Facilitation and allelopathy mediate phylogenetic and functional diversity under Atlantic Rainforest trees

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Running Title: Facilitation and allelopathy of trees in tropical forest

ABSTRACT

Plant phylogeny, diversity and production of germination inhibiting chemicals can be used as patterns for inferring key drivers of plant community construction and assembly. We conducted the study in a restoration area of Atlantic Rainforest from Southeast Brazil. In this context, we aimed to investigate community assembly rules by simultaneously evaluating the relationships of species with a phylogenetic, functional and ecophysiological (allelopathy) approach and multifaceted β diversity (taxonomic, phylogenetic and functional). We measured the plant canopy height and diameter at soil height for all individuals and determined successional group and dispersal syndrome for all species regenerating in open areas and below 18 adult individuals of each tree species *Bixa atlantica* Antar & Sano, *Inga laurina* (Sw.) Willd., *Joannesia princeps* Vell. and *Senna multijuga* subsp. *multijuga* var. *verrucosa* (Vogel) H.S.Irwin & Barneby. Phylogenetic and functional indexes of community structure were calculated with the net relatedness index and the nearest taxon index. Taxonomic, phylogenetic and functional diversities (respectively, TD, PD, and FD) for the regenerating community in each area were calculated and pairwise comparisons made for TD, FD, and PD components of β diversity. Tests of tree species allelopathy derived from leaf extract were performed with seeds of *Lactuca sativa* L. (Asteraceae). The effects of diversity and of extracts on seed germination were analyzed using generalized linear models. The phylogenetic and functional structure of the regenerating communities under the four tree species did not differ from random for the four studied tree species. The PD was significantly higher for the communities that regenerated under *Joannesia*, while the FD was higher under both *Joannesia* and *Senna*, compared to communities from open sites, evidencing a facilitation mechanism for these two species. Only *Senna* and *Inga* differed from random in relation to β TD and β FD, suggesting possible environmental changes in these areas. Seeds irrigated with the extracts of *Inga*, *Joannesia* and *Senna* inhibited germination in an intermediate way, whereas seeds irrigated with *Bixa* extract had only 1% germination, indicating allelopathic effects. In this way, the planted species directly influence the organization of communities that regenerate below their canopies. It is therefore important to choose species that can contribute to improving diversity, and thus favor the success of restoration projects.

Keywords: beta diversity; diversity partitioning; functional diversity; phylogenetic diversity; restoration; tropical forest

1. Introduction

Knowledge of the phylogenetic and functional relationships among plants in a given community (whether clustered or overdispersed) helps to infer the main drivers of their construction and assembly (Webb et al., 2002; Weiher and Keddy, 1995; Zhang et al. 2023). The search for the processes involved in the assembly of communities in different ecosystems of the world has grown (e.g., Carrión et al., 2017; García-Camacho et al., 2017; Guerin et al., 2021; Saito et al., 2016; Xu et al., 2021) and special attention has been given to communities during the process of succession of restored forests (e.g., Chang et al., 2015; de Lima et al., 2021; Sansevero et al., 2011; Schweizer et al., 2015; Verdú et al., 2009; Viani et al., 2015). However, the interpretation of structure depends on the phylogenetic signal in the evolution of traits (Blomberg and Garland, 2002; Wiens et al., 2010) and whether the observed structure differs from that expected by null models (Saito et al., 2016; Webb, 2000). In communities with conserved phylogenetic signals, clustered phylogenetic patterns (coexisting species more related phylogenetically) are shaped by environmental filters (Cavender-Bares et al., 2004; Webb et al., 2002). On the other hand, communities with overdispersed phylogenetic patterns (coexisting species are distantly related phylogenetically) can be formed by competition (Cavender-Bares et al., 2004; Webb et al., 2002) or facilitation (Valiente-Banuet and Verdú, 2007; Souza et al., 2015).

Plant diversity also explains how communities are structured. For many years diversity was assessed only with a focus on species (i.e., taxonomic diversity; TD) (Gentry, 1988). However, current diversity analyses are based on phylogenetic diversity (PD) and functional diversity (FD), and generate more robust results, which can be used to better understand current patterns of biodiversity because this approach considers the evolutionary history and phenotypic similarity among species (de Bello et al., 2010; Loewen et al., 2023; Mouquet et al., 2012). If functional traits are conserved along the phylogeny, communities with greater phylogenetic diversity are composed of species with a broad spectrum of functional traits, which provide more functions for the ecosystem (Navarro-Cano et al., 2016). In this sense, restoration practices can be more efficient if phylogenetic and functional information is considered (Jiang et al., 2022; Montoya et al., 2012; Verdú et al., 2012). Using species with traits of facilitators in restoration can benefit not only the recruitment of non-planted species, but also favor the dynamics of communities and ecosystem processes (Navarro-Cano et al., 2016; see also Le Stradic et al., 2014). For example, Navarro-Cano et al. (2016) observed that communities that regenerated below the facilitator species *Gypsophila struthium* Loefl. seven years after planting they were phylogenetically more diverse than other planting areas.

Another mechanism that may influence the structuring of plant communities is allelopathy, since chemical compounds produced by some plants may interfere with adjacent vegetation (Arroyo et al., 2018; Hierro and Callaway, 2021). The presence of harmful allelopathic compounds in the environment can inhibit or delay seed germination (Fernandez et al., 2013) and inhibit seedling growth (Arroyo et al., 2018; Linhart et al., 2015). Studies of allelopathy have been carried out mainly with controlled temperatures and/or luminosity (Dai et al., 2017; Hashoum et al., 2017; Stowe, 1979) and with species with fast, uniform, and sensitive germination, such as *Lactuca sativa* (Maraschin-Silva and Aqüila, 2006; Tigre et al., 2012).

The emergence of partitioning of diversity made it possible to better understand the processes that influence the distribution of species among taxonomic, functional and phylogenetic facets of biodiversity (de Belo et al., 2009, 2010; Jankowski et al., 2009; Gaüzère et al. 2022). Diversity can be portioned into alpha (diversity within local communities), beta (β; diversity among local communities) and gamma (regional diversity) (Pavoine et al., 2004; Ricotta, 2005). The measurement of beta diversity among sample units can reveal variability in composition (Anderson et al., 2006). This measure can also be performed for phylogenetic and functional diversity, in which cases variation in phylogenetic and functional composition, respectively, can be found.

