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High diversity mixed plantations of *Eucalyptus* and native trees: An interface between production and restoration for the tropics

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ABSTRACT

Despite the high diversity of trees in the tropics, very few native species have been used in plantations. In a scenario of high international demand for nature conservation, ecological restoration and for the provision of forest products, mixed species forestry in the tropics emerges as a promising option. In this study, we examine three large experiments in the Atlantic Forest region of Brazil that combine early *Eucalyptus* wood production with a high diversity (23–30 species) of native tree species. We tested the following hypotheses: (1) *Eucalyptus* growth and survival is higher in mixed plantations than in monocultures, while that of native species is lower when intercropped with *Eucalyptus*; (2) The diameter of target native trees is influenced by the size and by the identity of neighboring trees; (3) The negative effect of competition from *Eucalyptus* on native species is directly related to their growth rate. We compared mixtures of *Eucalyptus* and a high diversity of native tree species with *Eucalyptus* monocultures and with plots containing only native species, replacing *Eucalyptus* by ten native species. To test our hypotheses, we examined inventory data considering the stand- and the tree-levels. We calculated survival rate, diameter and height growth and basal area of whole stands and groups of species. We also used a neighborhood index analysis to separate the effect of total competition (i.e. stand density) and the influence of groups of species (intra- and inter-specific competition). The *Eucalyptus* trees in high diversity mixtures grew larger and yielded nearly 75% of the basal area produced by *Eucalyptus* monocultures even though this genus accounted for only 50% of seedlings in the mixtures. In the mixtures, *Eucalyptus* negatively affected the growth of native species proportionate to the native species' growth rate. With some exceptions, the mixed plantations had no overall negative effect on tree survival or height growth. We conclude that mixtures of *Eucalyptus* and a high diversity of native tree species are feasible and represent a potential alternative for establishing multipurpose plantations, especially in the context of forest and landscape restoration.

1. Introduction

Tropical forests host the vast majority of tree species on Earth (Beech et al., 2017; Slik et al., 2015), but this potential remains underutilized as modern tropical silviculture is still dominated by monospecific plantations of a few genera, especially *Eucalyptus*, *Pinus*, *Acacia*, and *Tectona* (Kelty, 2006). Apart from being simplified from a biodiversity perspective, monocultures can also have a lower capacity to provide the ecosystem goods and services provided by diverse forests (Bauhus et al., 2017a; Lindenmayer et al., 2012) in the context of forest landscape restoration. The combined outcomes of providing ecosystem services while delivering timber and non-timber products may be improved when production and conservation objectives are balanced and integrated. However, a complex set of factors currently hinder the adoption of alternative systems (Puettmann et al., 2015).

New forestry systems could be designed as stable mixes where species do not outcompete each other and may result in plantations that have ecological and economic resilience (Lamb, 2005). Commercial mixed plantations usually comprise two to four species and are often only preferred when they produce a higher quantity or quality of wood

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(or biomass) than monocultures (Kelty, 2006). Together with the demand for timber products, there is growing international demand for forest and landscape restoration and for forests that can be used to achieve multiple objectives (Brancalion and Chazdon, 2017; Chazdon et al., 2017; FAO, 2016). In this scenario, mixed species forestry in the tropics emerges as a promising option to meet international demands for production and conservation at the stand and landscape scales while contributing to restoration objectives and serving as complementary forest habitat for wild species (Lamb, 2005).

In this study, we explore a silvicultural option for the tropical region of Brazil that intercrops a fast-growing species of *Eucalyptus*, widely used by the industry and farmers in the tropics, with a high diversity of native tree species. In other tropical regions, mixtures of native tropical species, sometimes including *Eucalyptus*, have demonstrated that these systems can result in greater individual tree and stand productivity than monocultures and that the diversity of tree species is reflected in the diversity of growth responses and in the flexibility of potential silvicultural regimes (Erskine et al., 2006, 2005; Montagnini et al., 1995; Nguyen et al., 2014). For example, *Eucalyptus* can reduce establishment costs by providing early income from wood production, while planting native species can potentially enhance the conservation value of plantations and serve as an option for high value timber exploitation in the longer term (Brancalion et al., 2012).

An important challenge for the design of this new type of mixture is to prevent the seedlings of the native species from becoming suppressed by *Eucalyptus*, which may result in reduced growth and/or high mortality, thus compromising the potential of mixed plantings to reestablish diverse tree communities. The use of a fast-growing *Eucalyptus* species in this system aims to provide a rapid economic return due to its relatively short cycle but is a challenge for its conservation viability. *Eucalyptus* species have been subject to extensive genetic improvement programs and are managed under intensive silvicultural regimes to achieve high biomass yield (Gonçalves et al., 2013), which is associated with a high demand for local resources. Commercial varieties of *Eucalyptus* might be, in comparison to native fast-growing trees, more efficient in acquiring and using the available water, light and nutrients. Native species have not gone through breeding programs and show a wide range of growth rates. This genetic diversity is desired for conservation purposes but may compromise the use of native trees in plantation forestry. It is necessary to understand how *Eucalyptus* and native species interact in these mixed plantations and to further improve these systems to minimize competition while maximizing both wood production and restoration outcomes.

In this study we examined mixed plantations of *Eucalyptus* and a high diversity of native species using large experiments controlled for species diversity, stand density, age, disturbance regime and site characteristics such as soil type, topography and climate. We analyzed inventory data at the stand and tree levels from three different experimental sites in eastern Brazil containing (i) mixed plantations of *Eucalyptus* and a high diversity of native trees (23–30 species), (ii) *Eucalyptus* monocultures, and (iii) plantations composed exclusively of native trees, in which ten additional native tree species replaced *Eucalyptus* in the design of mixed plantings. To investigate the silvicultural viability of these mixtures both to produce high yields of *Eucalyptus* wood in mixed plantations and establish plantation stands with a high diversity of native tree species, our objective was to answer the following questions: What are the silvicultural consequences of intercropping *Eucalyptus* and native species? Do the size and identity of neighboring trees influence target tree diameter? How do different native species respond to the intercropping with *Eucalyptus*? We tested the following hypotheses: (1) *Eucalyptus* growth and survival is higher in mixed plantations than in monocultures, while that of native species is lower when intercropped with *Eucalyptus*; (2) The diameter of target native trees is influenced by the size and by the identity of neighboring trees; (3) The negative effect of competition from *Eucalyptus* on native species is directly related to their growth rate.

