

## RESEARCH ARTICLE

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# Clonal propagation, scale dependent assembly, and nucleation drives natural regeneration in a *restinga* sandy coastal plain

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## Abstract

On the sandy coastal plains, environmental filters that limit seedling establishment and survival create a naturally heterogeneous landscape, formed by vegetation patches inserted in a matrix of bare sandy soil. The succession processes in these ecosystems depend on some pioneer species that facilitate the recruitment and survival of other species. Here, we evaluated the spatial pattern and changes of vegetation patches of *restinga* (i.e., coastal sandy plain vegetation) over one decade (2011–2021). The research was carried out in Alagoas State, Northeast of Brazil. We considered as patches the vegetation islands inserted in a matrix of bare sandy soil and applied methodologies of photointerpretation. Landscape metrics included patch area, edge, shape, and core area. To test the effect of landscape metrics on species occurrence and species richness per patch, we applied generalized linear models (GLM) with binomial and quasi-Poisson distributions, respectively. We used the “betapart” package to evaluate the importance of turnover and nestedness as drivers of beta diversity among patches. Our data indicate that a key plant (*Myrciaria floribunda*), which can propagate by root suckers, initiates a succession process, creating regeneration nuclei, which seem to follow a deterministic succession pattern until the patch reaches 10 m<sup>2</sup> in area. In the successional sequence, the patches grow and coalesce with neighboring patches. Species richness of patches presented an unimodal response to patch size. Overall, there is a greater contribution of species turnover to among-patch beta diversity. However, for patches smaller than 10 m<sup>2</sup>, beta diversity was mostly driven by nestedness, reflecting a process of species addition to the growing patches. The succession pattern found in the study area should be considered for the formulation of nature-based restoration models, expected to be more efficient and effective for ecosystems with similar environmental filters.

## KEYWORDS

assembly line, coastal vegetation, ecological succession, landscape ecology, sandy soils, turnover

## 1 | INTRODUCTION

Coastal ecosystems, including sandy plains, mangrove swamps, and other wetlands, have been severely affected by human activities around the world, as coastal areas are the most densely populated

areas on the planet. Despite the existence of large extensions of degraded coastal areas, little is known about the patterns that guide the successional mechanisms in these environments. This lack of theoretical knowledge on succession hampers the application of effective large-scale restoration initiatives.

In Brazil, *restinga* is both a geomorphological and botanical term, applied to name coastal sandy plains dating from the Quaternary, as well as the vegetation that occurs in these areas (Zamith & Scarano, 2006). Previous studies in *restinga* have shown that few plants are able to establish themselves via seeds in bare sand, mainly due to high temperatures, luminosity, winds, low humidity, and lack of organic matter. Therefore, regeneration in the *restinga* depends on pioneer plants that facilitate the arrival and establishment of other species (Dias et al., 2005; Sampaio et al., 2005; Zamith & Scarano, 2006).

In some cases, the plants that become established in the early stages of succession are ramets of tree or shrub species that colonize bare sand through clonal growth. For example, root sucking has been reported for *restinga* areas (Cirne & Scarano, 2001; Scarano et al., 2004) and for other types of vegetation as the temperate rainforest and tropical dry-forest (Escandón et al., 2020; Vieira et al., 2006). However, ecological literature has underestimated this type of initial colonization importance, considering that it can be a successful pattern for local plant dispersal in many ecosystems, in which water and thermal stress conditions do not favor germination and initial plant growth (Silva & Moura, 2021). The first plants that establish themselves can serve as perches or offer resources such as food and shelter for seed-dispersing birds (Dias et al., 2005), or create physical or biological conditions for the establishment of other species throughout the succession, acting as nurse plants (Tirado et al., 2015), triggering the formation of vegetation cores. Positive interactions are cited as important factors in diversity maintenance as environmental stress increases (Bertness & Callaway, 1994; Cavieres & Badano, 2009; Filazzola & Lortie, 2014). Thus, many coastal areas, such as sandy plains, sandbanks, and dunes, exhibit aggregated patterns of species distribution, with areas comprising vegetation patches and areas of bare soil, especially those with recurrent impacts.

Natural succession patterns characterized by the emergence and subsequent coalescence of vegetation patches of varying sizes have also been reported for other types of vegetation in other parts of the planet (Correia et al., 2010; Cutler et al., 2008; Vieira et al., 2013; Visser et al., 2004). This succession model seems to follow a classic pattern of primary succession described by Yarranton and Morrison (1974), which is based on nucleation resulting from facilitation processes and is apparently more common in sandy soils (Brooker et al., 2008; Pugnaire et al., 2011; Vieira et al., 2013).

Some authors suggest that the spatial structure can mediate interactions between species (Bertness & Callaway, 1994) and diversity (He & Legendre, 2002). Many successional characteristics, such as the species richness of a community, are intricately linked to landscape structural patterns, especially concerning the size and number of patches (Bascompte & Rodríguez, 2001; Meloni et al., 2020). Thus, understanding how the spatial structure of an ecosystem develops and how assemblages respond to the size and number of patches in the landscape is central to predicting its long-term dynamics and may help predict their responses in the face of degradation scenarios (Matias et al., 2010), as well as support effective restoration proposals.

In this sense, we analyzed the succession process in an area of coastal sandy plain, located in a Protected Area (APA da Marituba), in

northeastern Brazil, through analyses of the spatial pattern and changes of vegetation patches of *restinga* over one decade (2011–2021), and the contributions of species turnover/nestedness to beta diversity (Socolar et al., 2016), in relation to landscape metrics.

We hypothesized that (1) there is a centrifugal growth pattern, initiated by key species that triggers the succession process; (2) the assembly of plants, throughout the successional process, is scale-dependent, and bigger patches will present different compositions in relation to the smaller ones since they will represent different stages of succession, and (3) initially, beta diversity variation will be driven by nestedness, as only a specific pool of species will be able to cope with the environmental constraints imposed by the sandy soils of the studied area. Subsequently, with the increase in patch size, beta diversity will be driven by turnover, as the arrival of the initial species will create suitable environments for the colonization of species from more advanced successional stages.

To test our hypotheses, we analyzed (i) the change in the total area of vegetation cover and its relationship with the expansion of existing patches and the emergence of new ones; (ii) patch species richness and the correlation between the species composition of the patch and the landscape metrics (area and shape, edge index, and core area); (iii) key plant assemblages in the initial stage of succession; (iv) changes in the patch species assemblages as a function of patch age and/or size; and (v) the partitioning of among-patches beta diversity between species turnover and nestedness.