In this context, we aimed to investigate community assembly rules by simultaneously evaluating the relationships of species with a phylogenetic, functional and ecophysiological (allelopathy) approach and multifaceted β diversity (taxonomic, phylogenetic and functional). Thus, more specifically, we investigated the effect of species planted in areas of restoration on the assembly and diversity of regenerating communities under their canopies. This knowledge increases the chances of optimizing the selection of species for planting in future restoration projects by identifying facilitating species to the establishment of seedlings (Chang et al., 2015), particularly in environments as diverse as the Atlantic Forest of Brazil. A previous study at the same location showed that some species interfere with the establishment of other plants in the community, such as: *Bixa atlantica* Antar & Sano (Bixaceae), *Joannesia princeps* Vell.

(Euphorbiaceae), *Inga laurina* (Sw.) Willd. (Fabaceae) and *Senna multijuga* subsp. *multijuga* var. *verrucosa* (Vogel) H.S.Irwin & Barneby (Fabaceae) (Spadeto et al., 2017), hereafter referred as *Bixa*, *Joannesia*, *Inga* and *Senna.* Higher species richness and abundance of individuals were found under *Joannesia* and *Senna*, while lower abundance of individuals was found below *Bixa* (Spadeto et al., 2017).

In this context, we tested the following hypotheses: (i) The structure of the plant community recruited below tree species is overdispersed, since according to Valiente-Banuet and Verdú (2007), facilitation can act as assembly rule favoring phylogenetic dispersion because facilitators tend to recruit species unrelated to each other; (ii) Greater functional and phylogenetic diversity is found in communities below tree species than in open areas given that some species behave as facilitators, and thus form communities of distantly related species, which increases phylogenetic (Valiente-Banuet and Verdú, 2007) and functional (Gazol and Camarero, 2016) diversity; (iii) β diversity (for all facets: taxonomic diversity, FD, PD) between tree species and open areas is greater than expected by random. We expect communities of dissimilar plants to establish themselves under tree species and in open areas. We also expect β diversity among the communities of each tree species to be greater than expected at random because, according to Padilla and Pugnaire (2006), each species can provide different conditions and facilitate the establishment of different communities; (iv) Lower germination of *L. sativa* seeds irrigated with *Bixa* leaf extract since a lower abundance of regenerants has been previously observed under this species (see Spadeto et al., 2017).

2. Material and methods

2.1. Study area

The study was conducted in a restoration area of Reserva Natural Vale (RNV) (9°06’ to 19°8’ S; 39°45’ to 40°19’ W), located in the state of Espírito Santo, Southeast Brazil. The region is within the domain of the Atlantic Forest, one of the world’s biodiversity hotspots (Myers et al., 2000; Resende et al., 2018), specifically the physiognomy of the lowland dense ombrophilous forest (IBGE, 2012). The climate is Tropical Wet and Dry (Aw), with two well-defined seasons. The rainy season occurs between the months of September and April and the annual averages for temperature and rainfall are 22 °C and 1,200 mm, respectively (Alvares et al., 2013). This restored area was a plantation of Eucalyptus spp. After wood extraction, the area became dominated by the exotic grasses *Urochloa* spp. The soil was prepared in 2004 and at the beginning of 2005, 170 native tree species were planted in the area, distributed in two spacings (2×2 and 3×3 m), delimited by plots of 50 x 50 m. The maximum distance between the two plots was 400 m, and planting was carried out in an area of 4.5 ha.

2.2. Study species

Bixa atlantica is a pioneer tree or treelet that reaches 6 to 11m in height, zoochoric and endemic to the Atlantic Rainforest (Antar et al., 2023). *Inga laurina* is an early secondary tree that reaches 10 to 20 m in height, zoochoric and widely distributed, occurring in different domains in Brazil, such as the Caatinga, Amazon, Cerrado, as well as the Atlantic Forest (Lorenzi et al., 2008; Garcia et al., 2023). *Joannesia princeps* is an early secondary tree 6-23m tall that occurs in the domains Caatinga, Cerrado and Mata Atlantica of southeast and northeast Brazil (Külkamp, 2023). *Senna multijuga* subsp. *multijuga* var. *verrucosa* is an early secondary tree that reaches 10 to 40 m tall, and this variety is endemic to the Atlantic Forest in the southeast and northeast regions of Brazil (Bortoluzzi et al., 2023).

2.3. Vegetation sampling

Eighteen individuals of each species were randomly selected eight years after planting: *Bixa*, *Joannesia*, *Inga* and *Senna*. These species were chosen because of their rapid growth in the area, because they produce large amounts of seeds or fruits attractive to the fauna and because they have been used in several restoration projects in Southeast Brazil (e.g., Botelho et al., 1996; Ferreira et al., 2009; Massad et al., 2011; Pedroza et al., 2011; Rolim et al., 2007). These factors, associated with the greater richness and abundance of individuals under *Joannesia* and *Senna* (Spadeto et al., 2017), led us to investigate more deeply the mechanisms that aid in the assembly and diversity of the community below these species.

A set of 18 open areas close to the focal species, but without being influenced by the canopy, were also established to serve as controls. Circular plots with a radius of three meters were established in these areas and under the study species to evaluate natural regeneration (Fig. 1). The plots marked under the study tree species were centered around individuals selected from *Bixa*, *Joannesia*, *Inga* or *Senna*. We counted and identified all shrubs and trees that regenerated within each studied plot and were taller than 30 cm and/or had a diameter at breast height lower than 5 cm.

2.4. Measures of species attributes

All species of regenerating shrubs and trees were considered to measure their attributes. The traits of height and diameter at soil height were recorded for all regenerating individuals, and the successional group and dispersal syndrome were determined for all regenerating species. The assessment of height and diameter growth of regeneration tree species is crucial for the evaluation of the success of forest restoration efforts (Freitas et al., 2019). Additionally, successional group and dispersal syndrome are important for forest tree species because they help understand how seed propagation occurs and the distribution pattern of species in the environment, informing decisions about forest management, conservation, and restoration (Massi et al., 2022).