2. Material and methods

2.1. The mixed forests and the control treatments

We implemented three experimental sites with three treatments, where mixture plots (hereafter MIX) contained rows of clonal *Eucalyptus* alternating with high diversity rows comprising of 23–30 native tree species (hereafter, diversity group); monospecific *Eucalyptus* stands (hereafter EUC) as the control for *Eucalyptus*; and plots planted with native species (hereafter NAT), as the control for native tree species, in which we used the same 23–30 native species (diversity group) that were intercropped with *Eucalyptus*, but *Eucalyptus* rows were replaced by rows containing a mix of 9–10 fast-growing, wide-canopy native tree species (Supplementary Fig. 1). All seedlings in each experimental site were planted at the same time and were cultivated with the same silvicultural techniques commonly used in short-rotation *Eucalyptus* plantations in the region. This includes fertilization according to *Eucalyptus* nutritional demands for the local soil conditions, grass control with glyphosate spraying, ant control with insecticide baits and replanting after very low mortality within 1–2 months. All treatments of a given experimental site had the same spacing between the rows and between trees within rows. The mixtures that intercrop *Eucalyptus* and a high diversity of native tree species were conceived as a strategy to provide early income from the exploitation of *Eucalyptus* wood to offset part of the costs of plantation and maintenance in tropical forest restoration but may also serve as a permanent production system. Although, for areas where ecological restoration is the final objective (and where *Eucalyptus* is exotic), *Eucalyptus* may remain as part of the system during one or a few rotations and then be harvested and replaced by several native species to increase diversity.

2.2. Study sites and experimental design

We implemented three experimental sites within the Atlantic Forest region along the Brazilian East coast, located in Aracruz, ES, Mucuri, BA, and Igrapiúna, BA. The geographic distribution of the experimental sites represents a gradient of latitude, altitude, precipitation and temperature (Supplementary Table 1; Table 1). To control for the variability of ecological interactions, each native species was planted in the same position within all plots. The list of species used in each treatment is shown in Supplementary Table 2. Stand development is illustrated in Fig. 1 and the visual difference between mixtures and native species plots is shown in Fig. 2.

2.3. Data collection

We measured the survival rate while considering planted trees of any size. The Diameter at Breast Height-DBH (cm) and total height (m) were measured for all planted trees ≥ 1.3 m tall. Dead trees were not measured. In the experimental sites of Aracruz and Mucuri, trees that branched below 1.3 m had up to five of the largest stems measured. In Igrapiúna, we measured up to three of the largest stems. Height data was not available for the experiment in Igrapiúna. We inventoried the experiment in Aracruz at 38, 51 and 57 months after planting; the one in Mucuri at 48 months; and the one in Igrapiúna at 31, 45, 53 and 60 months after planting.

2.4. Data analysis

We divided species into different functional groups within each site according to their taxonomic identity and growth rate. These included *Eucalyptus*, fast-growing, wide-canopy native tree species, and all other native species grouped in terms of fast- (DBH $>$ 10 cm), intermediate- (DBH between 5 and 10 cm), and slow-growth rates (DBH $<$ 5 cm). Native species growth-rate classification was based on the mean diameter of native species intercropped with fast-growing, wide-canopy

Table 1
Characteristics of study sites. MIX = native trees intercropped with *Eucalyptus*; NAT = native trees intercropped with fast-growing, wide-canopy native tree species; EUC = *Eucalyptus* monoculture.

	1 Aracruz-ES	2 Mucuri-BA	3 Igrapiúna-BA	References
Coordinates	19°49′12″S, 40°16′22″W	18°05′09″S, 39°33′03″W	13°49′0″S, 39°9′0″W	
Altitude	41 m	78 m	121 m	Alvares et al. (2013)
Annual average rainfall	1412 mm	1531 mm	2191 mm	Alvares et al. (2013)
Annual average air temperature	23.4 °C	23.9 °C	25.0 °C	Alvares et al. (2013)
Climate Köppen	Aw; with a dry cold winter and a hot wet summer	Af;	Af; without a dry season	Köppen (1936)
Water deficit	Feb-Sep	Jan-Apr	Nov-Mar	Sentelhas et al. (2013a, 2013b, 2013c)
Soil	Typical Yellow Argisol (Ultisol); sandy/medium/clayey texture	Argisol; clayey (40%)	Dystrophic Yellow-Red Oxisol; clayey	EMBRAPA. Centro Nacional de Pesquisa de Solos (2000), EMBRAPA (2013)
Relief	Flat	Flat	Rounded hills with soft slopes;	Ab'Sáber (2003)
Experimental design	Randomized block design; 5 blocks	Randomized block design; 4 blocks	Randomized block design; 6 blocks	
Treatments	MIX; NAT; EUC	MIX; NAT; EUC	MIX; NAT	
Planting date	July 2011	May 2012	June 2011	
Experimental area	11.23 ha	10.37 ha	3.24 ha	
Total number of seedlings	9600	11,520	5400	
Plot area	2160 m^2	2160 m^2	1080 m^2	
Number of seedlings in effective plot	120	120	130	
Plot design	10 rows of 24 trees; two outer rows as border	10 rows of 24 trees; two outer rows as border	15 rows of 12 trees; one outer row as border	
Seedlings per hectare	1,111	1,111	1,667	
Spacing	3 × 3 m	3 × 3 m	3 × 2 m	
Eucalypt planted	*E. grandis* × *E. urophylla*	Hybrid of *E. urophylla*	4 different clones	
Fast-growing, wide-canopy native tree species	10 species	10 species	9 species	Rodrigues et al. (2009)
Native species of the diversity group	30 species	28 species	23 species	Rodrigues et al. (2009)