## 2 | METHODS

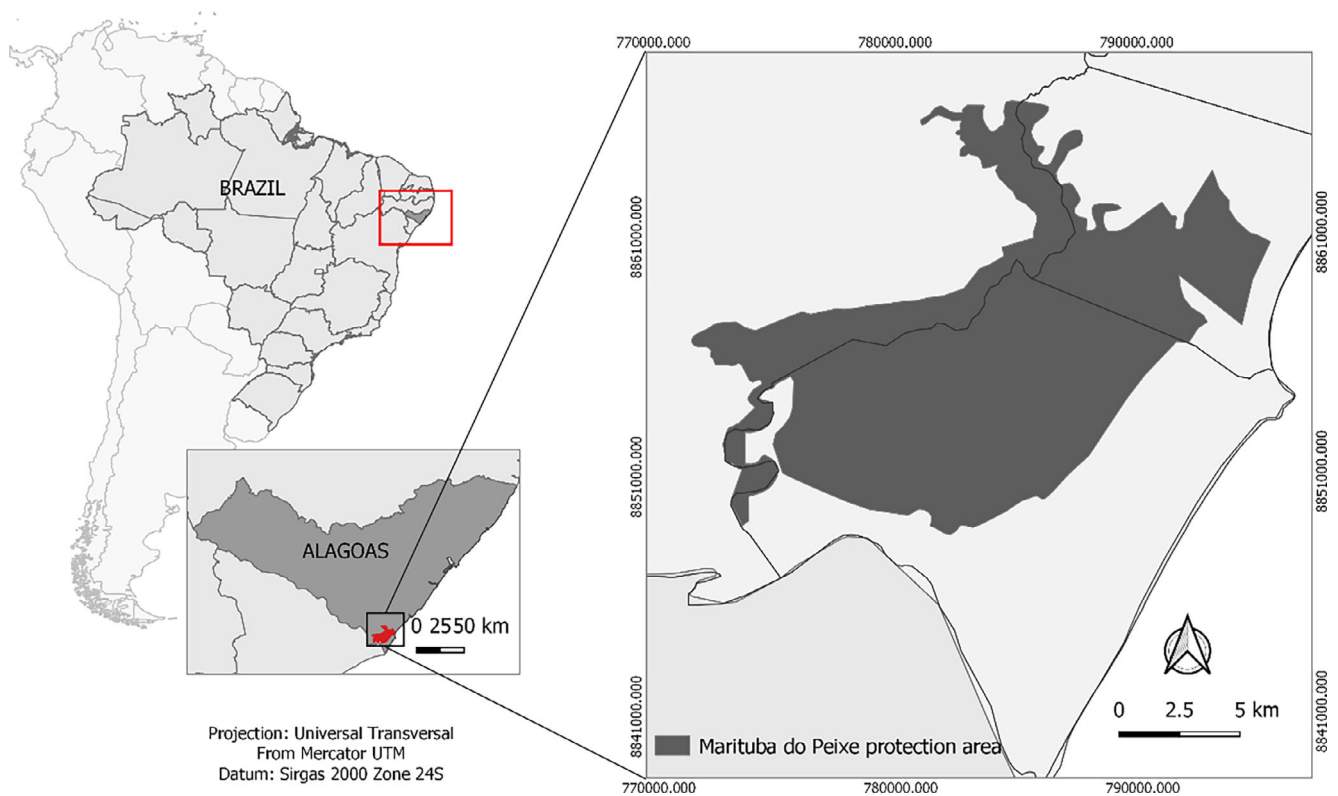
### 2.1 | Study area

This study was carried out in the *Marituba do Peixe* Environmental Protection Area, a sustainable use conservation unit (Figure 1), analogous to category VI management of protected areas of the IUCN (Dudley, 2008). The *Marituba do Peixe* EPA is partially covered by the Atlantic Forest and is situated within the *Piauí* and *Marituba* river basins, forming lakes during the rainy season in the floodplains (Lopes et al., 2022). The study area is located between sandy ridges of dense vegetation and neighboring areas of coconut monoculture, which occupies a large part of the territory of the conservation unit (Lopes et al., 2022). In these areas, there are constant impacts that are caused by fire, wood removal, and extensive grazing.

The area is located in the south of the State of Alagoas, Brazil, and is characterized by a sub-humid climate, with precipitation around 1100 mm. Its topography is relatively flat, and the soil is mainly composed of dystrophic quartz sand of marine origin (ALAGOAS, 2006).

### 2.2 | Image selection and sample design

We applied methodologies of photointerpretation, on images corresponding to the years 2011 and 2021. For the year 2011, we used a mosaic of images obtained through *Google Earth pro* Maxar



**FIGURE 1** Location of the Marituba do Peixe Environmental Protection Area, Alagoas, Brazil. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

Technologies, corresponding to the month of December 2011, using a maximum zoom of 49 m for manual vectorization of the patches. All the selected images had low cloud cover and were freely accessible.

For the year 2021, we used high-precision drone images obtained through an RPAS (Remotely Piloted Aircraft System—Phantom 4 PRO), equipped with a camera with a 20-megapixel on-board sensor and 1" CCD size, 94° FOV, an f/2.8 optical aperture, with a spatial resolution of 3 cm.

We marked and vectorized 110 patches of vegetation seen in images from 2011 and/or 2021, based on photointerpretation, considering elements of roughness and color in compatibility with arboreal and/or arboreal-shrubby vegetation. All the vegetation islands inserted in a matrix of bare sandy soil were considered as patches.

Each patch visualized in the 2021 images was visited in the field from January 2021 to December 2021. All plant species within each patch were identified to the lowest taxon possible and classified according to their habit (Table S1). For 104 of the 110 patches analyzed, it was possible to make a complete identification of the species.

### 2.3 | Structural characteristics of patches and determination of the patch expansion pattern

In the patches marked in the 2011 images, only the patch area was measured, and for the patches of 2021, the landscape metrics included patch area, edge, shape, and core area (considering 5 and

10 m of edge effect distances) (Table 1). These indices were calculated in Arcgis10.3 software with the help of the V-LATE 2.0 extension tool. The comparison of the patches aimed to verify if there was regression, expansion, coalescence, or suppression of patches over the years, as well as to assess the shape and growth pattern of these patches.

To answer if there is a pattern in the expansion of the patches, we superposed the images of 2011 and 2021 and analyzed if there were differences in patch areas for each studied patch. For this comparison, the landscape metrics Area, Edge, Shape, and Core Area (Table 1), selected for their influence on species richness in the patches, were considered and calculated using GIS software. In addition, these landscape metrics have characteristics that should be evaluated as interrelated variables, such as the Shape Index and Edge, for which irregular shape can increase the edge effect and could decrease species richness and also avoid the occurrence of species with a lower tolerance to extreme environmental conditions.