The height and diameter attributes of the focal species were measured *in situ*. We subsequently classified species according to their successional group as pioneer, early secondary or late secondary species (Gandolfi et al., 1995), and their dispersal syndrome as zoochoric, anemochoric or autochoric. Categorical variables were used for calculating FD, with quantitative variables (height and diameter) being categorized into four classes of similar size (i.e., composed of 24 species in each class).

2.5. Phylogenetic tree construction

The plant species sampled in all plots were used to construct a phylogenetic tree. All species were initially added to the phylogenetic tree using the software Phylomatic (Webb and Donoghue, 2005). The program generated a tree where the relationships of the species sampled followed APG IV (APG, 2016). Then, with the aid of Mesquite software (Maddison and Maddison, 2009) we corrected and improved tree resolution based on several recent molecular phylogenetic analyses. Finally, we used the 'bladj' algorithm implemented in Phylocom (Webb et al., 2008) to position the undated nodes evenly between dated nodes (Supplementary Material 1, Table S1, and Fig. S1).

2.6. Allelopathy effect of facilitators' leaf extract

Approximately 100 g of leaves of each species (*Bixa, Inga, Joannesia* and *Senna*) was collected in RNV to produce aqueous extract, which was used in the irrigation of seeds of *L. sativa* L. (Asteraceae) (Maraschin-Silva and Aqüila, 2006). The

L. sativa was used in this experiment because its germination is fast and uniform, and because it is a sensitive species capable of providing evidence of allelopathic effects (Maraschin-Silva and Aqüila, 2006; Tigre et al., 2012). To produce the extract, the leaves were dried in a forced air circulation oven at 40 °C and then mechanically crushed. Distilled water was added in the ratio of 1:10 (p/v) and maintained for 48 hours, after which the solution was filtered. The test of only one aqueous extract concentration (20%) was performed with the objective of approaching the realistic concentration of the natural leachate (Hashoum et al., 2017). Distilled water was used to irrigate the seeds in the control treatment.

The bioassays were mounted on sterile Petri dishes lined with two layers of filter paper moistened with approximately 3 ml of extract or distilled water (control treatment). Twenty-five seeds were seeded in each plate and each treatment had four replicates. The bioassays were kept in a B.O.D. incubator (Biochemical Oxygen Demand) humid germination chamber at a constant temperature of 25 °C and a photoperiod of 12 h. The number of germinated seeds was checked daily. Germinated seeds were considered those that produced a primary root of at least 2 mm in length. The experiment was set up in a completely randomized design with five treatments (control and leaf extracts of *Bixa*, *Joannesia*, *Inga* and *Senna*) × four replicates.

2.7. Data analysis

2.7.1 Similarity pattern of the plant community

To explore the similarity pattern of the plant community that regenerated in the control treatment and in the four facilitating species, we generated the Sorensen distance with the ‘vegdist’ function from the ‘vegan’ package (Oksanen et al., 2018) and used a principal coordinates analysis (PCoA) with presence and absence data, according to

Dray et al. (2003). To visualize the groups of plots under the four facilitator species in relation to the control, we made a factorial map using the ‘s.class’ function of the ‘ade4’ package (Dray and Dufour, 2007). To test whether there was a significant difference between the groups studied (control and fourth facilitator species) in terms of floristic composition, we used the previously calculated Sorensen distance, and then used the analysis of similarity (ANOSIM) test according to Quinn and Keough (2002), with the ‘with’ function of the ‘base’ package. These analyses were carried out in the R environment (R Core Team, 2021).

2.7.2. Phylogenetic and functional structure

After the tree was constructed, the mean distance between pairs (mean pairwise distance - MPD) and the mean distance of the nearest taxon (mean nearest taxon distance - MNTD) were calculated to evaluate the mean phylogenetic distance between all pairwise combinations of species and the mean phylogenetic distance of the nearest relative of all species, respectively. In addition, MPD and MNTD were used to calculate the net relatedness index (NRI) and the nearest taxon index (NTI). These metrics capture distinct aspects of the phylogenetic structure of communities. Values of NRI and NTI can also be calculated based on the functional dendrogram resulting from the phenotypical distance between species (Pontarp, 2021; Webb et al., 2008). While NRI reflects the structure of the phylogenetic tree or functional dendrogram as a whole, particularly the basal nodes, NTI is related to the pattern shown in the terminal part of the phylogenetic tree or functional dendrogram (Webb, 2000; Webb et al., 2002). Both NRI and NTI are standardized measures (standardized effect size) and are calculated with the following formula: [$NRI = –(MPD_{obs.}–MPD_{rand.})/MPD\sigma_{rand.}$], where $MPD_{obs.}$ is the mean of MPD observed in the local community; $MPD_{rand.}$ is the mean of MPD obtained by randomization in null communities; and $MPD\sigma_{rand.}$ is the standard deviation of $MPD_{rand.}$ (Webb et al., 2002). To calculate NTI it is only necessary to replace MPD with MNTD. Negative values of NRI or NTI indicate communities with overdispersed phylogenetic or functional structure (i.e., co-occurring species in the sample are phylogenetically less closely related or functionally less similar than expected by chance), whereas positive values indicate communities with clustered phylogenetic structure (i.e., co-occurring species in the sample are phylogenetically more closely related or functionally more similar than expected by chance). Values close to zero indicate communities with random structure (i.e., the phylogenetic or functional relationship of the co-occurring species in the sample does not differ from that expected by chance).

Information on the presence and absence of species in the communities was used in all analyses. The regional species bank was delimited as the sum of all the species occurring below all sampled plots (below the crowns of the evaluated tree species and in the open areas of the control plots). The null model used was generated with the independent permutation algorithm (independent swap; Gotelli and Entsminger, 2003), which maintains constant richness and frequency in the plots, while randomizing only patterns of species co-occurrence. The independent swap null model assumes that the probability of a species colonising a plot is proportional to its frequency in the total number of samples considered (Kembell and Hubbel, 2006). As well as being generally more biologically realistic, this null model has a low probability of type I error (Kembel 2009). The phylogenetic and functional structure analyses were performed with the package ‘picante’ (Kembel et al., 2010) in R software (R Development Core Team, 2016). We used the one-sample *t*-test (Kembel and Hubbel, 2006) to test whether phylogenetic or functional structure of each species (Control, *Bixa*, *Inga, Joannesia*, and *Senna*) differed from the null expectation (mean NRI or NTI = zero).