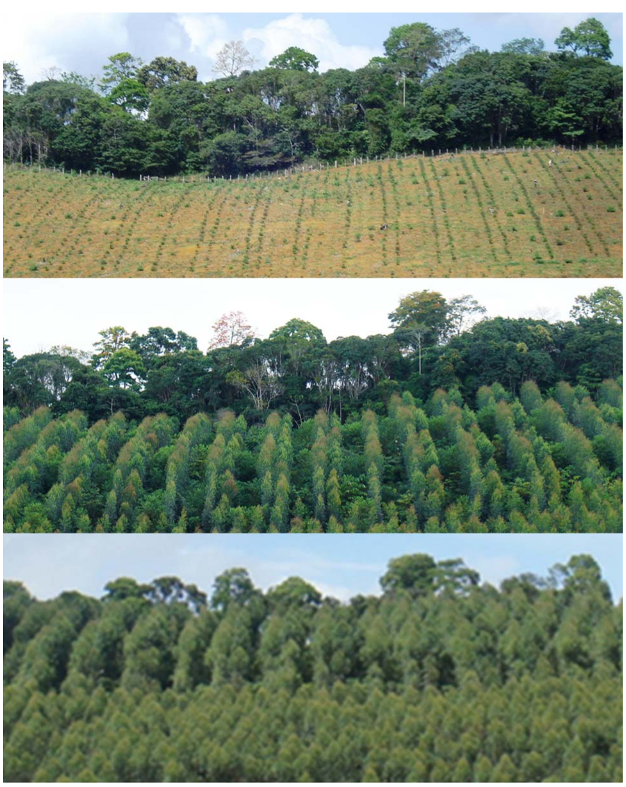

Fig. 1. Stand development at the experimental site in Igrapiúna, BA, Brazil. One week after planting (upper image), 30- (middle) and 44-months after planting (bottom).

native tree species in the native species plots recorded in the last inventory of each site (Supplementary Fig. 2).

2.4.1. Growth and survival in mixtures compared with Eucalyptus or native species plots

To test the hypotheses that *Eucalyptus* growth and survival is higher in mixed plantations than in monocultures, while that of native species was lower when intercropped with *Eucalyptus*, we compared their survival, diameter growth, height growth and basal area in all inventories and sites. We compared these variables between treatments at the stand level (community) using Welch's Two Sample *t*-test. We compared the total basal area of each treatment using ANOVA and Tukey ($\alpha = 0.05$).

2.4.2. The influence of neighbor size and identity on the diameter of target native trees

At the stand level, there were only three treatments, however at the neighborhood level, where a neighborhood could include the neighbors of a given target tree within different search radii, there is a much greater number of taxonomic diversity, functional diversity and stand density (due to differences in tree sizes). To test if the diameter of target native trees is influenced by the size (DBH) and by the identity (species functional group) of neighboring trees and the spatial scale (neighborhood search radii) to which these interactions occur, we examined the relationship between the diameter of target trees and a neighborhood index of target groups. We used inventory data to calculate neighborhood indices to quantify spatial (across site) and temporal tree interactions and growth dynamics. We performed tree-level analyzes to separate the effects of stand density from the effects of species composition on the growth of trees in the mixed species plots and used this to facilitate the interpretation of the stand-level analysis. This approach allows the partitioning of total competition effects into the effects of inter- and intra-functional group competition.

Trees were mapped at each site and we defined four neighborhood search radii to calculate the neighborhood index as the sum of neighbor diameters within a given radius. When there was no mortality, radius A

Fig. 2. View of mixture (MIX, left) and native species (NAT, right) plots 51 months after planting, in Aracruz, Espírito Santo State, Brazil. Notice the difference in height between *Eucalyptus* and native trees and the two-layered canopy in mixture plots, with *Eucalyptus* above and native species crowns below.

included the four first order neighbors and corresponded to 3.1 m; radius B included eight neighbors and corresponded to 4.3 m in Aracruz and Mucuri and to 3.7 m in Igrapiúna; radius C included 20 neighbors and corresponded to 6.1 m in Aracruz and Mucuri and 4.1 m in Igrapiúna; radius D included 24 neighbors and corresponded to 8.5 m in Aracruz and Mucuri and 6.1 m in Igrapiúna. We avoided neighborhoods that exceeded the effective plot borders. We used the *nlme* (Pinheiro et al., 2016) package to perform a linear mixed effects analysis of the relationship between the diameter of target trees and Neighborhood Index (NI) of the form shown in Eq. (1). All statistical analyses were performed in R 3.2.1 (R Core Team, 2016).

$$y_{tijkl} = X_{tijkl}\beta + Z_{ijkl}b_{ijkl} + e_{tijkl} \tag{1}$$

With random effects:

$$\left(b_{i}\underset{\sim}{\overset{iid}{}} N\left(0,\sigma_i^2\right); b_{ij}\underset{\sim}{\overset{iid}{}} N\left(0,\sigma_{ij}^2\right); b_{ijk}\underset{\sim}{\overset{iid}{}} N\left(0,\sigma_{ijk}^2\right); b_{ijkl}\underset{\sim}{\overset{iid}{}} N\left(0,\sigma_{ijkl}^2\right); \varepsilon_{tijkl}\underset{\sim}{\overset{iid}{}} N\left(0,\sigma^2\right)\right)$$

where y_{tijk} is the dependent variable (DBH), X_{tijkl} is the independent variables matrix (fixed effects matrix which included age, species functional groups (with an interaction term between NI and species group)), Z_{ijkl} is the random effects matrix, β and b are the parameters' vector of fixed and random effects, t is the index for time of measurement, i is the index for site, j is the index for block, k is the index for plot, l is the index for tree, e_{tijkl} is the error component, ρ is the autocorrelation coefficient and ε_{tijkl} is the within group error vector. Visual evaluation using residual plots did not reveal any obvious deviation from normality or homoscedasticity. We used mixed models to be able to analyze data from repeated inventories of the same sites in different ages and to control for differences between sites, blocks and plots.

2.4.3. Competitive effect of Eucalyptus in relation to native species growth rates

To test if the negative effect of competition from *Eucalyptus* on native species was related to their growth rate, we compared the diameters of trees in each diversity group in mixture and the control at the stand and tree-levels. At the stand level, this comparison was performed using a linear regression, by plotting the mean diameter of a species growing in mixture versus its mean diameter in control, for all different sites and ages measured. Then, we contrasted the fitted line against the null model (slope = 1). The lower the slope, the greater the competitive effect.

At the tree level, we performed a linear regression of tree diameter (DBH) as a function of total neighborhood index. The steeper the slope, the greater the effect of NI on DBH. We accounted for the effects of the different diversity groups based on the different growth rates (fast-, intermediate-, and slow-growth), the four different search radii, and the total neighborhood index as the sum of the diameters of all trees around a given target tree with a given search radius.