### 2.4 | Data analysis

We built distance-based linear models (distLM) using the function “adonis” from the vegan package in R software (Oksanen, 2013) to test whether variations in the composition of plant assemblages were determined by landscape metrics. In these models, the similarity matrix between the species of the sampled assemblages, calculated based on the Jaccard distance, was used as the response variable. The

**TABLE 1** Description of landscape metrics used.

Index	Formula	Explanation
Area	$AREA = 0.5 \cdot \sum (x_{i+1} - x_i) (y_{i+1} - y_i)$	Size of the patches.
Edge	$PERIM = \sum \sqrt{(x_{i+1} - x_i)^2 + (y_{i+1} - y_i)^2}$	The higher the value, the greater the edge effect.
Shape	$SHAPE = \frac{p}{\sqrt{\pi \cdot a}}$	Complexity of the patch based on a standard feature 1, high values can be advantageous when regular shapes are privileged.
Core area	$\frac{CY-NP-NCAI=0}{NCA}$	Sum of the central areas of the patches. The higher the index, the greater the core area, meaning a larger, less jagged patch. It is calculated considering determined edge effects areas. In our study, it was measured considering two possible edge sizes, 5 and 10 m.

Source: Adapted from: Langanke et al. (2005) and McGarigal (2002), cited and Lang and Blaschke (2009).

distance matrix of landscape metrics was calculated based on the Euclidean distance and was inserted as a predictor. The models were simplified to their simplest form by removing non-significant variables, considering an alpha = 0.05. For all tests performed, the correlations between the predictor variables were initially tested, to avoid the effect of autocorrelation in the construction of linear models.

To test the effect of landscape metrics on the probability of occurrence of each species in patches, we applied GLM with binomial distribution. The response variable was the presence (1) or the absence (0) of the species. The predictor variables were the significant variables for the distance-based linear model. Models were not built for species that occurred in all patches or whose occurrence frequency was lower than five patches since the inclusion of these species generated an effect of non-convergence of the models.

To test the effect of landscape metrics on species richness per patch, we used a generalized linear model with quasi-Poisson distribution, in which patch richness was used as the response variable and the landscape metrics as predictor variables.

To assess the effects of turnover and nesting on the beta diversity (Baselga, 2010) among the patches, we used the package “beta-part” (Baselga et al., 2021). The analyses were carried out for three subsets of patches: all the sampled patches; patches smaller than 10 m<sup>2</sup>; and patches found only in 2021, and therefore younger than 10 years regardless of their size.

To verify possible relationships among species pair occurrence we built Spearman correlation matrices and tested the correlation among the presence and absence of each species pair. The analyses were implemented with the functions “cor” and “cor.mtest” of the package “Hmisc” (Harrell, 2023).

After sampling we verified that *Myrcia guianensis* (Aubl.) DC. occurred in 78% of the sampled patches, so we also tested our data for the role of this species as a nurse plant. To test the effect of the presence of *M. guianensis* on species richness in patches above 10 m<sup>2</sup> we used generalized linear models with quasi-Poisson distribution in which the species richness of each patch was inserted as a response variable and the presence or absence of *M. guianensis* was entered as a predictor variable. For this analysis, we removed the registers of *Myrciaria floribunda* (H. West ex. Wild.) O. Berg LC. because this species occurred in all of the sampled patches.

To test whether the presence of *M. guianensis* may alter the composition of communities in patches above 10 m<sup>2</sup> we used a distance-based linear model (distLM). To implement this model, we constructed a distance matrix considering the species composition in each patch above 10 m<sup>2</sup>. This matrix was constructed using the Jaccard distance since we had records of the presence or absence of species per spot. This matrix was entered as a response variable and the presence or absence of *M. guianensis* was entered as a predictor variable. All analyses were performed in the R environment (R Core Team, 2021).