2.7.3. Functional and phylogenetic diversity and diversity partitioning

Taxonomic diversity of the recruited species was measured by species richness. In order to obtain FD and PD diversities, the dissimilarity matrix of the species was calculated using the "Gower approach" of the 'trova' function (see de Bello et al., 2010; Lepš et al., 2006). The matrix used in the calculation of FD was constructed with the attributes: height class, diameter class, successional group and dispersal syndrome. The Rao index was calculated with the dissimilarity matrix to estimate FD and PD considering the occurrence of the species in each sample plot.

We constructed generalized linear models (GLMs) to test the hypothesis about functional and phylogenetic diversities by comparing species and comparing each species with open area. The models with significant differences were submitted to contrast analysis (package RT4Bio; Reis Jr. et al., 2013) to identify the difference between species, and species and open area ($P < 0.05$).

To test the hypothesis for β diversity, we used the 'Rao' function (de Bello et al., 2010) to calculate TD, FD and PD and to make pairwise comparisons of diversity (TD, FD, PD) of the species (that is, the β diversity between pairs of samples). In this case, each sample was a treatment with a focal tree species, along with the open area treatment. Null models were constructed to test whether the observed values of β TD, β FD and β PD were different from those expected by chance. To do this, we used the 'permatfull' function of the 'vegan' package (Oksanen et al., 2018) to construct 999 matrices of random occurrence, respecting two rules: the number of species per treatment was always the same as observed and the number of treatments in which a species occurred was always the same as observed (randomization while maintaining the marginal sums of the matrix). We considered values to differ if they were outside the upper and lower range of 2.5% of the calculated values for the 999 random matrices.

For pairwise comparisons of TD that were higher than expected by chance, similarity percentage analysis (SIMPER) was used to quantify the relative contribution of each regenerating species. We used Bray-Curtis similarity index in the SIMPER analysis, considering abundance. The analysis was performed using PAST 2.16 software (Hammer et al., 2001).

2.7.4. Allelopathy test

We used GLMs to analyze the effect of different extracts on seed germination, with the models with significant differences being submitted to contrast analysis (package RT4Bio; Reis Jr. et al., 2013) to identify the extracts or control responsible for the differences ($P < 0.05$). All analyses were performed in R software (R Core Team, 2021).

3. Results

A total of 96 species from 35 families were recorded for the regenerated communities (Fig. 2). The most abundant family was Fabaceae with 24 species, followed by Myrtaceae (9) and Lecythidaceae (6). With regard to successional group, 19 species were classified as pioneers, while 39 species were early secondary and 38 were late secondary. There were no representatives of the climax group. With regard to dispersal syndrome, 66 species were zoochoric, 22 anemochoric and eight autochoric (Supplementary Material 1, Table S2).

There is no clear difference between species composition of regenerating plants in control plots compared to the plots under the facilitator plants (Supplementary Material 1, Figure S2). In agreement with this observation, the ANOSIM showed a significant but very weak differentiation between regenerating communities, since the R value was near zero (R = 0.05; $P = 0.006$).

The phylogenetic structure of the regenerating communities in open areas and under the facilitators were not significantly different from random (Fig. 3a). A similar pattern was observed for the functional structure (Fig. 3b). Phylogenetic diversity was higher in the communities regenerated below *Joannesia* ($P < 0.05$) (Fig. 4a). On the other hand, there were no significant differences for PD of natural regeneration between the other tree species and open areas (Fig. 4a). A significant difference was found for FD in the communities under *Joannesia* and *Senna* ($P < 0.001$), which had higher FD (Fig. 4b). Communities that regenerated in open areas and below other tree species did not differ statistically ($P > 0.05$) (Fig. 4b).

Only the regenerating community under the species *Senna* differed from that expected at random for β TD (Table 1). The communities that regenerated under other species did not differ from the null model and formed a community similar to those found in open areas. The species that contributed most to the dissimilarity between *Senna* and open areas were: *Byrsonima sericea* DC., *Byrsonima stipulacea* A.Juss., *Acacia mangium* Willd., *Protium heptaphyllum* (Aubl.) Marchand subsp. *heptaphyllum, Anacardium occidentale* L., *Vernonanthura phosphorica* (Vell.) H.Rob., *Inga laurina* (Sw.) Willd., *Goniorrhachis marginata* Taub., *Byrsonima crassifolia* (L.) Kunth, *Terminalia kuhlmannii* Alwan & Stace, *Acacia auriculiformis* Benth., *Ceiba pubiflora* (A.St.-Hil.) K.Schum. Similarly, β FD of the regenerating communities below the tree species did not differ from the open areas except for the regenerated community under

Inga (Table 1). This species causes the functional composition of species that regenerate under its canopy to be different from those that regenerate in open areas. The β FD of the regenerating community below *Senna* and *Joannesia*, and *Senna* and *Inga* were dissimilar. The phylogenetic composition (β PD) of the natural regeneration under the tree species did not differ from the open areas (Table 1).

The extracts of the tree species had significant effects on the germination rates of *L. sativa* ($P < 0.001$). In the control treatment 94% of the seeds germinated while only 1% of the seeds irrigated with the leaf extract of *Bixa* germinated. The seeds irrigated with extract of *Inga*, *Senna*, and *Joannesia* had intermediate germination percentages (22, 22 and 30% of seeds, respectively), and did not differ significantly among themselves (Fig. 5).

4. Discussion

Contrary to what we predicted, our analysis did not indicate that the structure of communities beneath tree species was governed by biotic interactions, both in phylogenetic and functional analyses. The mechanism of facilitation was expected to structure the communities, as previously observed in other studies (Carrión et al., 2017; Valiente-Banuet and Verdú, 2007; Verdú et al., 2009).