3. Results

3.1. Species' performance in mixtures of Eucalyptus and a high diversity of native trees

Total basal area was highest in stands of *Eucalyptus* monoculture, intermediate in mixtures and lowest in native species plots (Fig. 3). Despite the strong tendency of higher basal area of *Eucalyptus* monocultures compared to mixtures in Mucuri, considering $\alpha = 0.05$ significance, these means were only significantly different considering $\alpha = 0.1$ significance (data not shown).

Individual *Eucalyptus* trees had larger diameters in the mixed plantation than in monoculture ($p < 0.01$), achieving an average increase of 21.4% in Aracruz and of 18.2% in Mucuri. In the mixture (555 *Eucalyptus* trees/ha), *Eucalyptus* produced approximately 75% of the

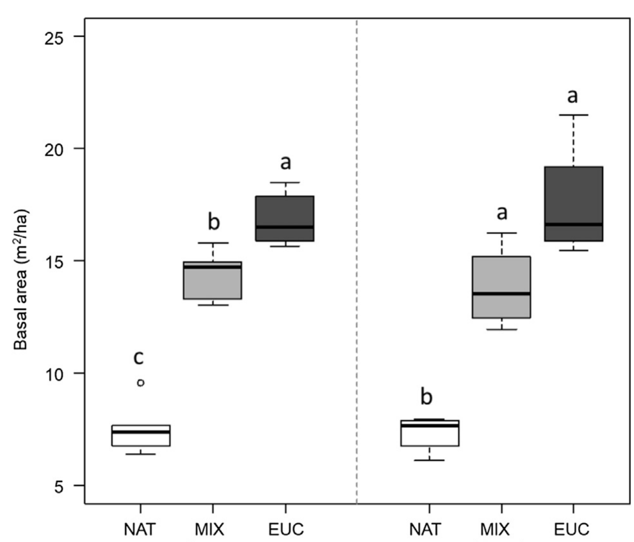

Fig. 3. Total basal area in three different forestry systems established in two experimental sites (Aracruz, ES, 57 months old; Mucuri, BA, 48 months old) in the Atlantic Forest of Eastern Brazil: Native species (NAT) (fast-growing, wide-canopy native tree species + native species of the diversity group, 1:1), Mixture (MIX) (*Eucalyptus* + native species of the diversity group, 1:1); *Eucalyptus* monoculture (EUC).

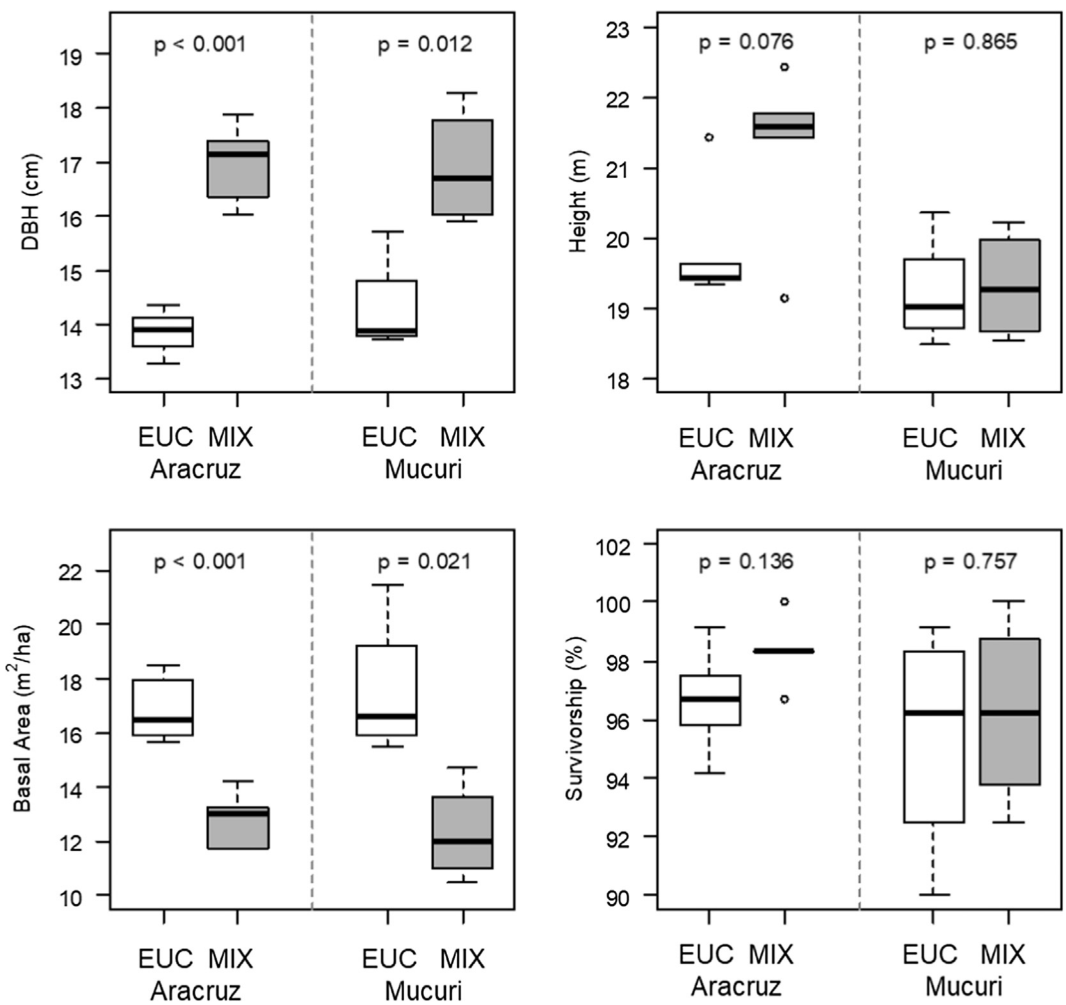

Fig. 4. Comparison of DBH, height, basal area and survivorship for *Eucalyptus* planted in monoculture (EUC) or intercropped (MIX) with 28–30 native tree species (diversity group) established in two experimental sites (Aracruz, ES, 57 months old; Mucuri, BA, 48 months old) in the Atlantic Forest of Eastern in Brazil.

basal area ($p < 0.001$) produced in *Eucalyptus* monocultures (1111 trees/ha). *Eucalyptus* survival and height were similar in monoculture and in mixtures with native trees (Fig. 4; Supplementary Fig. 3).