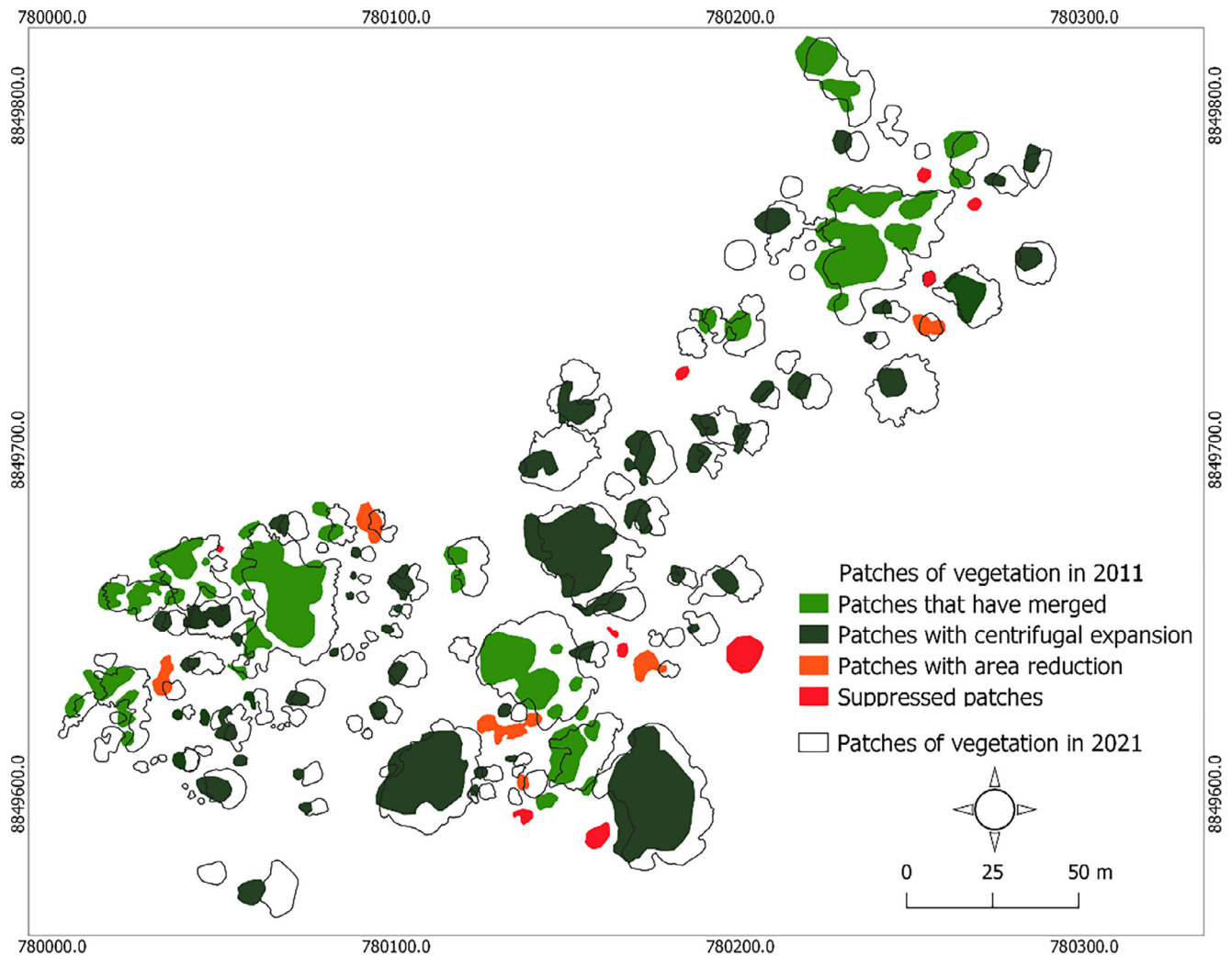
### 3 | RESULTS

The succession process appears to be triggered by *M. floribunda* which would act as a nurse plant. Patches richness and composition were scale dependent. The beta diversity was initially driven by nestedness in small patches, while the turnover gained importance with the increase in the patch area. For a better presentation, we divided the results into the following topics: (i) plant cover changes and patch metrics; (ii) species richness, correlation among species occurrence and effects of landscape features in patches plant assemblies; and (iii) ecological succession patterns on sandy coastal *restinga* assemblies and the partitioning of beta diversity.

#### 3.1 | Plant cover changes and patch metrics

Total plant cover increased by 58.09% from 2011 to 2021. Our results indicate that this increase is linked to the expansion of existing patches and the appearance of new patches. Of the 110 patches analyzed in the 2011 image, 94 exhibited centrifugal expansion, and 35 of these merged with neighboring patches. Six patches presented area decreases, and 10 patches were totally suppressed. We found that 28 new patches were formed during the study period and were identified only in the 2021 image (Figure 2). These new patches presented areas ranging from 1.83 to 34.84 m<sup>2</sup>, with a mean area of 13.52 ± 12.70 m<sup>2</sup>.

Patches with smaller areas tended to have shape index values closer to 1, which configures patches with rounded shapes. As patches grow, they exhibit irregularities in their shape and the index value tends to be higher.



**FIGURE 2** Plant cover of the observed vegetation patches ( $n = 100$ ) of *restinga* from 2011 to 2021. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/ldr.3057)]

Of the 100 patches viewed in 2021, only 5 displayed core area index considering 10 m of edge effect, and 15 patches displayed core area considering 5 m of edge effect.

### 3.2 | Species richness, correlation among species occurrence, and effects of landscape features in patch plant assemblies

We sampled a total of 36 species distributed in 25 botanical families (Table S1). The most representative families were Myrtaceae (presenting 5 species) and Anacardiaceae, Apocynaceae, and Rubiaceae (presenting 2 species each). All the other 21 sampled families were represented by one species each. Sampled species were distributed in many life forms ranging from herbs to trees, but the majority of sampled species were classified as trees. The vegetation patch seems to start in a predictable way, by a plant species, *M. floribunda*, that apparently establishes itself by clonal propagation, through sucker roots

released from individuals that make up an established vegetation nucleus (Figure 3).

Species richness per patch varied from one to 25 species, with a mean number of  $12 \pm 7$ . All patches with areas greater than  $200 \text{ m}^2$  presented more than 10 species, while all the patches with areas smaller than  $10 \text{ m}^2$  presented from 1 to 5 species. The relationship between species richness and patch area is unimodal (Figure 4) (Table S2), showing a tendency that peaks in patches with areas near  $600 \text{ m}^2$  and begins to decrease from this point. There was a positive effect of the presence of *M. guianensis* (Murta) on species richness in fragments larger than  $10 \text{ m}^2$  (Figure 5).

The assemblages present in the patches were influenced by landscape metrics such as patch area, core area, shape, and edge index (Table S3). However, species occurrence probabilities did not present uniform responses to landscape metrics, indicating that species-specific traits may be responsible for the colonization patterns in the study area (Table S4). Some species like *Anacardium occidentale* ( $p = 0.005$ ), *Cnidocolus urens* ( $p = 0.001$ ), *Lundia longa* ( $p = 0.0001$ ),





**FIGURE 3** Plant species are found early in the formation of plant patches in restinga areas. (a)—*Myrciaria floribunda*; (b)—*Myrciaria floribunda* and *Piloosceus catingicola*; and (c)—*Myrciaria floribunda*, *Piloosceus catingicola*, *Hohenbergia catingae* and *Xylopia laevigata*. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/ldr.3057)]

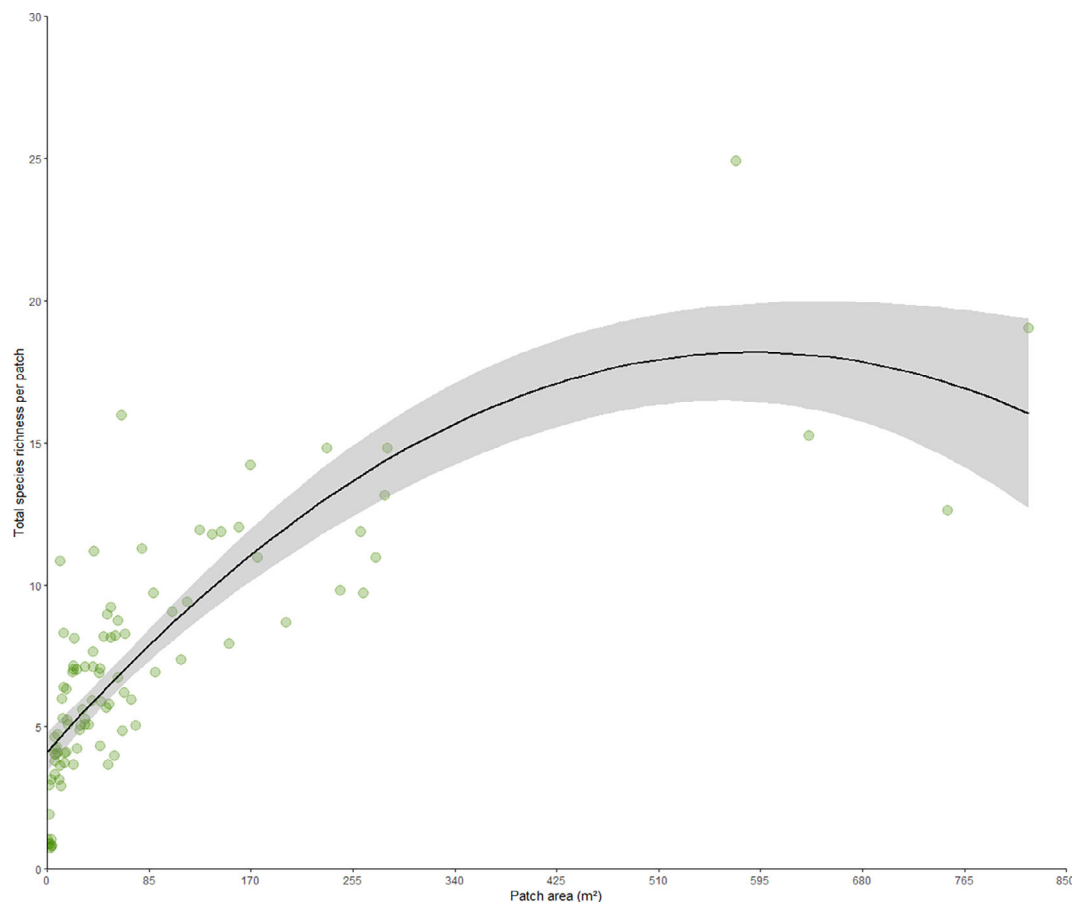
*Manilkara salzmannii* ( $p = 0.02$ ), *Passiflora cincinnata* ( $p = 0.007$ ) e *Protrium heptaphyllum* ( $p = 0.001$ ) presented positive relationships with patch area, while other species like *Himatanthus bracteatus* ( $p = 0.02$ ) presented negative relationships with patch area. Other landscape features of the patches as the edge index also affected species probability occurrence, like *Borreria verticilata* ( $p = 0.004$ ), *Hohenbergia catingae* ( $p = 0.008$ ), *Ocotea acutifolia* ( $p = 0.001$ ), and *Xylopia laevigata* ( $p = 0.0001$ ) that were positively influenced by irregular shapes. Some species were affected by more than one variable presenting different relationships with each of the measured landscape metrics. For example, *M. guianensis* and *Solanum paniculatum* probability occurrences were negatively affected by patch area and positively affected by the edge index.

