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ABANDONED EUCALYPTUS PLANTATIONS CAN BE USED AS CATALYSTS FOR NATURAL REGENERATION

MATHEUS CARVALHO DOS SANTOS

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Orientador: Prof. Dr. Luiz Fernando Silva Magnago

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SUMÁRIO

RESUMO	6
ABSTRACT	7
INTRODUÇÃO GERAL	8
REFERÊNCIAS	9
Abandoned Eucalyptus plantations can be used as catalysts for natural regeneration.	14
Abstract	15
Introduction	16
Materials and methods	18
Study area	18
Data collection	19
Measures of phylogenetic diversity and structure	20
Functional trait matrix	21
Phylogenetic signal of the functional traits	22
Data analysis	22
Results	23
Does Eucalyptus act as an environmental filter?	23
Does phylogenetic diversity increase over succession?	26
Are functional traits conserved across lineages?	28
Discussion	28
Does Eucalyptus act as an environmental filter?	29
Does phylogenetic diversity increase with succession?	30
Are functional traits conserved across lineages?	32
References	33
Data sources	42
SUPPLEMENTARY MATERIAL	47

RESUMO

A Mata Atlântica tem um elevado potencial de regeneração natural em áreas abandonadas sob plantios de eucaliptos. Hipotetizamos que a regeneração natural nas florestas tropicais começa com comunidades compostas por algumas espécies pioneiras, que exibem menor riqueza, diversidade e complexidade do que as comunidades de clímax encontradas no final da sucessão. Aqui, abordamos a diversidade e a estrutura filogenética nas florestas sob plantios abandonados de eucalipto e investigamos se o eucalipto atua como um filtro ambiental que seleciona as espécies mais aparentadas. Comparamos a diversidade (PD, MPD, MNTD) e a estrutura filogenética (sesPD, NRI, NTI) em áreas de regeneração natural da Mata Atlântica em dois tratamentos: i) tratamento misto, espécies nativas sob plantações abandonadas de eucalipto; ii) tratamento nativo, com a presença de espécies nativas. Estabelecemos 17 transectos no tratamento misto e 35 no tratamento nativo. Em cada transecto, amostramos 5-15 parcelas contíguas de 10 m x 10 m. Dentro de cada parcela, amostramos todos os indivíduos vivos com um diâmetro à altura do peito ≥ 10 cm. Não encontramos diferenças significativas entre tratamentos para nenhum dos índices de diversidade filogenética testados. As médias de NRI e NTI foram positivas, indicando agrupamento filogenética em ambos os tratamentos. Nenhum dos índices de diversidade filogenética e de estrutura filogenética foi significativamente afetado pelo aumento da área basal de acordo com os nossos modelos. As plantações de restauração têm objetivos que vão para além da restauração da cobertura florestal a uma área, assegurando a manutenção de espécies nativas evolutivamente únicas, e mantendo serviços e funções essenciais do ecossistema. Ao longo da sucessão, a diversidade filogenética aumentou em ambos os tratamentos sem diferenças significativas. Concluímos que os planos de restauração podem utilizar o eucalipto como ponto de partida para os planos de restauração, especialmente quando o sequestro de carbono juntamente com a biodiversidade é o principal objectivo do projecto de restauração.

Palavras-chave: Conservação da Biodiversidade; Diversidade e Estrutura Filogenética; Mata Atlântica; Plantações Florestais; Restauração Ecológica; Sinal filogenético de traços funcionais; Sub-bosque de Eucalipto; Sucessão secundária.

ABSTRACT

After abandonment, the Atlantic Forest has a high potential for natural regeneration in areas under eucalyptus plantations. We hypothesize that natural regeneration in tropical forests begins with communities composed of a few pioneer species, which exhibit lower richness, diversity, and complexity than climax communities found at the end of succession. Here, we address diversity and phylogenetic structure in eucalyptus understory forests and investigate whether eucalyptus acts as an environmental filter that selects for more phylogenetically related species. We compared diversity (PD, MPD, MNTD) and phylogenetic structure (sesPD, NRI, NTI) in natural regeneration areas of the Atlantic Forest in two treatments: i) mixed treatment, native species under abandoned eucalyptus plantations; ii) native treatment, with the presence of native species. We established 17 transects in the mixed treatment and 35 in the native treatment. On each transect, we sampled 5-15 contiguous 10 m x 10 m plots. Within each plot, we sampled all live individuals with a diameter at breast height ≥ 10 cm. We found no significant differences between treatments for any of the phylogenetic diversity indices tested. The means of NRI and NTI were positive, indicating phylogenetic clustering in both treatments. None of the phylogenetic diversity and phylogenetic structure metrics were significantly affected by increasing basal area according to our models. Restoration plantings today have goals that go beyond restoring forest cover to an area, ensuring the maintenance of evolutionarily unique native species, and maintaining key ecosystem services and functions. Throughout succession, phylogenetic diversity increased in both treatments without significant differences. We conclude that restoration plans can use eucalyptus as a starting point for restoration plans, especially when carbon sequestration along with biodiversity is the main goal of the restoration project.

Keywords: Atlantic Forest, Biodiversity Conservation, Diversity and Phylogenetic Structure, Ecological restoration, Eucalyptus understory, Forest Plantations, Phylogenetic characters of functional traits, Secondary succession.

INTRODUÇÃO GERAL

A restauração ecológica é o processo de contribuição para a recuperação de um ecossistema que foi degradado, danificado ou destruído (SER, 2004). Além de contribuir para a conservação da biodiversidade, a restauração de ecossistemas visa promover benefícios sociais, econômicos e ambientais, tais como a mitigação das alterações climáticas (CBD, 2019). A Organização das Nações Unidas (ONU) definiu a década 2021-2030 como a Década da Restauração, com o objetivo de deter a degradação dos ecossistemas e restaurá-los para atingir objetivos globais (ONU Brasil, 2021; WRI Brasil, 2021), como o Bonn Challenge (IUCN, 2021), e objetivos nacionais, como o Pacto de Restauração da Mata Atlântica no Brasil, lançado em 2009, que promove a recuperação de 15 milhões de hectares de áreas degradadas até 2050 (PACTO, 2021).

A Mata Atlântica foi identificada pela *Conservation International* como um *hotspot* global devido à fragmentação antrópica e ameaça à biodiversidade (Myers et al., 2000), restando 26,8% da sua cobertura florestal (MapBiomas, 2021). A degradação e o desmatamento na Mata Atlântica foram impulsionados pela expansão das terras agrícolas e monoculturas de árvores (Rodrigues et al., 2009; Rosa et al., 2021), com 57,1% da cobertura em uso extensivo agrícola e pecuário e 3,5% em uso florestal (MapBiomas, 2021). As plantações de eucalipto para fins comerciais no Brasil correspondem a 76,9% das florestas plantadas (IBGE, 2022). Após o abandono do uso da terra, a Mata Atlântica tem um elevado potencial de regeneração natural (Rozendaal et al., 2019; Poorter et al., 2021), quer em antigas áreas de pastagem (Benayas et al., 2007) ou sob plantações de eucalipto (Silva Júnior et al., 1995; Sartori et al., 2002; Souza Filho et al., 2007; Onofre et al., 2010; Viani et al., 2010; Ronquin, 2021).