Native trees of the diversity group had smaller diameters when intercropped with *Eucalyptus* than intercropped with fast-growing, wide-canopy native tree species (Fig. 5) at all sites and ages (Supplementary Fig. 4; $p < 0.01$). The mean reduction was −17.9% at Aracruz, −19.0% at Mucuri and −23.0% at Igrapiúna. Fast- and intermediate-growing species had smaller diameters in mixtures, except for the intermediate-growing species at Mucuri, which had similar values. The diameter of slow-growing species did not differ amongst sites and ages (Supplementary Fig. 4). The basal area of native trees intercropped with *Eucalyptus* was 61.8% of that produced in native species plots in Aracruz ($p = 0.019$), 45.7% in Mucuri ($p = 0.003$) and 48.6% in Igrapiúna ($p = 0.004$). Smaller basal areas occurred for native species in mixtures in all sites and ages for fast- and for intermediate-growing species, but not for the latter at Mucuri (Supplementary Fig. 5). We observed no difference in the basal area of slow-growing species at Aracruz or Igrapiúna at all ages, but this group presented a lower basal area in the mixture at Mucuri (Supplementary Fig. 5).

The survival of native trees of the diversity group did not differ between treatments, except at Mucuri, where mortality was higher in the mixture as a result of increased mortality of fast-growing native species (at 48 months; $p = 0.02$). The survivorship of intermediate-growing native species was not affected by mixing with *Eucalyptus*. No difference in survival was observed for slow-growing native species during the early stages of the experiments, but their survivorship became significantly lower in the mixtures at Aracruz as stands developed (at 51 and 57 months) (Fig. 5; Supplementary Fig. 6). Tree height was similar for native species of the diversity group in both treatments in the last inventory (Fig. 5) and changed through time is shown in Supplementary Fig. 7.

3.2. Target tree diameter is affected by size and identity of neighbors

Eucalyptus' diameter was negatively correlated with the size of the closest *Eucalyptus* neighbors, but was not influenced by native species neighbors, regardless of the search radii used (Table 2). Across sites, ages and treatments, the diameter of target native trees was negatively related to the size of neighbors (total neighborhood index) and this effect was modified by the identity of the neighbors (as indicated by the interaction between NI and species groups, data not shown).

3.3. Tree growth rate and mixing effect intensity

At the plot level, the competitive effect of *Eucalyptus* on diameter in mixtures was greater for native species of fast- than for species of intermediate- and slow-growth rates (Fig. 6). At the neighborhood level, the interaction between fast-growing, wide-canopy native tree species neighborhood index and the group of target tree species within radii including the nearest 8, 20 and 24 potential neighbors was important ($p < 0.01$) for the diameter reduction in mixtures. Fast-growing native

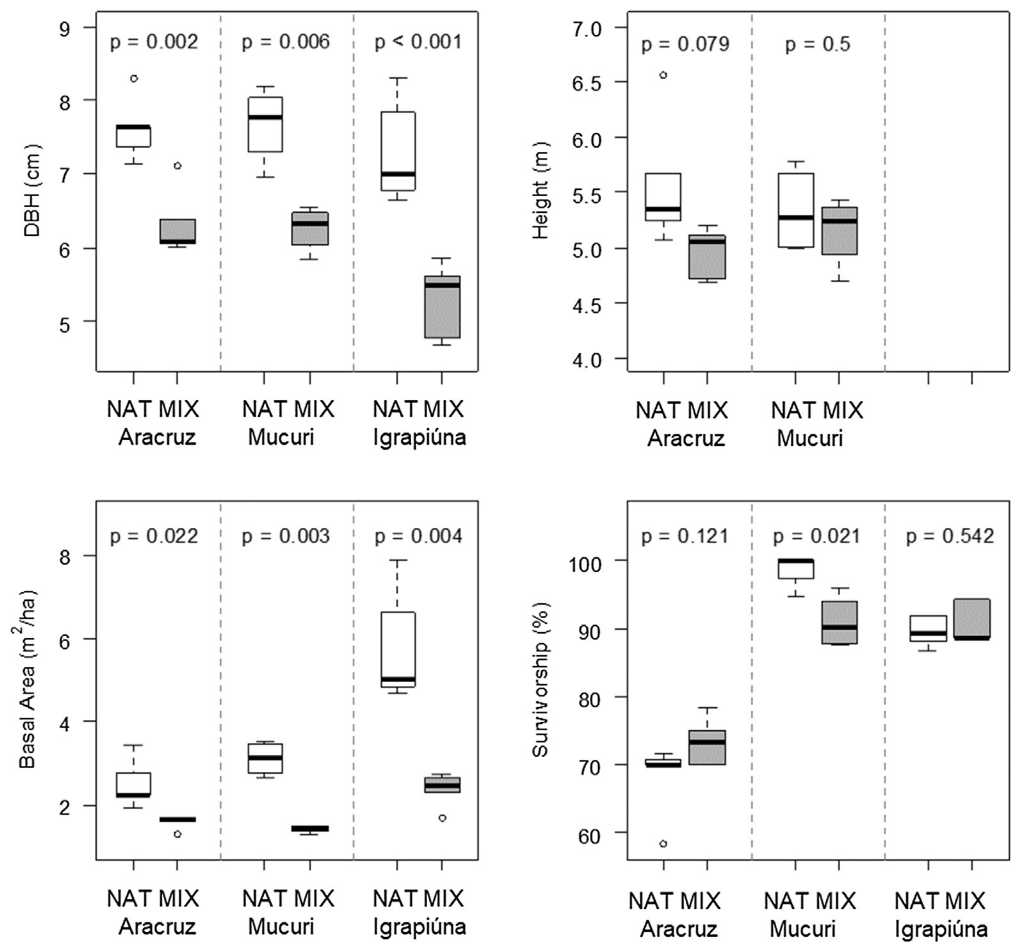

Fig. 5. Comparison of DBH, height, basal area and survivorship for native trees of the diversity group intercropped with fast-growing, wide-canopy native tree species (NAT) or with *Eucalyptus* (MIX) established in three experimental sites (Aracruz, ES, 57 months old; Mucuri, BA, 48 months old; and Igrapiúna, BA, 60 months old) in the Atlantic Forest of Eastern Brazil. Tree height was not available at Mucuri, BA.

species' diameter and total neighborhood index had the strongest negative relationship; whereas tree species of intermediate- and slow-growth showed a weaker negative relationship with the neighborhood index of fast-growing shading species (*Eucalyptus* or native) (Fig. 7), which is consistent with the differences shown in Fig. 6.