### 3.3 | Ecological succession patterns in restinga assemblies and beta diversity partition patterns

Considering the patch areas as a proxy for a chronosequence, in which small patches are presumably younger than great patches, the ecological succession in the area presented a predictable pattern in which the first species to establish in a forming nucleus is *M. floribunda*, that was the only species present in patches smaller than  $2 \text{ m}^2$ , besides its presence in all the sampled patches.

*M. floribunda* is found in association with *Pilosocereus catingicola*, the second species to arrive in the successional sequence, being present in 97% of patches with areas greater than  $2 \text{ m}^2$ . *H. catingae* is likely the third species to arrive, and was present in 98% of patches with areas greater than  $6 \text{ m}^2$  (Figure 3). *C. urens* and *B. verticilata* are also found in patches with areas smaller than  $10 \text{ m}^2$ , but the order in which they appear was not consistent in relation to patch area. These five species were consistently recorded in patches with less than  $10 \text{ m}^2$ . One exception was the presence of *X. laevigata* that occurred one time in a patch with an area smaller than  $10 \text{ m}^2$  and was found in 93% of the patches greater than  $10 \text{ m}^2$ , many times in co-occurrence with *M. guianensis*, found in 78% of patches bigger than  $10 \text{ m}^2$ . *A. occidentale* was found only in patches with an area bigger than  $160 \text{ m}^2$ .

The presence of *M. guianensis* altered the species composition of patches larger than  $10 \text{ m}^2$  ( $df = 1$ ,  $R^2 = 0.10$ ,  $F = 9.3154$ ,  $p < 0.001$ ) (Figure 6), and presented a positive correlation with many other species, like *X. laevigata* (Meru) ( $r = 0.69$ ,  $p < 0.05$ ) (Figure S1). *Philodendron acutatum* (Imbé) was positively correlated to tree species like *A. occidentale* L. (Caju) ( $r = 0.73$ ,  $p < 0.05$ ). Important species pairs of the initial successional process like *H. catingae* and *P. catingicola* were also highly correlated ( $r = 0.68$ ,  $p < 0.05$ ). These two species were recorded in 88% and 92% of the patches, respectively, and can be considered pioneer species for this environment, like *M. floribunda*.



**FIGURE 4** Species–area relationship in the studied *restinga* patches. The relationship shows a tendency that peaks in patches with areas near 600 m<sup>2</sup> and begins to decrease from this point. The line was adjusted using the best model fitted to the relationship and the gray area represents the 95% CI. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/for.3057)]

We verified a low number of negative correlations among species occurrence (Figure S1). Four species exhibited high and positive correlation coefficients but were not considered in our scenario since they were recorded in a low number of patches (1–6 patches) which may have caused the statistical relation without a correspondent ecological one. There were few cases of negative correlation and with inexpressive values (Figure S1).

The beta diversity partition analysis showed that when considering all the available patches, the contribution of turnover ( $\beta_{TU} = 0.90$ ) was higher than that of nestedness ( $\beta_{NE} = 0.07$ ) for beta diversity variation in the study area. This showed that there is a substantial species substitution among patches of different areas (Figure 7a). On the other hand, when considering only those patches smaller than 10 m<sup>2</sup>, presumably in the initial phase of ecological succession in *restinga* areas, we observed a different pattern, with the growth of nestedness contribution ( $\beta_{NE}$  foi 0.54), superior to turnover ( $\beta_{TU}$  de 0.33) (Figure 7b). The species composition is extremely similar at the beginning of a patch formation until it reaches a size of 10 m<sup>2</sup>.

