*** (2020) suggest that disturbance excludes similar sets of regionally abundant species existing across large numbers of patches. Furthermore, disturbance removes regionally abundant species, but only some of them across different local patches, leaving new or rare species less susceptible to the climatic conditions of the open areas in these new ones, which results in different floristic compositions (**Stewart & Globig**, 2016). We found rare species at all sampling sites, including alien taxa. In Sanguaré, beta diversity should increase because disturbance promotes spatial variation in population establishment via environmental heterogeneity, which provides new habits for rare species. **Stewart and Globig** (2016) pointed out that disturbed sites exhibited higher frequencies of rare species and, thus, higher beta diversity than undisturbed sites. Therefore, disturbance induces colonization of new species in such a way that each species colonizes a small number of patches, like the sampling units in Sanguaré.

Conclusions

The initial set of species present in Sanguaré was removed due to disturbance. Nevertheless, the establishment of native species such as *Spondias mombim* or *Bursera simaruba* has contributed to the recovery of diversity levels to those before the anthropic impact representing a positive result of the restoration process that is being carried out in the study area. However, we also found alien species, likely due to the removal of the natural cover that has left empty areas more easily colonized by alien species better adapted to anthropogenic disturbance.

Our results show that diversity will be low at both extremes of the disturbance degree: weedy grassland and mature forest. The lower alpha diversity is presumably due to a reduction in the generalist species and the loss of rare and native species. Diversity appears to peak at an intermediate level of disturbance in low shrubs, which we attribute to the coexistence of dominant competitors and rapid colonizers (**Svensson *et al.***, 2012). The IDH has been validated in areas under ecological restoration. In the paper that originally proposed the IDH, the hypothesis is primarily concerned with richness, i.e., the number of species. However, here, we found that other aspects of diversity, such as the relative abundance of species, evenness, and dominance, also follow the IDH predictions.

Although our initial prediction was that biotic homogenization had occurred in Sanguaré, we suggest that the results of beta diversity cannot be used to unambiguously identify homogenization changes in assembly mechanisms that influence clumping of species in disturbed and undisturbed landscapes. Thus, relationships among beta diversity, disturbance, and community assembly are not yet generalizable. Our results are relevant to ecosystem management and conservation. A rich understanding of the mechanisms by which disturbance alters beta diversity would not only help advance community assembly theory but also our knowledge of how to preserve and restore biodiversity in human-modified ecosystems.

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Conflict of interest

There have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

Author contributions

MGJ: Conceptualization, formal analysis, methodology, writing of the original draft, review, and editing; **GFH:** Conceptualization and methodology; **BG:** Conceptualization, formal analysis, methodology, data curation, and investigation.

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