Para que ocorra a regeneração natural, é necessário o recrutamento de plântulas durante a sucessão natural através do banco de sementes do solo, dispersão de sementes ou rebrotas (Baider et al., 2001; Tabarelli & Peres, 2002; Viani et al., 2015). A montagem de comunidades dirige a sucessão natural através de processos evolutivos e ecológicos baseados na teoria do nicho (concorrência e filtros ambientais) ou teoria neutra (Webb et al., 2002; Cavender-Bares et al., 2009; Meiners et al., 2015). Os filtros ambientais atuam para selecionar espécies dentro de uma comunidade com base na sua capacidade de persistir sob certas condições, limitando a composição de espécies com características ecológicas-funcionais semelhantes (Webb et al., 2002; Cavender-Bares et al., 2002; Cavender-Bares et al., 2007). A regeneração natural é eficaz em plantações abandonadas de eucaliptos, que podem catalisar a sucessão florestal no subsolo, mesmo em áreas sem florestas nativas (Viani

et al., 2010; Ronquin, 2021). Por outro lado, o eucalipto pode atuar como um filtro ambiental, influenciando a estrutura filogenética das comunidades através da selecção de espécies semelhantes e estreitamente relacionadas (Kraft et al., 2008; Myers & Harms, 2009).

Duas abordagens revelaram-se promissoras na detecção de respostas na montagem de comunidades às mudanças ambientais: a diversidade filogenética e a funcional. A diversidade filogenética é uma medida que incorpora as relações entre espécies numa comunidade (Magurran, 2004), enquanto que a diversidade funcional incorpora a variação entre espécies e os seus traços que influenciam o modo como as comunidades funcionam (Tilman, 2001). Assim, as medidas que incorporam relações filogenéticas ou traços funcionais podem ser superiores às medidas tradicionais de diversidade (Cianciaruso et al., 2009) e revelaram-se úteis em estudos de restauração florestal (Rother et al., 2019). A diversidade filogenética tem sido utilizada na ecologia de comunidades para inferir a montagem, organização e co-ocorrência de espécies (Webb et al., 2002). Os esforços de restauração visam restaurar um ecossistema com diversidade e função adequadas (Aerts & Honnay, 2011). Isto requer uma compreensão das características funcionais das espécies e pode ajudar a avaliar o sucesso da restauração de acordo com os objetivos e necessidades (Díaz et al., 2013).

Abordamos estas importantes lacunas no conhecimento da diversidade e estrutura filogenética das florestas em sub-bosque de eucalipto na Mata Atlântica, investigando se o eucalipto pode atuar como um filtro ambiental, selecionando espécies filogenéticamente mais relacionadas que outras espécies na comunidade. Como pressuposto, podemos considerar que nas florestas tropicais, a regeneração natural começa com comunidades compostas por poucas espécies pioneiras, com menor riqueza, diversidade e complexidade do que as comunidades clímax encontradas no final da sucessão (Horn, 1974; Magnago et al., 2011; Greenberg et al., 2011; Chazdon, 2012; Crouzeilles et al., 2017; César et al., 2018; Poorter et al., 2021). Assim, esperamos que em áreas abandonadas, o eucalipto possa atuar como um catalisador para a sucessão de espécies nativas no sub-bosque, aumentando a diversidade filogenética à medida que a sucessão avança.

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Abandoned Eucalyptus plantations can be used as catalysts for natural regeneration¹

Matheus C. Santos¹, Jeanpierre R. Mirano², Nathália V. H. Safar³, Luiz Fernando S. Magnago^{2*}

¹ Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Universidade Estadual de Santa Cruz, Ilhéus, Bahia, Brazil; ² Centro de Formação em Ciências e Tecnologias Agroflorestais, Universidade Federal do Sul da Bahia, Ilhéus, Bahia, Brazil; ³ Departamento de Botânica, Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil.

* Corresponding author. E-mail: m_oak@outlook.com

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¹ Title page. The manuscript will be submitted to the journal Functional Ecology.

Abstract

- 1. After abandonment, the Atlantic Forest has a high potential for natural regeneration in areas under eucalyptus plantations. We hypothesize that natural regeneration in tropical forests begins with communities composed of a few pioneer species, which exhibit lower richness, diversity, and complexity than climax communities found at the end of succession. Here, we address diversity and phylogenetic structure in eucalyptus understory forests and investigate whether eucalyptus acts as an environmental filter that selects for more phylogenetically related species.
- 2. We compared diversity (PD, MPD, MNTD) and phylogenetic structure (sesPD, NRI, NTI) in natural regeneration areas of the Atlantic Forest in two treatments: i) mixed treatment, native species under abandoned eucalyptus plantations; ii) native treatment, with the presence of native species. We established 17 transects in the mixed treatment and 35 in the native treatment. On each transect, we sampled 5-15 contiguous 10 m x 10 m plots. Within each plot, we sampled all live individuals with a diameter at breast height \geq 10 cm.
- 3. We found no significant differences between treatments for any of the phylogenetic diversity indices tested. The means of NRI and NTI were positive, indicating phylogenetic clustering in both treatments. None of the phylogenetic diversity and phylogenetic structure metrics were significantly affected by increasing basal area according to our models.
- 4. Restoration plantings today have goals that go beyond restoring forest cover to an area, ensuring the maintenance of evolutionarily unique native species, and maintaining key ecosystem services and functions. Throughout succession, phylogenetic diversity increased in both treatments without significant differences.
- 5. We conclude that restoration plans can use eucalyptus as a starting point for restoration plans, especially when carbon sequestration along with biodiversity is the main goal of the restoration project.

Keywords: Atlantic Forest, Biodiversity Conservation, Diversity and Phylogenetic Structure, Ecological restoration, Eucalyptus understory, Forest Plantations, Phylogenetic characters of functional traits, Secondary succession.

Introduction

Ecological restoration is the process of contributing to the recovery of an ecosystem that has been degraded, damaged or destroyed (SER, 2004). In addition to contributing to biodiversity conservation, ecosystem restoration aims to promote social, economic, and environmental benefits, such as climate change mitigation (CBD, 2019). The United Nations (UN) has defined the decade 2021-2030 as the Decade of Restoration, with the aim of halting the degradation of ecosystems and restoring them in order to achieve global goals (UN Brazil, 2021; WRI Brazil, 2021), such as the Bonn Challenge (IUCN, 2021), and national goals, such as the Atlantic Forest Restoration Pact in Brazil, launched in 2009, which promotes the recovery of 15 million hectares of degraded areas by 2050 (PACTO, 2021).

The Atlantic Forest has been identified by Conservation International as a global hotspot for anthropogenic fragmentation and threats to biodiversity (Myers et al., 2000), with 26.8% of its forest cover remaining (MapBiomas, 2021). Degradation and deforestation in the Atlantic Forest have been driven by the expansion of agricultural land and monoculture tree plantations (Rodrigues et al., 2009; Rosa et al., 2021), with 57.1% of the cover in extensive agricultural and livestock use and 3.5% in forestry use (MapBiomas, 2021). *Eucalyptus* plantations for commercial purposes in Brazil correspond to 76.9% of planted forests (IBGE, 2022). After land use abandonment, the Atlantic Forest has a high potential for natural regeneration (Rozendaal et al., 2019; Poorter et al., 2021), either in former pasture areas (Benayas et al., 2007) or under *Eucalyptus* plantations (Silva Júnior et al., 1995; Sartori et al., 2002; Souza Filho et al., 2007; Onofre et al., 2010; Viani et al., 2010; Ronquin, 2021).