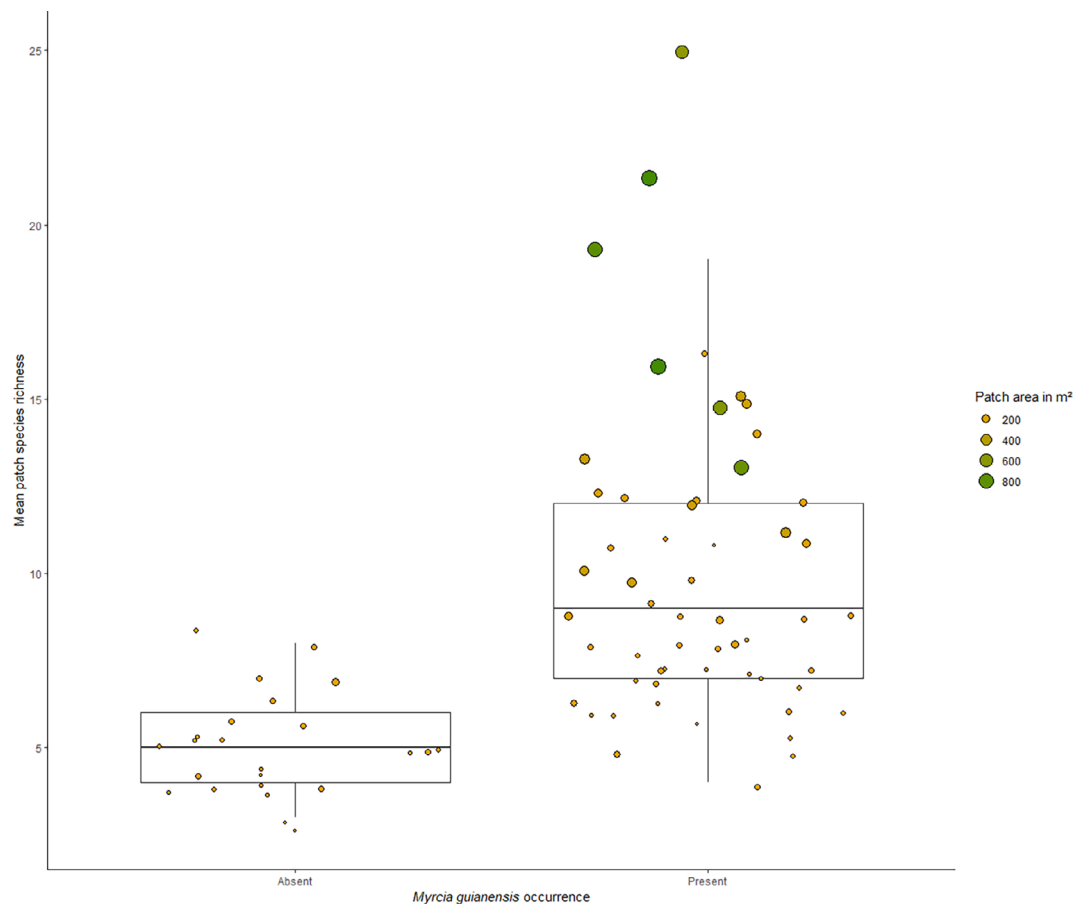
In relation to the time of appearance of the patches on the satellite images, those patches that were only observed in 2021, thus younger than 10 years old, and whose areas varied from 0.88 to 43 m<sup>2</sup>, the turnover component of beta diversity variation was also

higher ( $\beta_{TU} = 0.67$ ) than the one related to nestedness ( $\beta_{NE} = 0.24$ ) (Figure 7c).

## 4 | DISCUSSION

### 4.1 | Spatial dynamics of plant cover

The centrifugal growth and the fusion between patches indicate that ecological succession is driven by species that agglomerate in patches. This patch expansion and coalescence with neighbor patches generate more uniform forest patches in the most advanced successional stages. The succession based on patch formation has been reported by several authors studying a plethora of different ecosystems that were mainly located in arid regions (Tirado et al., 2015; Zaluar et al., 2000; Zhang & Tielbörger, 2019). Most of these studies link the pattern of species aggregation to a sum of two key processes: (1) facilitation mechanisms promoted by nurse plants and (2) the difficulties of plant recruitment in open areas, that impose more severe environmental filters. There is a high need for a better understanding of the facilitation mechanisms in our study area, but in the face of processes that occur in similar environments they may be linked to decreases in



**FIGURE 5** Comparison of species richness in patches with the presence and absence of *Myrcia guianensis*. The boxes represent 75% of the data, the line represents the median and the whiskers represent the standard error. Dots represent the sampled patches and dot size, and color are related to the sampled patch area. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/for.3057)]

soil temperature, increases in nutrient availability, and feed for frugivorous. Also, vegetation patches can be a seed trap for anemocoric seeds. Also, vegetation patches can be a seed trap for anemocoric seeds. In patch areas, a greater deposition of seeds by the feces of frugivorous animals, such as lizards and small mammals, is also expected (Filazzola & Lortie, 2014; Loureiro et al., 2022). The tendency of initial colonization of plant species in patches is also described for coastal environments, where the aggregation is a strategy through which plant communities become more complex, increasing their diversity and plant cover based on a key nurse plant presence (Zaluar et al., 2000).

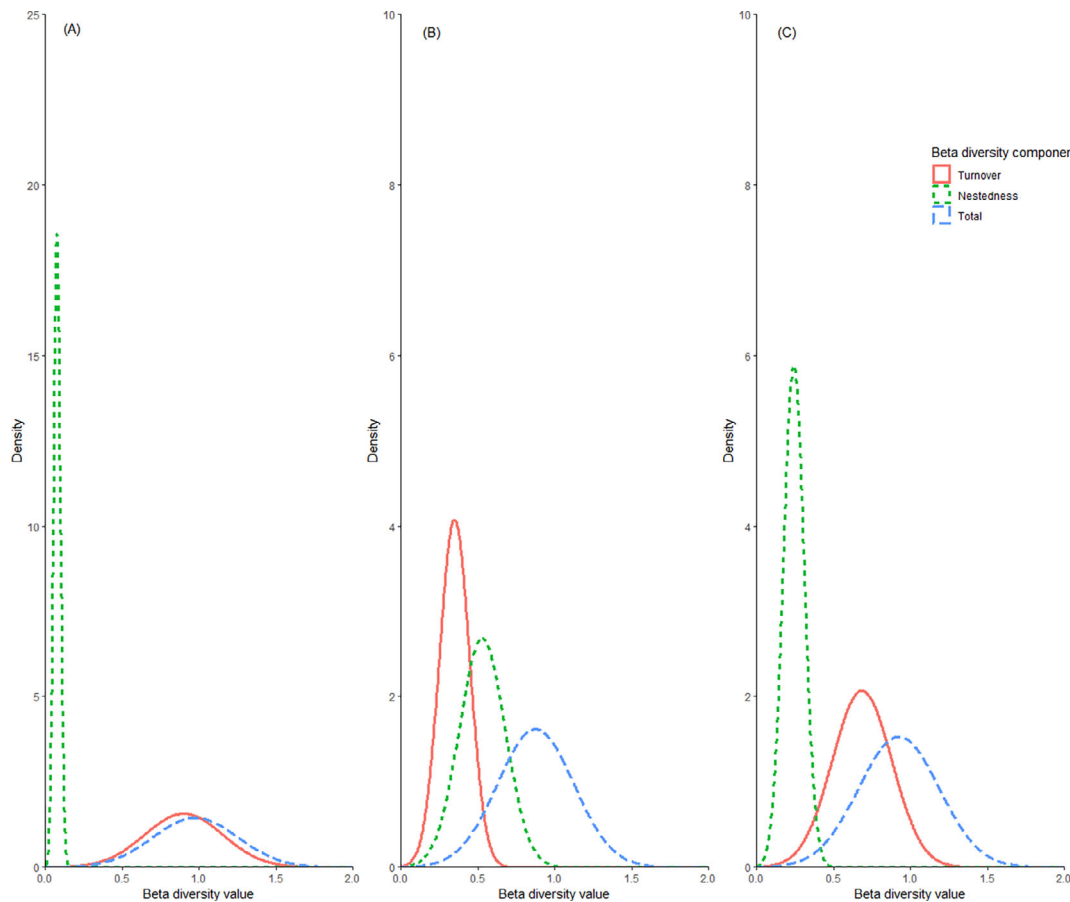
The plant individuals that start patch formation are, in general, more resistant pioneer species or ramets from individuals that inhabit neighboring patches. In this process, which seems very common, although poorly described in the literature, shrubs or trees that bear sucker's roots propagate to open areas, initiating a new patch. These roots possibly act as a drain, sustaining the plantlet in its establishment phase. In other species that present clonal growth, ramets that remain attached to their parental plants may receive nutritional boosts from the reserves from the parental individual (Coelho et al., 2007; Demetrio & de Freitas Coelho, 2023). In this sense, clonal growth may play a key role in *restinga* habitats, once a few species are able to