4. Discussion

Commercial *Eucalyptus* species are well known in Brazil for their fast growth and high productivity in large-scale monocultures (Gonçalves et al., 2013). However, very little is known about the performance of *Eucalyptus* in mixed plantations with several native trees, as well the performance of native trees when intercropped with *Eucalyptus* (Erskine et al., 2006, 2005) or other tropical species (Montagnini et al., 1995; Nguyen et al., 2014; Parrotta, 1999), which compromise the design and management of multipurpose mixed plantations. This study shows that it is feasible to establish a mixture of *Eucalyptus* and native tree species in high diversity plantations. Our first hypothesis was supported, since *Eucalyptus* grew faster in the mixtures while native species did not perform as well in mixtures. Our second hypothesis was also supported because both the size and the identity of neighbors were important factors influencing the diameter of target native trees. The results also supported the third hypothesis that *Eucalyptus* had a greater competitive effect on the fastest growing group of native species and a smaller competitive effect on the species with slower-growth rates. Even though competition slowed the diameter growth of native species, their survivorship and height were not affected.

At the stand level, our results showed that, in mixtures, *Eucalyptus* produced nearly 75% of the basal area produced by *Eucalyptus* monocultures, even though mixtures had only 50% of the density of *Eucalyptus* seedlings (555 trees ha^{-1}) compared to monocultures (1,111 trees ha^{-1}). This resulted from the considerably greater diameters that individual *Eucalyptus* trees grew when intercropped with native species. Similar results were found for mixtures of *Eucalyptus* and *Acacia* (Forrester et al., 2004; Santos et al., 2016) and *Eucalyptus* and *Falcataria* (Binkley et al., 2003), in which individual *Eucalyptus* trees grew larger than in monocultures and produced disproportionately higher biomass per hectare than in monospecific stands. This outcome is advantageous when larger trees are worth more than smaller trees or when earlier harvesting can be anticipated because trees reach merchantable sizes earlier. In the mixture, *Eucalyptus* trees were much larger and taller than in *Eucalyptus* monoculture, and we found no evidence of competition from the smaller and shorter neighboring native species. The *Eucalyptus* species that are grown in plantations are often strong competitors and commonly benefit from growing in mixtures (Forrester et al., 2006). However, there are exceptions where *Eucalyptus* has been planted on sites where other species have been able to compete strongly enough to reduce the growth of the *Eucalyptus*, even if this was only for part of the rotation (Bouillet et al., 2013; Forrester et al., 2007). Therefore, even for *Eucalyptus*, careful consideration of site and the mixed species is critical for success.

In this study, individual *Eucalyptus* trees may have benefited from more access to light especially at the lateral parts of their crowns above the rows of shorter native species canopies, as illustrated in Fig. 2. These results clearly show that *Eucalyptus* benefited from the mixture plantations, which could be explained by competitive reduction and/or

Table 2
Effect of neighboring trees on the diameter of target trees in three experimental sites in the Atlantic Forest of Eastern Brazil (Aracruz, ES, 38, 51 and 57 months old; Mucuri, BA, 48 months old; and Igrapiúna, BA, 31, 45, 53 and 60 months old). Bold letters, indicating the number of potential neighbors included in the search radii, followed by asterisks mean a significant effect; plain text letters indicate no significant effect for that search radius. For details on search radii and the number of neighboring trees within the given radius, refer to the Data analysis section.

Group of target tree	Factor influencing target tree diameter	Number of potential neighbors
Eucalyptus	Neighborhood index of *Eucalyptus*	**4***** **8*** 20 24
Eucalyptus	Neighborhood index of Diversity group	4 8 20 24
Diversity group	Total neighborhood index (including all species)	**4***** **8***** 20 24
Diversity group	Neighborhood index of *Eucalyptus* or fast-growth shading native species	4 **8***** 20 24
Diversity group	Identity of neighbor (species group neighbors belong to: *Eucalyptus*; fast-growth shading native species; native species of fast-; intermediate-; or slow-growth)	**4***** **8***** **20***** **24*****

* $p < 0.05$.
*** $p < 0.001$.

facilitation interactions (Kelty, 2006; Vandermeer, 1989), often collectively described using the term complementarity. The competitive advantage of *Eucalyptus* over native species that led to a potential reduction in competition, originates from many years of artificial selection and genetic improvement, which enabled *Eucalyptus* to capture more resources than native trees (Gonçalves et al., 2013). The competitive reduction would also be related to a density effect because the native trees contribute a relatively low proportion of the stand basal area even though they represent about half the number of trees. That is, the basal area of the *Eucalyptus* monocultures was significantly greater than that of the mixtures. Facilitation could arise from higher soil nitrogen availability incorporated into the system by the abundant N-fixing native trees in our experiments (roughly 25% of the native trees). However, the role of biological N fixation in these plantations is still unknown and it is possible that the initial nitrogen fertilizer application interfered with the nodulation capacity of some of the tree species we planted. It is also possible that the rate of litter decomposition and nutrient cycling was higher in the mixtures (Gartner and Cardon, 2004; Hättenschwiler et al., 2005; Richards et al., 2010; Rothe and Binkley, 2001). Further research is needed to decouple competitive reduction from facilitation in this silvicultural system so that these processes can be efficiently manipulated and utilized by managers.

Stand-level analyzes showed that the mixture with *Eucalyptus* negatively affected the size of native species (diameter, but not height). Thus, the mixtures were intermediate in productivity between the more productive *Eucalyptus* monocultures and the less productive native species stands. Similarly, the productivity of tropical plantations in the Philippines was related more to the productivity of the species within the plantation than to the tree species richness of the plantation (Nguyen et al., 2012). Tree-level analyzes showed that in these systems, the effect of neighbor size on target tree diameter depends both on the identities of target trees and neighbors. The growth of native species was influenced by fast-growing, wide-canopy native tree species and by *Eucalyptus*, and the effect of treatment was important, meaning that using *Eucalyptus* instead of fast-growing, wide-canopy native tree species, resulted in greater competition. Similarly, previous research on mixtures of *Eucalyptus* and *Acacia* showed that competition slowed the diameter growth but not height of *Acacia* (Laclau et al., 2008). Amazonas et al. (in press) showed that native species may face stronger water limitation in these mixtures. This could cause shifts in carbon partitioning from above to belowground, ultimately resulting in less wood production (Nouvellon et al., 2012).