Communities in the early stages of succession, such as the community evaluated in this study, may have random structure for several reasons. Some authors have suggested that the phylogenetic pattern for tropical forests in the early years of succession is driven by stochastic factors, moving to clustered (driven by abiotic factors) or overdispersed (resulting from limiting similarity or other biotic interaction processes) over the years (Chang et al., 2015; Letcher, 2010; Schweizer et al., 2015). However, other studies have indicated that stochastic factors are more important than deterministic factors in environments with higher productivity and higher species richness (Chase, 2010; Wang et al., 2010). Soliveres et al. (2012) postulated that climatic conditions along with biotic interactions affect the phylogenetic pattern, with one potentially overriding the other, thus leading to random structure. Similarly, Swenson and Equist (2009) found that a random phylogenetic pattern is not due to the lack of mechanistic process, but instead is due to the simultaneous influence of abiotic filters and limiting similarity. Therefore, despite finding random phylogenetic and functional structure for all communities under tree species, PD was higher below *Joannesia* and FD was higher under *Joannesia* and *Senna*, suggesting a mechanism of facilitation. In other words, the communities that regenerate under *Joannesia* and *Senna* are formed by species that cover a wide spectrum of functional attributes, thus suggesting the provision of more ecosystem functions (Navarro-Cano et al., 2016).

When species act as facilitators they can promote the establishment of other distantly related species, considering that in order to coexist they must differ in their traits, at least in the regeneration phase. This mechanism organizes the community and enables an increase in PD and FD (Navarro-Cano et al., 2016; Valiente-Banuet and Verdú, 2007). Furthermore, these plant species may have had priority effects on the structure and function of this community, as they were previously planted at the study site, positively or negatively affecting the establishment, growth or reproduction of later arriving species (Fukami, 2015; Weidlich et al., 2021). Furthermore, the comparison between tree species and open areas suggested that only the communities under the species *Senna* and *Inga* had β TD and β FD values, respectively, higher than expected at random. These two studied species modified the TD and FD of the communities formed below them, with the presence of species and functional attributes differing from those found in open areas. These attributes are fundamental to ensure a successful restoration.

The composition of species under facilitating plants can differ from that in open areas, as observed by Flores and Jurado (2003) and Schöb et al. (2013). Dissimilar communities between facilitating plants and in open areas are due to the environmental changes that under these facilitating plants. Such changes are highlighted by those involving: luminosity and temperature (Lima and Gandolfi, 2009; Padilla and Pugnaire, 2006); availability of water and nutrients (Koorem and Moora, 2010; Liu et al., 2014; Mihoč et al., 2016; Pueyo et al., 2016; Ramírez et al., 2015); protection against herbivores (Gómez-Aparicio et al., 2004); and reduction of competition with herbaceous species (Avendaño-Yáñez et al., 2014). A reduced stress under facilitators creates an environment conducive to the germination and development of species that could not colonize open areas. Species that comprise the upper stratum of a plant community form a cover that affects the diversity and structure of the lower stratum (Foré et al., 1997; Souza et al., 2015). In the present work, the species *Senna* and *Inga*, and *Joannesia* and *Inga*, seemed to form different microenvironmental conditions, because the communities under these species were functionally dissimilar between each other. In these cases, the communities regenerating below these tree species are comprised of species that provide different ecosystem functions. Paterno et al. (2016) previously described the importance of high diversity in restored areas. In restored environments, beneficiary species make different associations with facilitating plants, so the greater the diversity of species used in planting, the greater the different sets of beneficiary species, which increases species richness and β diversity (Paterno et al., 2016).

Another mechanism that could be acting in the structuring of communities under the tree species in the studied restoration area is allelopathy since germination was reduced in the presence of all species, especially below *Bixa*. Aqueous leaf extract of this species showed an inhibitory effect on the germination of *L. sativa* seeds, with only

1% of the seeds irrigated with this extract germinating. Although there is no record in the literature of possible allelopathic effects of *Bixa*, the present study, along with the reported low richness and abundance of individuals regenerating under *Bixa* (Spadeto et al., 2017), suggest an allelopathic effect. The community that regenerated below *Bixa* resembled the community formed in open areas, with respect to species richness and abundance. The allelopathic effect of a species can be evaluated by the relative density of plants regenerating below its crown and by seed germination tests in laboratories. The Mediterranean plant *Artemisia herba-alba* Asso was described as potentially having allelopathic effects because of the low relative density of plants that regenerated under its crown and the results of seed germination tests in laboratories. A later study carried out in natural areas (Arroyo et al., 2018) corroborated this hypothesis with the first signs of allelopathy and demonstrated the reduction of vitality of plants neighboring *A. herba-alba* (Arroyo et al., 2018). Therefore, the investigation of *Bixa*'s allelopathic activities should be included in future research to evaluate the role of this plant species in structuring communities in Atlantic Forest restoration projects.

We found evidence that facilitation structured the communities that regenerated under the studied tree species but only when we analyzed FD and PD and performed pairwise comparison of β diversity. We also found evidence that the communities were influenced by the mechanism of allelopathy. In areas such as that of the present study, planted species directly influence the organization of communities that regenerate below their canopies. It is therefore important to choose species that can contribute to improving diversity, and thus favor the success of restoration projects.

CRediT authorship contribution statement

CS, SHK: Conceptualization; CS, DN: Data curation; CS, DN, CAN: Formal analysis, Visualization; CS, SHK, DN, CAN, GWF: Methodology; CS: Writing - original draft; CS, DN, CAN, CCP, LAOPG, SHK, GWF: Writing- Reviewing and Editing.

Declaration of Competing Interest

The authors declare no conflict of interest with the content of this work.

Data availability

Data will be made available on request.

Acknowledgements

We would like to thank the Reserva Natural Vale for logistical support and the Instituto Capixaba de Pesquisa, Assistência Técnica e Extensão Rural (Incaper) in Domingos Martins – ES for the availability of the site to perform the seed germination test. We thank Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq; 406757/2022-4), Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG), and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for financial support. DN thanks scholarship from CNPq (151341/2023-0). CCP thanks scholarship from CNPq (173800/2023-8).

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Table 1. Pairwise comparisons of β diversity. Cells with the abbreviation TD or FD are significantly different than expected at random (*P* < 0.05). TD: taxonomic diversity and FD: functional diversity

	Control	*Bixa*	*Joannesia*	*Inga*	*Senna*
Bixa					
Joannesia					
Inga	FD				
Senna	TD		FD	FD	

Figure Legends

Fig. 1. Example of a plot showing regenerating plants below a canopy of a facilitator species in restoration areas of the Atlantic Forest located in the state of Espírito Santo, Southeast Brazil. (a) *Bixa atlantica* plot. (b) *Senna multijuga* subsp. *multijuga* var. *verrucosa*.