For natural regeneration to occur, seedling recruitment is required during natural succession through the soil seed bank, seed dispersal, or stem regrowth (Baider et al., 2001; Tabarelli & Peres, 2002; Viani et al., 2015). Community assembly directs natural succession through evolutionary and ecological processes based on niche theory (competition and environmental filters) or neutral theory (Webb et al., 2002; Cavender-Bares et al., 2009; Meiners et al.,

2015). Environmental filters act to select species within a community based on their ability to persist under certain conditions, limiting the composition of species with similar ecological-functional traits (Webb et al., 2002; Cavender-Bares et al., 2009; Kraft & Ackerly, 2010; Bennett et al., 2017). Natural regeneration is effective in abandoned *Eucalyptus* plantations, which can catalyze forest succession in the understory, even in areas without native forests (Viani et al., 2010; Ronquin, 2021). On the other hand, *Eucalyptus* can act as an environmental filter, influencing the phylogenetic structure of communities by selecting similar and closely related species (Kraft et al., 2008; Myers & Harms, 2009).

Two approaches have shown promise in detecting community responses to environmental change: phylogenetic and functional diversity. Phylogenetic diversity is a measure that incorporates the evolutionary relationships among species in a community (Magurran, 2004), whereas functional diversity incorporates variation among species and their traits that influence how communities function (Tilman, 2001). Thus, measures that incorporate phylogenetic relationships or functional traits may be superior to traditional diversity measures (Cianciaruso et al., 2009) and have proven useful in forest restoration studies (Rother et al., 2019). Phylogenetic diversity has been used in community ecology to infer the assembly, organization, and co-occurrence of community species (Webb et al., 2002). Restoration efforts aim to restore an ecosystem with appropriate diversity and function (Aerts & Honnay, 2011). This requires an understanding of the functional traits of species and can help assess restoration success according to goals and needs (Díaz et al., 2013).

We address these important gaps in our knowledge of the diversity and phylogenetic structure of *Eucalyptus* understory forests in the Atlantic Forest by investigating whether *Eucalyptus* may act as an environmental filter, selecting phylogenetically more closely related species than other species in the community. As an assumption, we can consider that in tropical forests, natural regeneration starts with communities composed of few pioneer species, with lower richness, diversity and complexity than climax communities found at the end of succession (Horn, 1974; Magnago et al., 2011; Greenberg et al., 2011; Chazdon, 2012; Crouzeilles et al., 2017; César et al., 2018; Poorter et al., 2021). Thus, we expect that in abandoned areas, *Eucalyptus* may act as a catalyst for the succession of native species in the understory, increasing phylogenetic diversity as succession progresses.

Materials and methods

Study area

This study was conducted in the state of Espírito Santo, in the southeast of Brazil. Within the region, we focused on the areas surrounding BR 262, from Viana (km 19) to the district of Vítor Hugo (km 72), and in the basin of the Jucu River (north arm) (Figure 1). The climate is tropical (Aw, Köppen-Geiger classification), with an annual rainfall of 1500 mm and an average annual temperature of 18 °C, ranging from 9.4 °C to 29.6 °C (Feitoza, 1986; Alvares et al., 2013). The vegetation is classified as dense ombrophyllous forest and submontane (50-500 m) or montane (500-1500 m), based on the altitude criteria of Garbin et al. (2017). Traditional agricultural use has altered the forests in the region, which have been replaced by forest regeneration or *Eucalyptus* plantations (Simonelli et al., 2021).



Figure 1. Study sites in the Atlantic Forest of Brazil.

Data collection

We conducted the fieldwork in two natural succession treatments: i) mixed treatment, native species under abandoned *Eucalyptus* plantations; ii) native treatment, with the presence of native species. We sampled 17 transects in the mixed treatment and 35 transects in the native treatment. In each transect, we sampled 5-15 contiguous plots of 10 m x 10 m (0.01 ha), for a total of 494 plots (4.94 ha). Within each plot, we sampled all individuals living and rooted within our plots with a diameter at breast height (DBH; 1.30 m above ground level) \geq 10 cm. Species not identified in the field were collected, vouchered and subsequently identified through consultations at the Herbarium of Vale (CVRD), Herbarium VIES of the Federal

University of Espírito Santo (UFES) and Professor Mello Leitão Biology Museum (MBML). We classified taxonomy and occurrence in Brazilian biomes based on the Flora of Brazil database (BFG, 2021); We checked spellings, taxonomic status and establishment in PlantMiner (Carvalho et al., 2010).

Measures of phylogenetic diversity and structure

To construct our phylogeny, we generated a list of all our species, genera, and families based on the Angiosperm Phylogeny Group IV (APG, 2016). We omitted *Araucaria* Juss. and *Pinus* L. (Gymnosperms) because of their very distinct and ancient phylogenetic lineages. The list elaborated with the selected species was added to the GBOTB.extended.tre phylogenetic tree using the V.PhyloMaker package (Jin & Qian, 2019) in R, version 4.2.2 (R Core Team, 2022).

To explain phylogeny, we use the following metrics (Faith, 1992; Webb et al, 2002; Swenson, 2014): (i) Phylogenetic Diversity (PD), found by summing phylogenetic branches for all species and expressed in millions of years; (ii) Mean Pairwise Distance (MPD), mean phylogenetic distance between all combinations of pairs of individuals; (iii) Mean Nearest Taxon Distance (MNTD), mean phylogenetic distance between an individual and the closest related (nonspecific) individual. In addition, we calculated the standardized effect size (ses) of PD, Net Relatedness Index (NRI), and Nearest Taxon Index (NTI) to eliminate the wealth effect based on a null model. Negative values indicate phylogenetic clustering and positive values indicate phylogenetic overdispersion. We calculated these six metrics using the Picante package (Kembel et al., 2010) in R, version 4.2.2 (R Core Team, 2022). For standard effect size calculations, we compared our tree to 999 random null models using the taxa.labels algorithm, which incorporates the labels from the community data matrix, and without considering the relative abundance of species in the communities (abundance.weighted = FALSE).

Functional trait matrix

We examined four traits (Table 1) related to morphological and physical adaptations of trees in their role as dispersers, food resources, forest structure and carbon storage: i) dispersal syndrome according to Van der Pijl (1982); ii) seed size according to Tabarelli & Peres (2002); iii) maximum height; iv) wood density. We classified the maximum height and wood density traits as follows: small/low (1 < (μ - σ)); medium ((μ - σ) ≤ 2 < (μ + σ)); large/high (3 ≥ (μ + σ)), where μ = mean and σ = sample standard deviation.