colonize and establish in sand (Liebig et al., 2001; Zaluar et al., 2000). For example, in *restinga* areas of the Restinga de Jurubatiba National Park, Scarano et al. (2004) found a colonization pattern that was based on patches initially formed by ramets of *Clusia hilariana* Schldl, *Aechmea nudicaulis*, and *Allagoptera arenaria*, after which other species were able to colonize the area.

The three species cited in this study, *M. floribunda*, *P. catingicola*, and *H. catingae* seem to play similar functions. *M. floribunda*, for example, present a similar system of sucker roots, like *C. hilariana*. Both can start the formation of a new patch by the establishment of clonal individuals that are sustained by their parental clones, located in neighbor patches, in the initial phases of succession. These ramets may also participate in labor division processes with other attached ramets (Alpert & Stuefer, 1997). This may enhance ramet survival and success because different ramets may be linked to different ecological functions at different times (Demetrio et al., 2014). Ramets also present more sustentation tissues in comparison to seedlings of the same size (Cirne & Scarano, 2001), which allows their better establishment in unstable habitats like dunes and sand ridges, enhancing the use of clonal species as triggers for restoration processes in these habitats.

Plants of the family Bromeliaceae are thought to be excellent nurse plants in sandy *restinga* soils (Scarano, 2002), playing a central





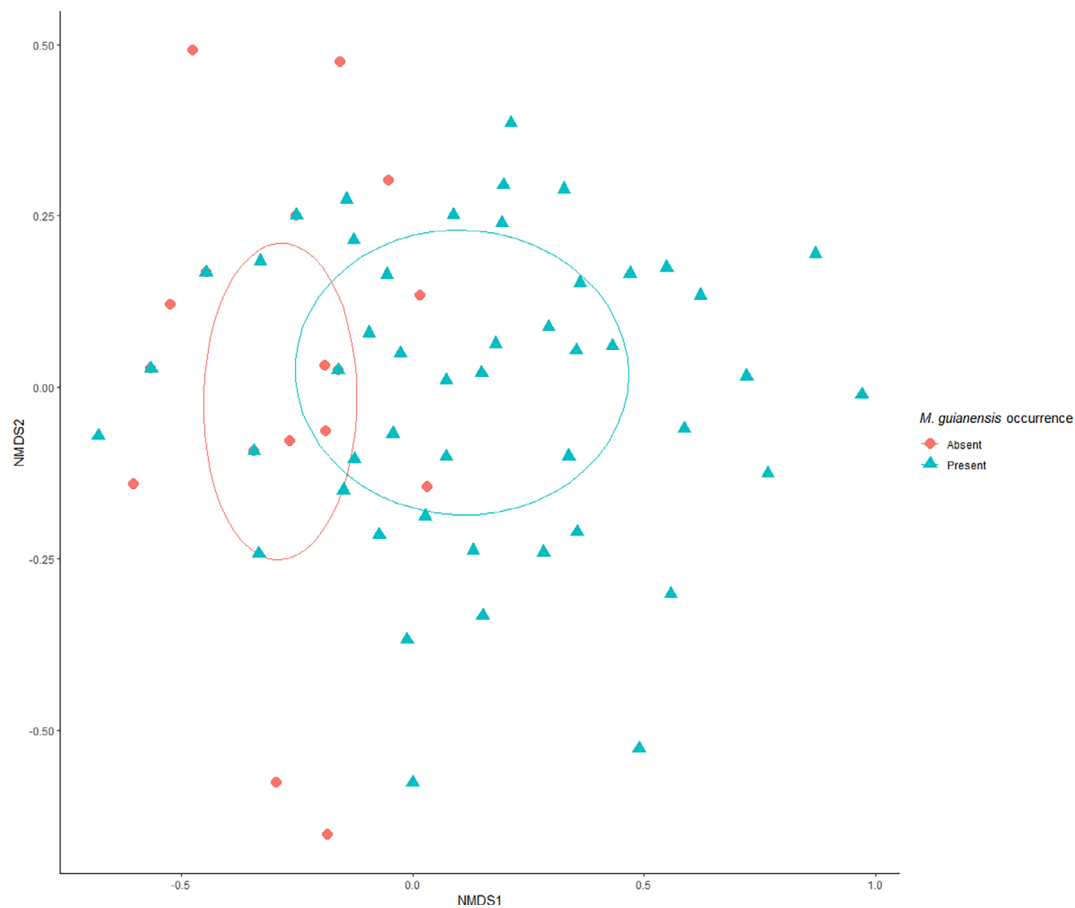
**FIGURE 6** NMDS representing the assemblies sampled in patches bigger than 10 m<sup>2</sup> with the presence and absence of *Myrcia guianensis*. Sampled patches are represented by triangles (patches where *M. guianensis* was present) and circles (patches where *M. guianensis* was absent) along their 95% ellipses. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/for.3057)]

role in the facilitation of the establishment of many other plant species (Scarano et al., 2004). Another species in our study area, *P. catingicola*, is a representative of the Cactaceae family, is saline-tolerant and bears a root system that is able to reduce the loss of nutrients by soil lixiviation (Menezes & Araujo, 2000), in a similar role of *A. arenaria* registered for Brazilian southeastern *restingas* (Scarano et al., 2004). The other two species found in patches smaller than 10 m<sup>2</sup> are the ruderal plants *C. urens* and *B. verticillata*. From 10 m<sup>2</sup> upward, two other species, *X. laevigata* and *M. guianensis* (Aubl.) DC., compose the assembly in the initial stage of the succession process. Species found in the greater patches, like *A. occidentale*, are suggested to belong to later succession stages.