Fig. 2. Phylogenetic tree assembled for the regenerating plant species sampled in a restored Atlantic Forest located in Espírito Santo, southeast Brazil. Light and dark green denote, respectively, absence and presence in the control and under the crowns of the four studied species.

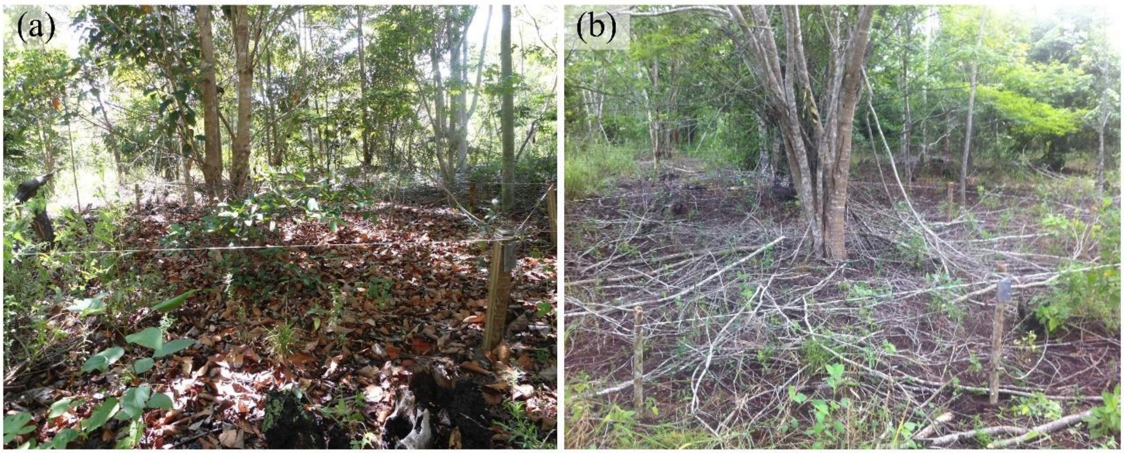
Fig. 3. Boxplot showing the phylogenetic (a) and functional (b) community structure using the net relatedness index (NRI; gray columns) and the nearest taxon index (NTI; black columns) in the recruiting communities under open areas (Control) and under *Bixa*, *Inga*, *Joannesia*, and *Senna*.

Fig. 4. Average phylogenetic diversity (a) and average functional diversity (b) in the recruiting communities in open areas (Control) and under *Bixa*, *Inga*, *Joannesia*, and *Senna*. The vertical lines represent standard deviation. Different letters above the bars denote significant difference between treatments (GLMs, $P < 0.05$).

Fig. 5. Effect of the leaf extracts of *Bixa*, *Inga*, *Joannesia*, and *Senna* on seed germination of *Lactuca sativa*. The vertical lines represent standard error. Different letters above the bars denote significant difference between treatments (GLMs, $P < 0.05$).

FIGURES

Figure 1:



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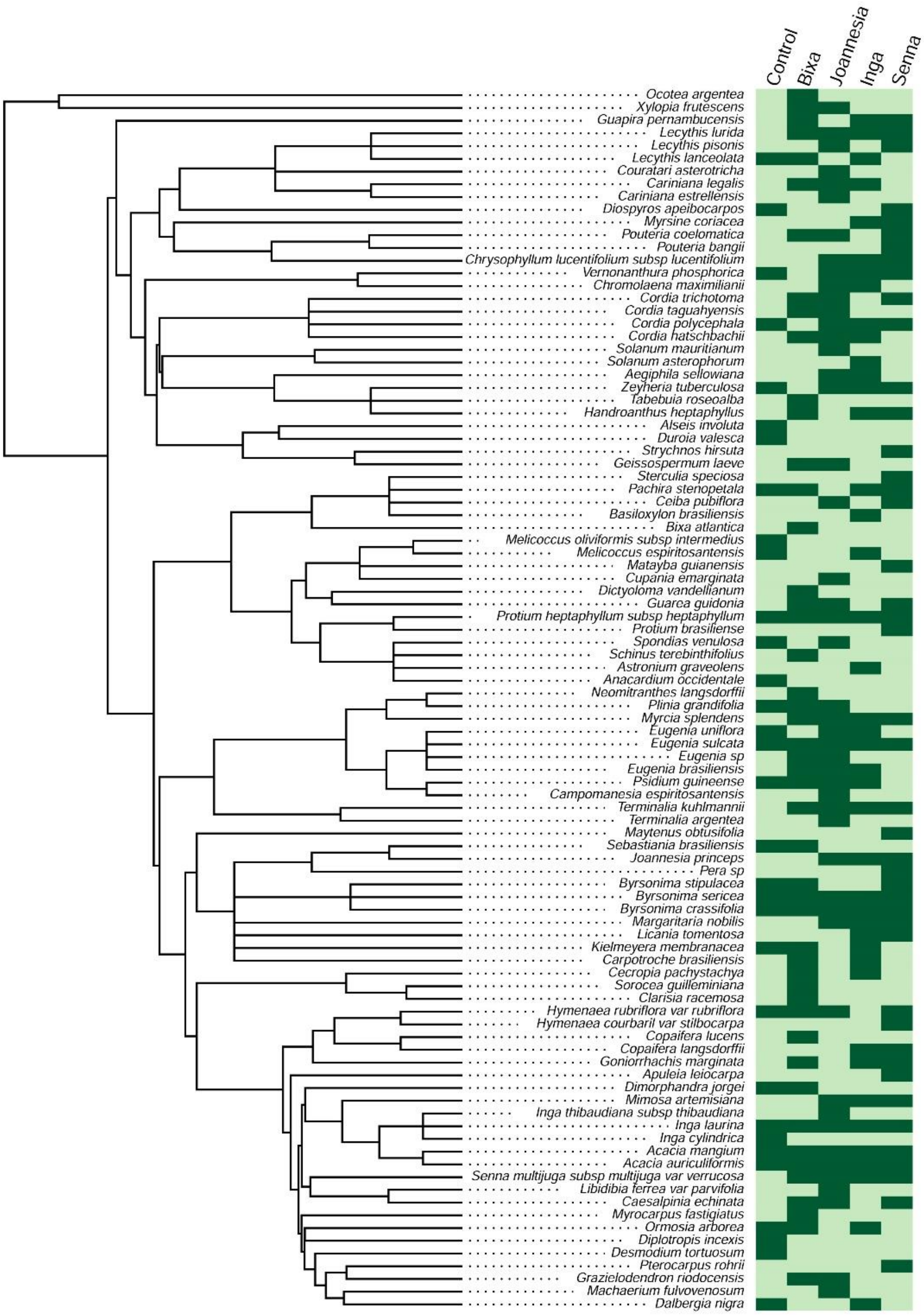
Control
Bixa
Joannesia
Inga
Senna
Ocotea argentea
Xylopia frutescens
Guapira pernambucensis
Lecythis lurida
Lecythis pisonis
Lecythis lanceolata
Couratari asterotricha
Cariniana legalis
Cariniana estrellensis
Diospyros apeibocarpos
Myrsine coriacea
Pouteria coelomatica
Pouteria bangii
Chrysophyllum lucentifolium subsp lucentifolium
Vernonanthura phosphorica
Chromolaena maximilianii