Functional trait	Relevance	Unit	Categories			
Disporsal syndroma	Colonization consoity	cotl	1. zoochoric			
Dispersar syndrome	Colonization capacity	Cal	2. non-zoochoric			
			1. small (< 0.6)			
Soudaiza	Quantity and type of		2. medium (0.6-1.6)			
Seed Size	food resource	CIII	3. large ($\geq 1.6-3.0$)			
			4. extremely large (> 3.0)			
	Compatitive potential		1. small (< 9.64)			
Maximum height	competitive potential	m	2. medium (9.64-29.78)			
	and growin period		3. large (≥ 29.78)			
	Dotontial for control		1. low (< 0.438)			
Wood density	allocation in biomass	g cm- ³	2. medium (0.438-0.708)			
	anocation in biomass		3. high (≥ 0.708)			

Table 1. Functional traits used to calculate the functional diversity value.

¹ cat = categorical.

Data for dispersal syndrome, seed size, and maximum height were obtained from the TRY database, the REFLORA program, and the literature, in addition to collecting field material. We obtained data for wood density from the Global Wood Density Database (Chave et al., 2009; Zanne et al., 2009) through the BIOMASS package (Réjou-Méchain et al., 2017) in R, version 4.2.2 (R Core Team, 2022), in the Tropical South America subsection. The list of data sources used in the study can be found in the Data sources section.

Phylogenetic signal of the functional traits

To quantify the phylogenetic signal in the functional trait data, we used the K statistic (Blomberg et al., 2003), which compares the observed signal to another under a Brownian motion model of trait evolution in a phylogeny. In this model, K = 0 indicates a lack of phylogenetic signal; K > 1 indicates that lineages are more similar than expected, causing clustering; K < 1 indicates that lineages are more divergent than expected, indicating overdispersal. The statistical significance of the phylogenetic signal was evaluated by comparing the observed patterns of trait-independent contrast variance with a null model of taxon label shuffling at the top of the phylogeny. We computed K-statistics and randomizations with the multiPhylosignal function using the Picante package (Kembel et al., 2010) in R, version 4.2.2 (R Core Team, 2022).

Data analysis

To assess how phylogenetic diversity differed between treatments, we compared the means of the phylogenetic metric indices (PD, MPD, MNTD, sesPD, NRI, NTI) in the mixed and native treatments using Student's t-test with a significance level less than or equal to 0.05 ($P \le 0.05$) through the stats package in R, version 4.2.2 (R Core Team, 2022). We tested the normality of the residuals using the Shapiro-Wilk test with the RVAideMemoire package in R, version 4.2.2 (R Core Team, 2022).

To assess how phylogenetic diversity affects succession, we used basal area of individual trees as a proxy for succession ($BA = \frac{\pi DBH^2}{40000}$; Soares et al., 2006) and phylogenetic indices as response variables. We then constructed generalized linear models with Gaussian error distributions, implemented in the glm function of the statistics package in R, version 4.2.2 (R Core Team, 2022). We also considered possible interactions between the predictor variables (treatments*basal area). The regression models were visualized using the visreg package in R,

version 4.2.2 (R Core Team, 2022).

Results

In total, we recorded 3240 individuals of 215 tree species from 140 genera and 51 families according to APG IV (2016). The mean and standard deviation of species richness for the mixed treatment was 16.05 ± 5.78 (range: 6-29 species), and 17.40 ± 7.42 (range: 4-37 species) for the native treatment. The most representative species in the both treatments were *Moquiniastrum polymorphum* (291), *Croton floribundus* (254), and *Piptadenia gonoacantha* (206). The most representative families in the both treatments were Fabaceae, Asteraceae, and Euphorbiaceae. The phylogenetic tree was constructed with 215 tips and 183 internal nodes (Figure S1). The mean and standard deviation of basal area of native species was 23.75 m²/ha ± 13.89 m²/ha (range: 2.87-54.74 m²/ha) in the mixed treatment, and 24.29 m²/ha ± 8.83 m²/ha (range: 6.58-48.09 m²/ha) in the native treatment. We verified the average time to abandonment of the *Eucalyptus* plantations based on the mean DBH, which ranged from 20.05 cm to 52.01 cm, with a mean of 37.22 cm ± 8.52 cm. The mean DBH value for *Eucalyptus* plantations in the state of Espírito Santo is 35.6 cm after 21 years of planting (Nutto et al., 2006). Therefore, we can estimate that the *Eucalyptus* species have at least 20 years of abandonment.

Does Eucalyptus act as an environmental filter?

We found that PD (Pearson: r = 0.969, P < 0.05) and MNTD (Pearson: r = -0.592, P < 0.05) were significantly correlated with species richness. We found no significant correlation between SR and MPD (Pearson: r = 0.244, P = 0.08), sesPD (Pearson: r = 0.088, P = 0.53), NRI (Pearson: r = -0.248, P = 0.07) and NTI (Pearson: r = 0.016, P = 0.9066). Thus, standardized values minimized the effects of species richness (Figure S2).

We found no significant differences between treatments for any of the phylogenetic diversity

metrics tested (Table S1). The mean PD was 0.11% higher in the mixed treatment than in the native treatment, harboring phylogenetic diversity with a species composition spanning 1536.02 million years (Fig. 2a). The mean MPD was 0.33% lower in the mixed treatment than in the native treatment, with more related species and a mean distance of 235.10 million years (Fig. 2b). The mean MNTD was 3.17% smaller in the mixed treatment than in the native treatment, with a species composition with a mean nearest neighbor distance of 135.98 million years, indicating that the terminal species in this treatment are more closely related (Fig. 2c).

We found no significant differences between treatments for any of the phylogenetic structure indices tested (Table S1). The means of sesPD were negative, indicating a lower PD than expected by chance (Fig. 2d). The means of NRI and NTI were positive, indicating phylogenetic clustering in both treatments (Figs. 2e-2f).





Figure 2. Patterns of a) Phylogenetic Diversity (PD), b) Mean Peer Distance (MPD), c) Mean Nearest Taxon Distance (MNTD), d) Standardized Effect Size (ses) of PD, e) Net Relatedness Index (NRI), and f) Nearest Taxon Index (NTI), in mixed and native treatments of natural regeneration in the Atlantic Forest.

Does phylogenetic diversity increase over succession?

None of the phylogenetic diversity (i.e., PD; MPD and MNTD) and phylogenetic structure (i.e., sesPD, NRI and NTI) metrics were significantly affected by increasing basal area according to our models. The interactions between the predictor variables were also not significant.

For phylogenetic diversity, our models showed that PD was positively affected by increasing basal area in the mixed (slope: 6.380) and native (slope: 20.974) treatments (Fig. 3a). MPD was positively affected by increasing basal area in the mixed (slope: 0.013) and native (slope: 0.299) treatments (Fig. 3b). The MNTD data did not show normality of residuals, so we removed outliers older than 200 million years (Figure S3). MNTD increased with increasing basal area in the mixed and native treatments (Fig. 3c).

For phylogenetic structure, our models showed that sesPD was positively affected by increasing basal area in the mixed (slope: 0.018) and native (slope: 0.033) treatments (Fig. 3d). PD was correlated with species richness (Figure S2). When the effect of richness was eliminated and the observed PD values were compared with those of communities generated by the null models (Table S2), communities with higher PD are expected to have positive sesPD values and communities with lower PD are expected to have negative sesPD values (Figs. 3a-3d).