In relation to patch shape patterns, smaller patches showed a more regular shape (round) in comparison to more irregular shapes in bigger patches. This seems to be a common pattern for native vegetation in coastal environments (Carranza et al., 2010). In these environments, Carboni et al. (2009) and Malvasi et al. (2018) hypothesized that natural formations are more irregular and parallel to the coastline. In our study area the patches elongate following the beach ridge plain, thus avoiding depressions that periodically flood.

## 4.2 | Species richness and occurrence in relation to landscape features

The species composition was similar to those of other *restinga* areas of Brazil (Souza & Morim, 2008), with the Myrtaceae family appearing as the richest family. The increase in species richness with the increase in patch area is possibly related to more favorable conditions of bigger patches, which would allow colonization by new species (Triantis et al., 2012). The species–area relationship, in which as the area increases the number of species tends to increase or remain constant, can be influenced by indirect factors or mechanisms such as local environmental variation (Benayas et al., 1999), environmental heterogeneity and scale (Turner & Tjørve, 2005). These factors can affect species richness through their effect on both species abundance and spatial distribution (He & Legendre, 2002). Our data suggest that the initial stage species may alter the environment, facilitating later species' arrival and growth. These initial species, such as *M. floribunda*, and *P. catingicola*, present vegetative reproduction structures, that would allow them to colonize and establish themselves in harsher environments. Furthermore, we suggest that the observed variability in richness in small and medium-sized patches



**FIGURE 7** (a) Beta diversity partition graph showing the contribution of turnover (dashed line) and nestedness (dotted line) to the total beta diversity variation (solid line). (b) Beta diversity partition graph showing the contribution of turnover (dashed line) and nestedness (dotted line) to the total beta diversity variation (solid line) in patches smaller than 10 m<sup>2</sup>. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/for.3057)]

may be a result of their proximity to larger patches that function as source areas.

The greater number of species related to a less regular shape of the patch may occur due to the model of patches lateral spread over areas of sandy ridges. This patch expansion pattern probably avoids areas of depression between sandy ridges, which flood periodically. Furthermore, some species can be adapted only to larger patch areas with more complex shapes (Malavasi et al., 2018; Varela et al., 2018).

The edge index and the patch shape were not the main drivers of species occurrence, and the relationship of these variables with the species composition of the plant assemblies was weak. These results do not corroborate findings for big fragments of tropical rain forests, in which the edge and shape indexes are important drivers of community assembly (Santana et al., 2021). In coastal forest communities, the assembly seems to be more related to the abiotic characteristics of these habitats and to the natural disturbances associated with these places, as well as the physical stressors (Fenu et al., 2013; Lins et al., 2021). In the succession model observed in the studied *restinga*, it is expected that isolated patches would be substituted by continuous lines of vegetation along sandy ridges during more advanced stages of ecological succession.

### 4.3 | Correlation among species and community assembly rules and beta diversity partition

Most correlations between species occurrence were positive. The few negative correlations were very low, showing that the presence of a species, in general, does not imply the exclusion of others. This suggests that competitive interactions were not determinant in the studied ecosystem, at least in the recorded successional stages. On the contrary, the positive correlations were strong, especially those among initial species like *M. guianensis* and many other species, which indicates a role of facilitation by these species. *M. guianensis* is also cited as one of the most common species in *restinga* habitats (Nunes-Freitas et al., 2006).

The coexistence pattern found can be linked to positive and negative interactions and to environmental heterogeneity (Chelli et al., 2019; Conti et al., 2017). This last factor is important to species coexistence on small scales, presenting a positive influence on species diversity and affecting species assembly (Bergholz et al., 2017).

In this sense, our results show that the variation of beta diversity among patch assemblies is basically ruled by the species turnover.

However, nestedness seems to be an important force in small patches, acting as a force of species selection from greater pools (Ulrich & Gotelli, 2007) in these areas. In this sense, we found that the variation in assembly composition is scale dependent, and the study area presents the influence of both processes.

Patches with smaller areas are subject to greater influence from the edge and few species are able to establish themselves. Thus, small patches exhibited the same group of species and the same pattern of species arrival triggered by *M. floribunda*. As the patch grows, it is assumed that environmental conditions become more favorable, so the initial species begin to be replaced by the turnover process, as  $\beta$  diversity is mainly influenced by environmental conditions (Jiang et al., 2022).

This result corroborates our hypothesis of the existence of an assembly rule initiated by key species. Apparently, the species composition of the patches is very consistent in patches smaller than 10 m<sup>2</sup>, following a clementian pattern.

The nestedness verified in young patches was lower than that recorded for small patches, independent of age, suggesting that the patch size is more decisive for the composition along the successional gradient than the age of the patch. Small patches with compact formats, presented a much more predictable successional pattern that was reflected by the higher nestedness level. Besides these factors, environmental, spatial, and historical conditions can also influence these variations in species composition differences (Qian et al., 2005).

Our results showed that larger, irregularly shaped patches present higher species richness. The conservation of these patches must therefore have the highest priority in the area to capture this variation. To begin restoration projects in the study area, we suggest that initially the three following key species are used: *M. floribunda*, *Pilosocereus catingicola* e *Hohenbergia catingae*, adopting a nature-based solution so as to create nuclei that favor the process of natural regeneration. However, to adopt these models, it is necessary to evaluate the survival rate of *M. floribunda* when planting seedlings, since it is possible that a large part of the plants of this species that begin the natural colonization process is ramets. Authors have reported the low survival rate of seedlings of species from the Myrtaceae family when planted in restinga (Zamith & Scarano, 2006).

Once these plants are established, the succession process would begin through various mechanisms already discussed in this study. One of these mechanisms, the action as perches, has already been successfully tested in other restinga areas (Loureiro et al., 2022).

We also suggest paying special attention to species with sucker roots, which seems to be a mechanism that allows early colonization of sandy habitats. Ramets of an adult plant can colonize a bare area and trigger the succession process in areas where seedlings originating from seeds would have few opportunities (Scowcroft & Yeh, 2013). We suggest that further studies should focus on this possible pattern in the colonization and regeneration of tropical sandy soils.

The main limitation of our study is the lack of environmental conditions sampling, and future studies should consider the influence of environmental factors and the effects of plant functional traits.

## AUTHOR CONTRIBUTIONS

FM conceived and designed the research, LM undertook the field study, extracted the data, and undertook most of the analyses, supported by GD, MDS, and FM; and LM, GD, and FM drafted the manuscript equally. All authors contributed to revisions and gave final approval for publication.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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