Cordia trichotoma
Cordia taguahyensis
Cordia polycephala
Cordia hatschbachii
Solanum mauritianum
Solanum asterophorum
Aegiphila sellowiana
Zeyheria tuberculosa
Tabebuia roseoalba
Handroanthus heptaphyllus
Alseis involuta
Duroia valesca
Strychnos hirsuta
Geissospermum laeve
Sterculia speciosa
Pachira stenopetala
Ceiba pubiflora
Basiloxylon brasiliensis
Bixa atlantica
Melicoccus oliviformis subsp intermedius
Melicoccus espiritosantensis
Matayba guianensis
Cupania emarginata
Dictyoloma vandellianum
Guarea guidonia
Protium heptaphyllum subsp heptaphyllum
Protium brasiliense
Spondias venulosa
Schinus terebinthifolius
Astronium graveolens
Anacardium occidentale
Neomitranthes langsdorffii
Plinia grandifolia
Myrcia splendens
Eugenia uniflora
Eugenia sulcata
Eugenia sp
Eugenia brasiliensis
Psidium guineense
Campomanesia espiritosantensis
Terminalia kuhlmannii
Terminalia argentea
Maytenus obtusifolia
Sebastiania brasiliensis
Joannesia princeps
Pera sp
Byrsonima stipulacea
Byrsonima sericea
Byrsonima crassifolia
Margaritaria nobilis
Licania tomentosa
Kielmeyera membranacea
Carpotroche brasiliensis
Cecropia pachystachya
Sorocea guilleminiana
Clarisia racemosa
Hymenaea rubriflora var rubriflora
Hymenaea courbaril var stilbocarpa
Copaifera lucens
Copaifera langsdorffii
Goniorrhachis marginata
Apuleia leiocarpa
Dimorphandra jorgei
Mimosa artemisiana
Inga thibaudiana subsp thibaudiana
Inga laurina
Inga cylindrica
Acacia mangium
Acacia auriculiformis
Senna multijuga subsp multijuga var verrucosa
Libidibia ferrea var parvifolia
Caesalpinia echinata
Myrocarpus fastigiatus
Ormosia arborea
Diplotropis incexis
Desmodium tortuosum
Pterocarpus rohrii
Grazielodendron riodocensis
Machaerium fulvovenosum
Dalbergia nigra