In the mixed treatment, NRI was negatively affected and NTI was positively affected with increasing basal area (Figs. 3e-3f). However, the trend line remained positive for both NRI and NTI, indicating more phylogenetically clustered species than expected by chance.

In the native treatment, NRI and NTI were negatively affected with increasing basal area (Figs. 3e-3f). When the effect of richness was removed (Figs. 3b-3c), NRI and NTI tended to be negative throughout succession, indicating phylogenetic overdispersion with less closely related species than expected by chance.



Figure 3. Plots of models of basal area of native species (BA) in relation to diversity indices and phylogenetic structure: a) Phylogenetic Diversity (PD), b) Mean Peer Distance (MPD), c) Mean Nearest Taxon Distance (MNTD), d) Standardized Effect Size (ses) of PD, e) Net Relatedness Index (NRI), and f) Nearest Taxon Index (NTI), in mixed and native treatments of natural regeneration in the Atlantic Forest. The red line represents the fitted curve and the gray areas are the 95% confidence intervals.

Are functional traits conserved across lineages?

We found a phylogenetic signal for all traits in the mixed and native treatments, with K values less than 1, indicating that the traits are more phylogenetically clustered than expected by chance (Table 2). The P-value was less than 0.05 for most functional traits (except for maximum tree height), indicating that most of the traits analyzed were less variable than expected from the random phylogeny of the community (Table 2). Given that most traits had significant phylogenetic sign, close relatives generally have more similar trait values than would be expected by chance.

Functional Traita	Mixed to	reatment	Native treatment		
Functional Traits	K	Р	Κ	Р	
Dispersal syndrome	0.537	0.001	0.709	0.001	
Seed size	0.292	0.001	0.213	0.002	
Maximum height	0.189	0.057	0.205	0.002	
Wood density	0.561	0.001	0.399	0.001	

Table 2. Results of phylogenetic signal analysis in functional traits using

 Blomberg's K.

K = Blomberg's K index; P = significance level (≤ 0.05).

Discussion

The potential of abandoned *Eucalyptus* plantations as a catalyst for natural regeneration has been evaluated in several studies, but it is not known how these communities are structured and what the phylogenetic diversity of the *Eucalyptus* understory is (Viani et al., 2010; Ronquin, 2021). Knowledge of the evolutionary history of species and their functions in ecosystems helps to guide restoration strategies (Aerts & Honnay, 2011). Currently, restoration plantings have goals beyond restoring forest cover in an area, such as ensuring the maintenance of evolutionarily unique native species (Rodrigues et al., 2009; Charles, 2018) and maintaining key ecosystem services and functions, such as carbon stocks (Pan et al., 2011; Magnago et al., 2015; Koch & Kaplan, 2022). Here, we show that for most metrics tested, phylogenetic diversity does not change in areas where natural regeneration has occurred in abandoned *Eucalyptus* plantations compared to areas that regenerated under other conditions (pasture or abandoned coffee plantations). During succession, phylogenetic diversity increased in both treatments, with closely related species sharing similar traits. Our results therefore suggest that restoration plans can use *Eucalyptus* as a starting point for restoration plans, especially when carbon sequestration is the main goal of the restoration project along with biodiversity (Brancalion et al., 2018; Brancalion et al., 2020).

Does Eucalyptus act as an environmental filter?

Our results showed that there was no significant difference between the means of the phylogenetic diversity indices in the treatments, with similar PD, MPD and MNTD values in the mixed and native treatments. Some studies have shown that the negative effects of Eucalyptus on the regeneration of native species, suggesting that for species with certain life history traits, the Eucalyptus understory may be ineffective for regeneration, acting as an environmental filter (Durigan et al., 2004; Ostertag et al., 2008; Pairo et al., 2021). In other biomes, such as the Cerrado, natural regeneration under *Eucalyptus* plantations has had poorer results due to cover and biomass interference (see Durigan et al., 2004). In ecosystems in other countries, the Eucalyptus understorey was dominated by exotic species from Hawaii due to light conditions (see Ostertag et al., 2008). There are several filters acting on the development of understory regeneration, both in *Eucalyptus* plantations and in native forests. In planted monocultures, there are additional filters to those already acting in native forests, such as: historical and environmental factors, canopy density, light availability in the understory, age of planting, planted forest species, distance to remnants of native vegetation, management of planted forests, and history of use of the area, which can directly or indirectly influence the richness, density, and structure of natural regeneration under Eucalyptus plantations (Geldenhuys, 1997; Parrotta, 1999; Viani et al., 2010).

Our results showed that there was no significant difference between the means of the

phylogenetic structure indices in the treatments, with similar sesPD, NRI and NTI values in the mixed and native treatments. The observed PD values are similar to those obtained for the simulated communities with the redistribution of species names in the phylogeny, with only 13% of the communities showing a P < 0.05 value (Table S2). On average, NTI and NRI indicate the occurrence of phylogenetic clustering in both treatments, with ecologically similar and more phylogenetically related species. This means that the species represent communities with an analogous amount of evolutionary history. A possible explanation, is due to the proximity of regenerating areas with matricial forests (250 meters) in the Central Mountainous Zone of Espírito Santo, with about 80.26% of its area presenting potential to receive propagules (Simonelli et al., 2021). The distance of the area to be restored from forest fragments providing propagules is strategic for the success of natural regeneration (Chazdon, 2012; Simonelli et al., 2021). *Eucalyptus* plantations can increase landscape connectivity, i.e., the dispersal and movement of native species. In many tropical regions, animals are the main seed dispersers and are therefore important for the dynamics of plant regeneration (Parrotta et al., 1997; Lindenmayer & Hobbs, 2004; Coelho et al., 2022).

Does phylogenetic diversity increase with succession?

We found no significant differences in diversity indices and phylogenetic structure as succession progressed in the treatments. In both treatments, we observed that phylogenetic diversity remained constant throughout the succession. The use of *Eucalyptus* as a facilitator species for the restoration of native forest vegetation has shown positive results, as they can act as pioneer species and trigger the initial successional process (Viani et al., 2010; Ronquin, 2021). This technique of intercropping *Eucalyptus* species with native species is an effective tool for forest restoration (Brancalion et al., 2018; Brancalion et al., 2020), especially in degraded areas where native species would not perform well due to major barriers to growth, such as drought, fire, and functional degradation of soil fertility and structure (Campello,

1998; Magnago et al., 2011; Ronquin, 2021). Our results confirm that competition with native trees does not appear to be strong enough to affect their survival or to suppress native trees during succession, which could have reduced species diversity and their evolutionary history (see Brancalion et al., 2020). These results may provide a new strategy for initiating forest restoration plans, as Brazilian native tree species grow more slowly than species of the genus *Eucalyptus* (Ronquin, 2021), although competition for resources with *Eucalyptus* can slow the growth of native species (Durigan et al., 2004; Brancalion et al., 2020; Pairo et al., 2021). Thus, in addition to the arrival of invertebrate and vertebrate species (da Rocha et al., 2012; Chazdon, 2012; Martin et al., 2012; Timo et al., 2015; Jacoboski et al., 2016) that provide important seed dispersal services in the early stages of restoration, abandoned *Eucalyptus* areas provide important habitat for native species (Viani et al., 2010; Ronquin, 2021; Coelho et al., 2022).