The different groups of native trees were affected differently by the competition with *Eucalyptus* according to their growth rate. The faster the native species grew, the more (in relative and absolute terms) their growth was constrained by competition with *Eucalyptus*. This may simply be because the faster species require correspondingly more resources to maintain their growth, and therefore they are more likely to be negatively affected by a faster growing and highly competitive tree species, like *Eucalyptus*. This effect may also be related to shade tolerance and could thus explain why the growth decrease of native species was related to growth rate with shade-tolerant late-successional species (which are slower growing) being less affected by the mixture.

At our experimental sites, *Eucalyptus* survived equally well in monospecific stands and in the mixtures. Native species had lower survival rates than *Eucalyptus* in general, but we found almost no difference between their survivorship in the mixtures and in the controls. Our results show that intercropping with *Eucalyptus* instead of fast-growing, wide-canopy native tree species does not cause additional mortality to native species seedlings, except for fast-growing species at the Mucuri site. Tree mortality varied in different studies examining mixtures of two species. Survival rates did not change amongst treatments or sites for mixtures of *Eucalyptus* and *Acacia* in Brazil and the Congo (Bouillet et al., 2013). Similar survival rates were observed between monocultures and mixtures of *Eucalyptus* and *Albizia* in Hawaii (DeBell et al., 1997) while *Acacia* had higher survival rates in mixtures with *Eucalyptus* than in monocultures in Australia (Forrester et al., 2004).

This study shows that mixed species plantations can be established with *Eucalyptus* and a high diversity of native tropical Brazilian tree species. The economic and restoration success of these plantations will also depend on the silvicultural approach that follows. Many silvicultural options are likely to be appropriate for diverse mixtures such as these, depending on the objectives. A selective thinning regime that removes poorly formed and suppressed, trees as well as trees that have reached merchantable sizes has been recommended for other tropical mixed species plantations (Erskine et al., 2005; Nguyen et al., 2014). In contrast, thinning the smallest trees will likely reduce the tree species richness by removing the slower growing species (Erskine et al., 2005). Thinning would release the retained trees from competition, provide some income and may also be used to encourage regeneration of the native species in the canopy gaps (Erskine et al., 2005; Nguyen et al., 2014). If necessary, the regeneration may be supplemented by enrichment planting (Bertacchi et al., 2016). In addition, while the planting design worked on each site, other designs could be tested such as where the slower growing species are planted a year earlier to give them a head start (Kelty and Cameron, 1995; Nguyen et al., 2014).

Plantation design is essential for the further development of these systems and different spatial and temporal strategies could be used to optimize ecological interactions (Kelty and Cameron, 1995). One option to cope with possible incompatibilities between the *Eucalyptus* and fast-growing native species, regarding competition for water, nutrients and light, would be to establish high diversity mixtures without these sensitive native species, and then to add these native species when the *Eucalyptus* is removed from the system, assuming there is still enough light available for them to establish between the other species. We harvested eucalypts five years after planting to maximize timber production and the quality of fiber for wood pulp production, thus integrating native trees into a commercial silvicultural system already