855 **Figure 3:**

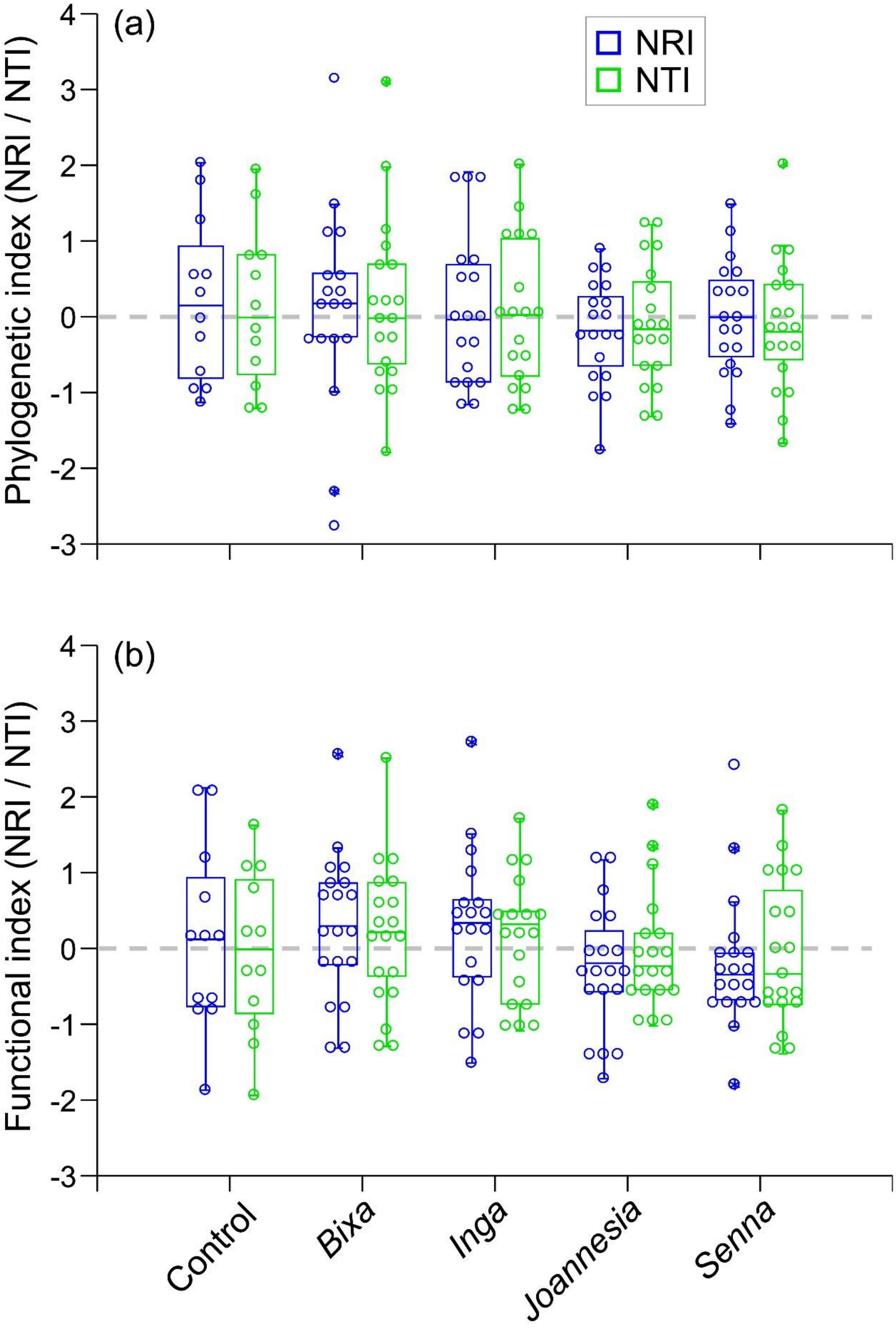

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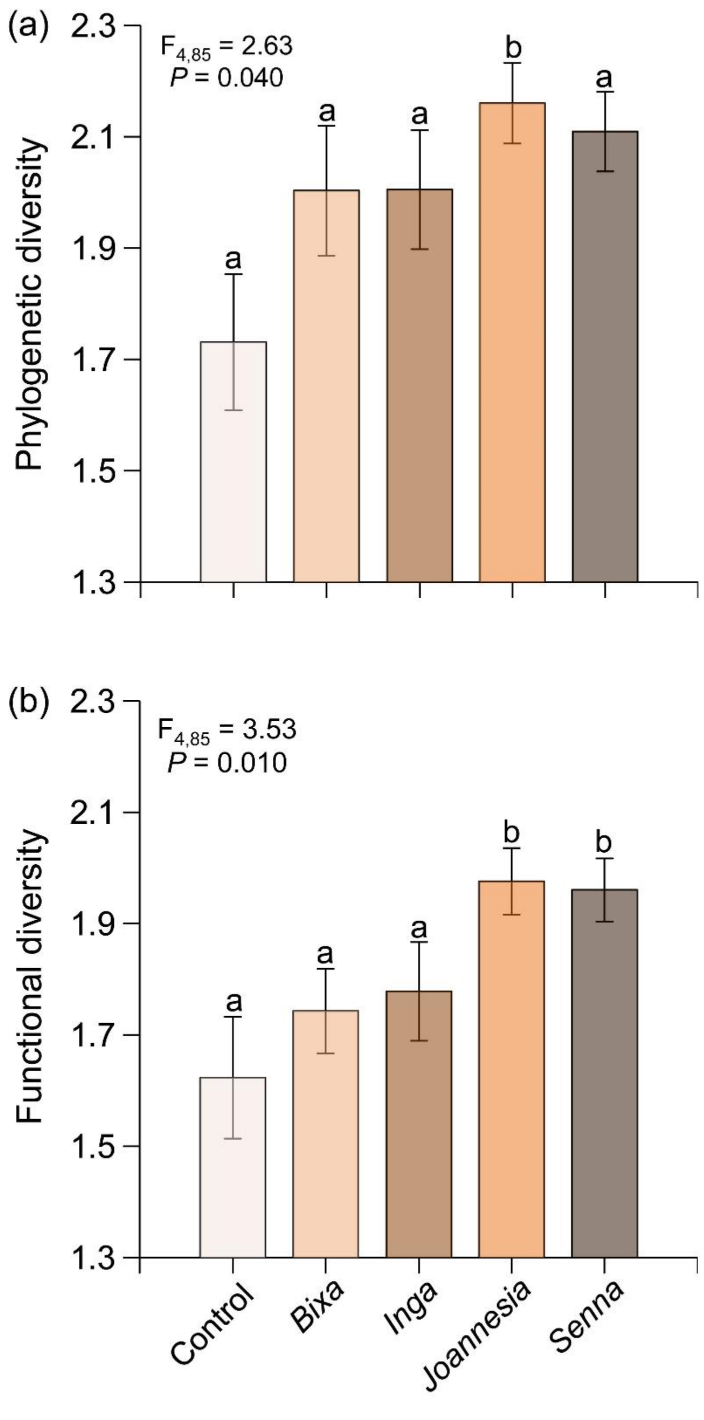
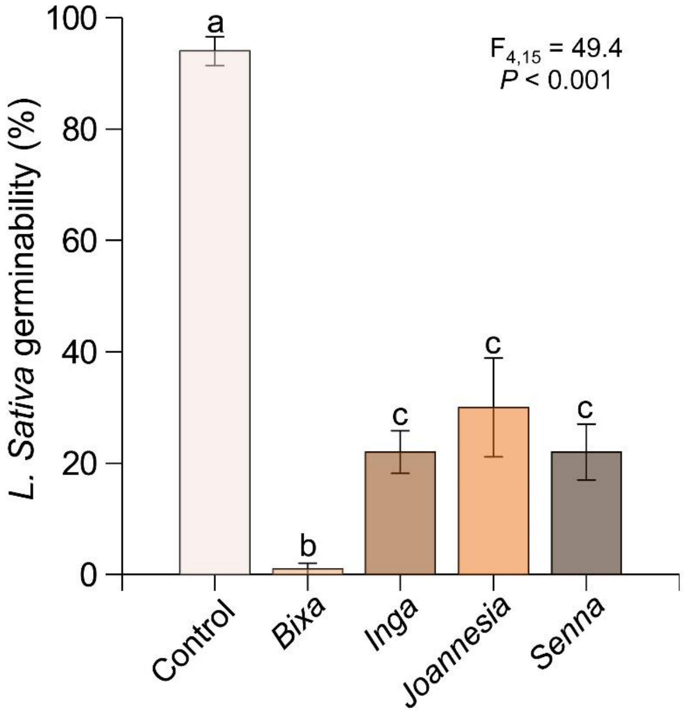
Figure 4:


(a)
Phylogenetic diversity
2.3
2.1
1.9
1.7
1.5
1.3
$F_{4,85}$ = 2.63
P = 0.040
a
a
a
b
a
(b)
Functional diversity
2.3
2.1
1.9
1.7
1.5
1.3
$F_{4,85}$ = 3.53
P = 0.010
a
a
a
b
b
Control
Bixa
Inga
Joannesia
Senna

861 **Figure 5:**



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