In the native treatment, we observed increased phylogenetic diversity during succession. We also observed that as succession progresses, species increase their relatedness by introducing species that are phylogenetically more distant throughout the succession. Thus, in early successional stages, communities are clustered by the effect of the environmental filter, whereas in advanced successional stages they exhibit phylogenetic dispersal due to limiting similarity (Letcher et al., 2012), resulting in the competitive exclusion of ecologically similar and phylogenetically close species (Webb et al., 2002; Cavender-Bares et al., 2009). We did not find this trend in *Eucalyptus* plantations due to the age of the regenerating community, which recruits pioneer species in younger plantations and subsequently starts to favor the establishment of species later in the ecological succession (Carneiro & Rodrigues, 2007; Pairo et al., 2021). The most abundant pioneer species were *Croton floribundus*, *Myrcia splendens*, *Piptadenia gonoacantha*, and *Senna multijuga* (see Carvalho, 2014; Lorenzi, 2021).

Are functional traits conserved across lineages?

Because most of our functional traits had significant phylogenetic signal, close relatives generally share more similar trait values than would be expected by chance. We quantified the phylogenetic signal of four functional traits for the species in the mixed and native treatments, which describes how selective pressures and life history act on the phenotypic evolution of species (Blomberg et al., 2003). All K values (Table 2) for the phylogenetic signal were less than one, suggesting that the traits are more labile than expected under a Brownian model of trait evolution. Thus, environmental filters would select functionally similar species based on their ability to adapt to the same environmental conditions, bringing together species with similar ecological niches (Cavender-Bares et al., 2009). The results for the phylogenetic signal of the traits analyzed indicate that wood density and dispersal syndrome are phylogenetically less convergent than expected by the Brownian model, but phylogenetically more conserved than a random association between traits and phylogeny. In addition, related species tend to be more similar than random in wood density and dispersal syndrome in the mixed treatment, and dispersal syndrome in the native treatment.

Dispersal syndrome is a trait associated with the establishment and distribution of species in new areas, and is related to dispersal distance and community structure (Cornelissen et al., 2003). Of the species found in our study area, 74.88% have animal dispersal (Data sources). Some studies cite the predominance of zoochoric species among regenerating individuals (Viani et al., 2010; Callegaro et al., 2013; Simonelli et al., 2021; Ronquin, 2021; Coelho et al., 2022), dispersal with greater influence in tropical forests due to the complexity of the environment and the co-evolutionary relationships between species (Silva et al., 1996). On the other hand, seed arrivals of non-zoochoric species tend to decrease as eucalypts grow because they become an obstacle to wind flow (Keenan et al., 1997).

Wood density follows successional trends: early in succession, pioneer species with acquisitive strategies and low wood density; throughout succession, slow-growing species

with conservative strategies and high wood density (Chazdon, 2012; Poorter et al., 2019). Younger *Eucalyptus* plantations are expected to have greater recruitment of pioneer species, which gradually decreases with increasing shading, favoring the establishment of species later in the ecological succession. (Carneiro & Rodrigues, 2007). This may explain the high representation of pioneer species in the mixed treatment, as they have similar characteristics and are functionally similar to *Eucalyptus*.

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Data sources

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30 Cabralea canjerana Meliaceae 0.4775 genus 40 Try zoo Try 2 REFLORA	Cabralea can	njerana	Meliaceae	0.4775	genus	40	Try	ZOO	Try	2	REFLORA
31 Cariniana estrellensis Lecythidaceae 0.5476 genus 11.82 Safar et al., 2022 nzoo Try 0.72 Safar et al., 2022	Cariniana est	trellensis	Lecythidaceae	0.5476	genus	11.82	Safar et al., 2022	nzoo	Try	0.72	Safar et al., 2022
32Cariniana legalisLecythidaceae0.5476genus35Safar et al., 2022nzooSafar et al., 20220.82Safar et al., 2022	2 Cariniana leg	galis	Lecythidaceae	0.5476	genus	35	Safar et al., 2022	nzoo	Safar et al., 2022	0.82	Safar et al., 2022
33 Caryota urens Arecaceae 0.5604 family 10 REFLORA zoo Try 0.15 Pimenta, 2015	3 Caryota uren	18	Arecaceae	0.5604	family	10	REFLORA	ZOO	Try	0.15	Pimenta, 2015
34 Casearia arborea Salicaceae 0.6777 genus 32.48 Try zoo Try 0.2 Marquete & Vaz, 200	Casearia arbo	orea	Salicaceae	0.6777	genus	32.48	Try	ZOO	Try	0.2	Marquete & Vaz, 2007
35 Casearia commersoniana Salicaceae 0.6777 genus 12.7 Try zoo Try 0.6 Safar et al., 2022	5 Casearia con	nmersoniana	Salicaceae	0.6777	genus	12.7	Try	Z00	Try	0.6	Safar et al., 2022
36 Casearia decandra Salicaceae 0.6777 genus 20 Try zoo Safar et al., 2022 0.7 Marquete & Vaz, 200	5 Casearia dec	candra	Salicaceae	0.6777	genus	20	Try	Z00	Safar et al., 2022	0.7	Marquete & Vaz, 2007
37 Casearia espiritosantensis Salicaceae 0.6777 genus 6 BDC zoo Try 0.2 REFLORA	/ Casearia espi	iritosantensis	Salicaceae	0.6777	genus	6	BDC	ZOO	Try	0.2	REFLORA
38 Casearia javitensis Salicaceae 0.6777 genus 18 Try zoo Try 0.4 Marquete & Zappi, 20	3 Casearia javi	itensis	Salicaceae	0.6777	genus	18	Try	ZOO	Try	0.4	Marquete & Zappi, 2018
39 Casearia sylvestris Salicaceae 0.6777 genus 21.85 Try zoo Try 0.25 Marquete & Vaz, 200	Casearia sylv	vestris	Salicaceae	0.6777	genus	21.85	Try	Z00	Try	0.25	Marquete & Vaz, 2007
40 Casearia ulmifolia Salicaceae 0.6777 genus 20 Try zoo Try 0.15 Safar et al., 2022) Casearia ulm	nifolia	Salicaceae	0.6777	genus	20	Try	ZOO	Try	0.15	Safar et al., 2022
41 Cathedra rubricaulis Aptandraceae 0.5604 SouthAmerica 8 Lucena et al., 2020 zoo Lucena et al., 2020 0.2 Lucena et al., 2020	Cathedra rub	oricaulis	Aptandraceae	0.5604	SouthAmerica	8	Lucena et al., 2020	ZOO	Lucena et al., 2020	0.2	Lucena et al., 2020
42 Cecropia glaziovii Urticaceae 0.3077 genus 23.75 Try zoo Try 0.15 FFESP	2 Cecropia gla	ziovii	Urticaceae	0.3077	genus	23.75	Try	ZOO	Try	0.15	FFESP
43Cecropia hololeucaUrticaceae0.3077genus20.71Safar et al 2022zooTry0.18FFESP	3 Cecropia hol	loleuca	Urticaceae	0.3077	genus	20.71	Safar et al., 2022	Z00	Try	0.18	FFESP
44 Cecropia pachystachya Urticaceae 0.3077 genus 15.06 Safar et al. 2022 zoo Try 0.61 Safar et al. 2022	Cecropia pac	chystachya	Urticaceae	0.3077	genus	15.06	Safar et al., 2022	ZOO	Trv	0.61	Safar et al., 2022