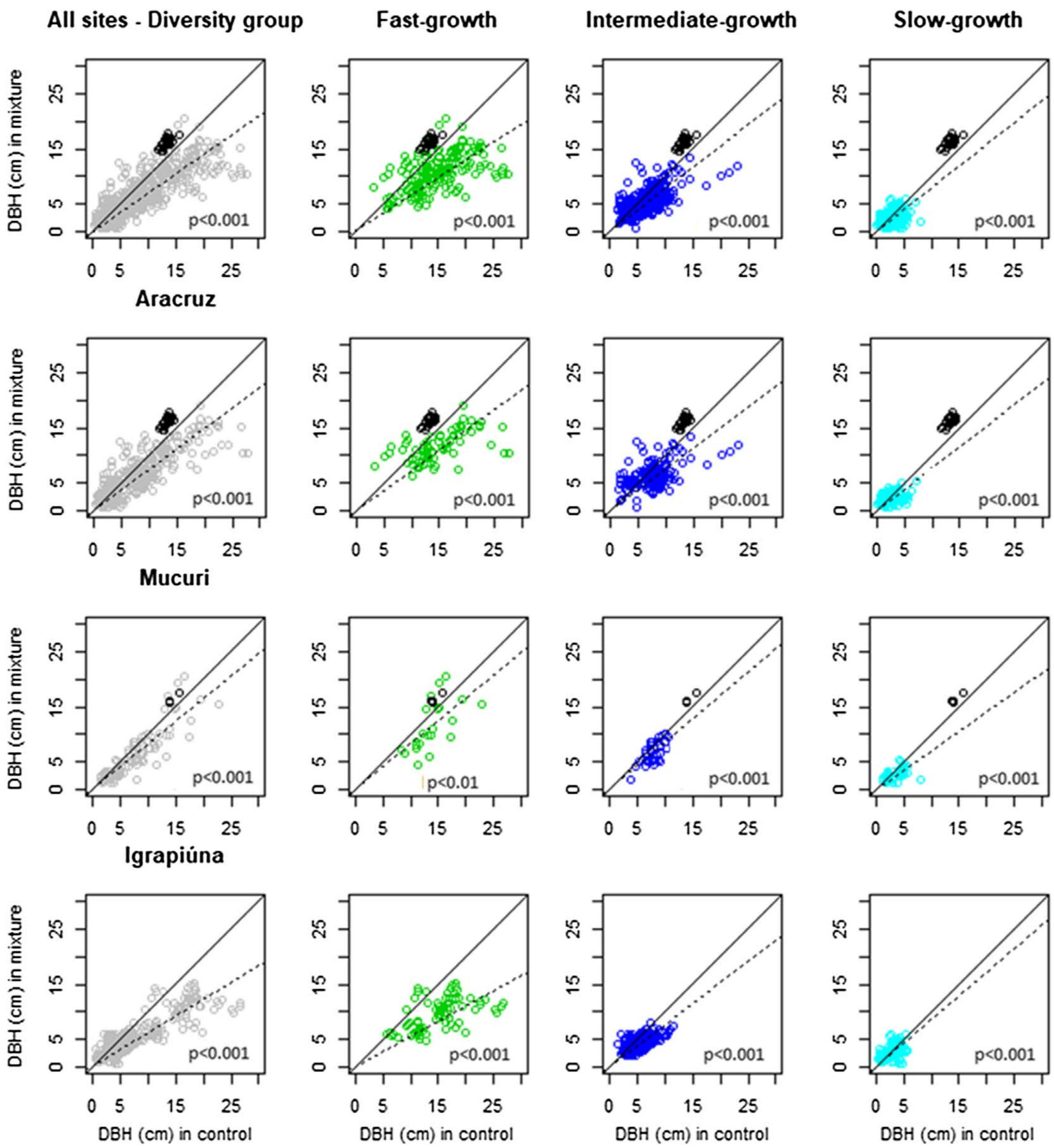

Fig. 6. Mixing effect on tree diameter for *Eucalyptus* (black) and native species of the diversity groups (grey), classified at fast-, intermediate- and slow-growing species in plantations established in three experimental sites in the Atlantic Forest of Eastern Brazil (Aracruz, ES, 38, 51 and 57 months old; Mucuri, BA, 48 months old; and Igrapiúna, BA, 31, 45, 53 and 60 months old). The points are the mean for all trees of the given diversity group in a given plot at a given age. Note that points above the diagonal continuous line indicate that diameters were often larger in mixtures and points below the line indicate that species had smaller diameters in the mixture than in control treatments (*Eucalyptus* monoculture or native species plots). The dashed lines are fitted to the native species and not to *Eucalyptus* (black circles), which are shown only to indicate the corresponding *Eucalyptus* Diameter at Breast Height (DBH) in the same treatments. The p-values provided indicate that the diameter of native species in mixtures is significantly smaller than in native species plots. Data from all experimental sites are shown in the first row; from Aracruz in the second row; from Mucuri in the third row; and from Igrapiúna in the fourth row, which does not have a *Eucalyptus* monoculture as a treatment. Data includes all inventories.

used across the approximately 5.7 Mha of *Eucalyptus* plantations in Brazil (Indústria Brasileira de Árvores, 2017). Alternatively, *Eucalyptus* could be harvested earlier to provide firewood and poles, in the cases where there is a local market for smaller eucalypt logs. Balancing silvicultural designs and markets is critical for promoting mixed tree plantations in the tropics (Nguyen et al., 2014), so the multiple uses of eucalypt wood is an advantage to increase the flexibility of its management in mixed plantations focused on both conservation and production. Another option is the implementation of mixtures in different spatial arrangements using an intermediate- or a coarse-, instead of a fine-grid design, to minimize competition between *Eucalyptus* and native trees (Bauhus et al., 2017b; Kelty and Cameron, 1995). For example, planting double or triple rows of *Eucalyptus* intercropped with double or triple rows of native tree species. Different designs could, however, increase competition between *Eucalyptus* trees and result in decreased *Eucalyptus* wood production, or compromise restoration when this is the final objective.

5. Conclusions

The mixed plantations we studied are beneficial for the growth of *Eucalyptus*, which produced almost 75% of the basal area of monocultures using only 50% of the number of *Eucalyptus* seedlings. Even though competition for resources with *Eucalyptus* slowed the growth of native species, it was not strong enough to affect their survival or outcompete the native trees. The slower growth of native species is not of major concern in the short-term and may be reversed if the forests are managed for purposes other than the production of *Eucalyptus* in the future, but this reversal still needs to be assessed. We conclude that mixtures of *Eucalyptus* and a high diversity of native tree species are

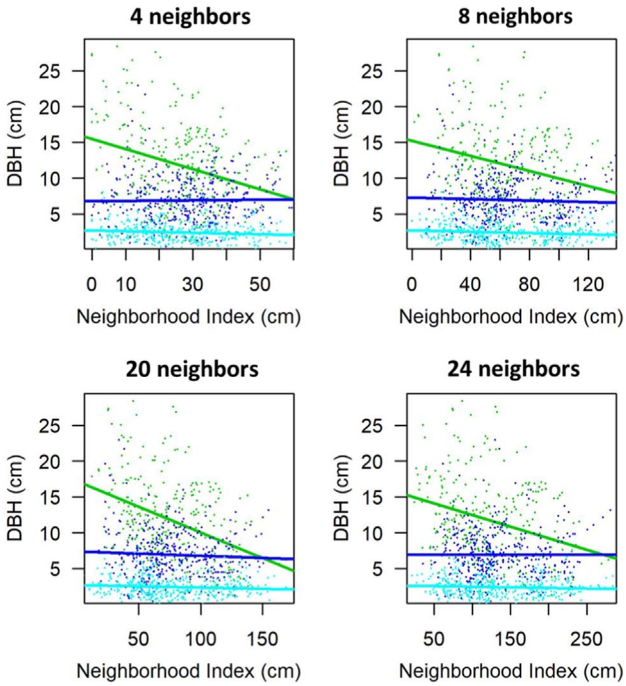

Fig. 7. Relationship between tree diameter at breast height (DBH) and total neighborhood index for species of fast- (green), intermediate- (dark blue) and slow-growths (pale blue) in mixed plantations established in three experimental sites in the Atlantic Forest of Eastern Brazil (Aracruz, ES, 38, 51 and 57 months old; Mucuri, BA, 48 months old; and Igrapiúna, BA, 31, 45, 53 and 60 months old). Fast: $p < 0.001$ (4, 8, 20 and 24 potential neighbors); $R^2 = 0.08$ (4 potential neighbors), 0.06 (8 potential neighbors), 0.15 (20 potential neighbors), and 0.09 (24 potential neighbors). Slow-growth: $p < 0.05$ (4, 8 potential neighbors); $R^2 = 0.0115$ (4 potential neighbors), 0.0145 (8 potential neighbors). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

technically feasible and represent an important alternative for establishing multipurpose plantations, especially in the context of forest and landscape restoration.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2018.03.015.

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