45	Cedrela fissilis	Meliaceae	0.3988	genus	30	Try	Z00	Safar et al., 2022	4	REFLORA
46	Chrysophyllum	Sapotaceae	0.7677	genus	25	Safar et al., 2022	ZOO	Safar et al., 2022	2.2	Safar et al., 2022
47	Citronella	Cardiopteridaceae	0.5604	family	11	BDC	ZOO	Safar et al., 2022	1.15	Safar et al., 2022
48	Clarisia ilicifolia	Moraceae	0.5302	genus	18	Safar et al., 2022	ZOO	Try	1.09	Safar et al., 2022
49	Clitoria fairchildiana	Fabaceae	0.5604	family	12	Lorenzi, 2021	nzoo	Try	0.16	Embrapa
50	Clusia spiritu-sanctensis	Clusiaceae	0.6000	genus	8	FFESP	ZOO	FFESP	0.15	FFESP
51	Copaifera langsdorffii	Fabaceae	0.6081	genus	22.33	Safar et al., 2022	ZOO	Try	1.18	Safar et al., 2022
52	Cordia magnoliifolia	Boraginaceae	0.4874	genus	7.5	Safar et al., 2022	ZOO	Safar et al., 2022	0.66	Safar et al., 2022
53	Cordia trichotoma	Boraginaceae	0.4874	genus	11.33	Safar et al., 2022	ZOO	Safar et al., 2022	1.1	Safar et al., 2022
54	Couepia	Chrysobalanaceae	0.8046	genus	25.59	Safar et al., 2022	ZOO	Safar et al., 2022	2.2	Safar et al., 2022
55	Coussapoa microcarpa	Urticaceae	0.4623	genus	24.68	Try	ZOO	Try	1.2	Safar et al., 2022
56	Coussarea contracta	Rubiaceae	0.6103	genus	19.95	Try	ZOO	Try	2.24	Safar et al., 2022
57	Croton floribundus	Euphorbiaceae	0.4071	genus	10.86	Safar et al., 2022	nzoo	Safar et al., 2022	0.33	Safar et al., 2022
58	Cupania	Sapindaceae	0.6193	genus	16	BDC	ZOO	Safar et al., 2022	2	REFLORA
59	Cupania oblongifolia	Sapindaceae	0.6193	genus	6.5	Safar et al., 2022	ZOO	Try	1.5	FFESP
60	Cupania racemosa	Sapindaceae	0.6193	genus	13.92	Safar et al., 2022	ZOO	Try	2	FFESP
61	Cupania rugosa	Sapindaceae	0.6193	genus	18.36	Safar et al., 2022	Z00	Safar et al., 2022	2	REFLORA
62	Cupania scrobiculata	Sapindaceae	0.6193	genus	22	Try	Z00	Try	1.1	Safar et al., 2022
63	Cupania vernalis	Sapindaceae	0.6193	genus	23.75	Try	Z00	Try	1.7	FFESP
64	Cupania zanthoxyloides	Sapindaceae	0.6193	genus	15	REFLORA	Z00	Try	2.7	FFESP
65	Dalbergia nigra	Fabaceae	0.8084	genus	20	Try	nzoo	Safar et al., 2022	0.48	Safar et al., 2022
66	Dialium guianense	Fabaceae	0.8673	genus	40	Try	Z00	Try	0.56	Safar et al., 2022
67	Dictyoloma vandellianum	Rutaceae	0.5604	family	13.77	Safar et al., 2022	nzoo	Embrapa	0.21	Safar et al., 2022
68	Didymopanax calvus	Araliaceae	0.5750	genus	30	REFLORA	Z00	Barbosa et al., 2016	0.6	FFESP
69	Endlicheria paniculata	Lauraceae	0.5011	genus	21.85	Try	ZOO	Try	2.5	FFESP
70	Eriotheca candolleana	Malvaceae	0.4407	genus	18.42	Safar et al., 2022	nzoo	Try	0.73	Safar et al., 2022
71	Eriotheca macrophylla	Malvaceae	0.4407	genus	30.34	Safar et al., 2022	nzoo	Safar et al., 2022	0.57	Safar et al., 2022
72	Erythroxylum pulchrum	Erythroxylaceae	0.7100	genus	5.5	Safar et al., 2022	ZOO	Safar et al., 2022	0.65	Safar et al., 2022
73	Eschweilera ovata	Lecythidaceae	0.8253	genus	27.97	Safar et al., 2022	ZOO	Safar et al., 2022	1.77	Safar et al., 2022
74	Eucaliptus	Myrtaceae	0.5604	family	40	REFLORA	nzoo	REFLORA	0.25	REFLORA
75	Eugenia	Myrtaceae	0.7219	genus	25	Safar et al., 2022	ZOO	Safar et al., 2022	1.81	Safar et al., 2022
76	Eugenia zuccarinii	Myrtaceae	0.7219	genus	25	Safar et al., 2022	ZOO	Safar et al., 2022	2	REFLORA
77	Euphorbiaceae	Euphorbiaceae	0.5604	family	6.79	Safar et al., 2022	ZOO	Safar et al., 2022	3.27	Safar et al., 2022
78	Euterpe edulis	Arecaceae	0.4065	genus	19	Try	ZOO	Try	1.1	Safar et al., 2022
79	Fabaceae	Fabaceae	0.5604	family	7.54	Safar et al., 2022	nzoo	Safar et al., 2022	1.18	Safar et al., 2022
80	Ficus	Moraceae	0.3956	genus	40	Try	ZOO	Try	0.1	Safar et al., 2022
81	Ficus clusiifolia	Moraceae	0.3956	genus	40	Try	ZOO	Try	0.05	REFLORA
82	Ficus insipida	Moraceae	0.3956	genus	40	Try	ZOO	Try	0.05	REFLORA
83	Gallesia integrifolia	Phytolaccaceae	0.4800	genus	30	Try	nzoo	Try	3	REFLORA
84	Garcinia gardneriana	Clusiaceae	0.6567	genus	8.5	Safar et al., 2022	ZOO	Safar et al., 2022	1.48	Safar et al., 2022
85	Geissospermum laeve	Apocynaceae	0.7823	genus	31	Try	ZOO	Try	1.1	Safar et al., 2022
86	Guapira	Nyctaginaceae	0.4923	genus	25	Safar et al., 2022	ZOO	Try	0.63	Safar et al., 2022
87	Guapira noxia	Nyctaginaceae	0.4923	genus	9	Safar et al., 2022	ZOO	Try	0.2	Safar et al., 2022
88	Guapira opposita	Nyctaginaceae	0.4923	genus	25	Safar et al., 2022	Z00	Try	0.63	Safar et al., 2022
89	Guarea guidonia	Meliaceae	0.6319	genus	40	Try	ZOO	Try	1	REFLORA
90	Guatteria	Annonaceae	0.5554	genus	12.23	Safar et al., 2022	ZOO	Safar et al., 2022	0.4	Safar et al., 2022
91	Guatteria sellowiana	Annonaceae	0.5554	genus	36.08	Safar et al., 2022	Z00	Safar et al., 2022	0.65	Safar et al., 2022
92	Guettarda viburnoides	Rubiaceae	0.7067	genus	8.49	Safar et al., 2022	ZOO	Safar et al., 2022	1.33	Safar et al., 2022

93	Himatanthus bracteatus	Apocynaceae	0.5021	genus	13.83	Safar et al., 2022	nzoo	Safar et al., 2022	0.98	Safar et al., 2022
94	Hirtella insignis	Chrysobalanaceae	0.7955	genus	7	Safar et al., 2022	ZOO	Safar et al., 2022	0.8	Safar et al., 2022
95	Hyeronima alchorneoides	Phyllanthaceae	0.5604	family	40	Try	Z00	Try	0.5	Lorenzi, 2021
96	Inga capitata	Fabaceae	0.5813	genus	30	Try	Z00	Safar et al., 2022	0.73	Safar et al., 2022
97	Inga laurina	Fabaceae	0.5813	genus	30	Try	Z00	Try	1	REFLORA
98	Inga marginata	Fabaceae	0.5813	genus	30	Try	Z00	Try	1	REFLORA
99	Inga subnuda	Fabaceae	0.5813	genus	14.56	Safar et al., 2022	Z00	Try	1	Safar et al., 2022
100	Inga vera	Fabaceae	0.5813	genus	50	Try	Z00	Try	1.5	REFLORA
101	Jacaranda puberula	Bignoniaceae	0.3954	genus	23.49	Try	nzoo	Safar et al., 2022	0.677	Safar et al., 2022
102	Jacaratia heptaphylla	Caricaceae	0.2650	genus	17.68	Safar et al., 2022	Z00	Safar et al., 2022	0.3	Safar et al., 2022
103	Jacaratia spinosa	Caricaceae	0.2650	genus	40	Try	Z00	Try	0.7	REFLORA
104	Kielmeyera	Calophyllaceae	0.5604	family	8	Ramos, 2011	Z00	Try	1	Ramos, 2011
105	Ladenbergia hexandra	Rubiaceae	0.4900	genus	11	FFESP	nzoo	FFESP	0.11	FFESP
106	Lamanonia ternata	Cunoniaceae	0.5604	family	19	Try	nzoo	Try	0.05	Oliveira et al., 2019
107	Lauraceae	Lauraceae	0.5604	family	22.04	Safar et al., 2022	ZOO	Safar et al., 2022	2.09	Safar et al., 2022
108	Licania kunthiana	Chrysobalanaceae	0.8287	genus	45	Try	ZOO	Try	1.98	Safar et al., 2022
109	Licaria guianensis	Lauraceae	0.7726	genus	19	Try	ZOO	Safar et al., 2022	0.2	Safar et al., 2022
110	Lonchocarpus cultratus	Fabaceae	0.7073	genus	19.9	Safar et al., 2022	nzoo	Safar et al., 2022	0.57	Safar et al., 2022
111	Machaerium aculeatum	Fabaceae	0.4947	genus	12	Lorenzi, 2021	nzoo	Try	1.5	Lorenzi, 2021
112	Machaerium hirtum	Fabaceae	0.4947	genus	12	IPÊ	nzoo	Try	1.4	Martins et al., 2016
113	Machaerium nyctitans	Fabaceae	0.4947	genus	18	Lorenzi, 2021	nzoo	Try	1.4	Filho et al., 2006
114	Mangifera indica	Anacardiaceae	0.5604	family	30	Try	ZOO	Try	8.42	Coral & Garcia, 2021
115	Matayba guianensis	Sapindaceae	0.7713	genus	24	Try	ZOO	Try	0.82	Safar et al., 2022
116	Maytenus	Celastraceae	0.7446	genus	6	Barbosa et al., 2016	ZOO	Barbosa et al., 2016	4.5	REFLORA
117	Miconia	Melastomataceae	0.6229	genus	14.05	Safar et al., 2022	Z00	Safar et al., 2022	0.6	Safar et al., 2022
118	Miconia calvescens	Melastomataceae	0.6229	genus	8	Try	ZOO	Try	0.75	Chagas, 2012
119	Miconia cinnamomifolia	Melastomataceae	0.6229	genus	24.7	Try	ZOO	Safar et al., 2022	0.6	Safar et al., 2022
120	Miconia holosericea	Melastomataceae	0.6229	genus	7.75	Try	ZOO	Try	0.2	Chagas, 2012
121	Miconia prasina	Melastomataceae	0.6229	genus	15.25	Try	ZOO	Try	0.63	Safar et al., 2022
122	Micropholis	Sapotaceae	0.6568	genus	33.41	Safar et al., 2022	ZOO	Safar et al., 2022	0.8	Safar et al., 2022
123	Monteverdia obtusifolia	Celastraceae	0.7446	genus	8.68	Safar et al., 2022	ZOO	Safar et al., 2022	0.5	Safar et al., 2022
124	Moquilea tomentosa	Chrysobalanaceae	0.5604	family	20	REFLORA	ZOO	Coradin et al., 2018	6	Coradin et al., 2018
125	Moquiniastrum polymorphum	Asteraceae	0.5604	SouthAmerica	10	REFLORA	nzoo	Faria, 2016	0.3	Faria, 2016
126	Myrcia neoglabra	Myrtaceae	0.8068	genus	13	Safar et al., 2022	ZOO	Safar et al., 2022	1	Safar et al., 2022
127	Myrcia splendens	Myrtaceae	0.8068	genus	30	Try	ZOO	Try	0.46	Safar et al., 2022
128	Myrcia vittoriana	Myrtaceae	0.8068	genus	9.62	Safar et al., 2022	ZOO	Try	0.35	Safar et al., 2022
129	Myrciaria tenella	Myrtaceae	0.6575	genus	6	REFLORA	ZOO	Try	0.4	REFLORA
130	Myrsine coriacea	Primulaceae	0.5604	family	21.85	Try	Z00	Try	0.24	Safar et al., 2022
131	Myrsine guianensis	Primulaceae	0.5604	family	11.23	Safar et al., 2022	ZOO	Try	0.26	Safar et al., 2022
132	Myrtaceae	Myrtaceae	0.5604	family	16.5	Safar et al., 2022	ZOO	Safar et al., 2022	0.48	Safar et al., 2022
133	Nectandra membranacea	Lauraceae	0.5207	genus	35	Try	ZOO	Try	0.1	Goldenberg & Moraes, 2009
134	Nectandra oppositifolia	Lauraceae	0.5207	genus	28.5	Try	ZOO	Try	0.15	Goldenberg & Moraes, 2009
135	Neoraputia alba	Rutaceae	0.5604	family	16	Safar et al., 2022	nzoo	Safar et al., 2022	0.71	Safar et al., 2022
136	Ocotea	Lauraceae	0.5195	genus	16.09	Safar et al., 2022	Z00	Safar et al., 2022	1.12	Safar et al., 2022
137	Ocotea aciphylla	Lauraceae	0.5195	genus	19.95	Try	Z00	Safar et al., 2022	2	Brotto et al., 2013
138	Ocotea argentea	Lauraceae	0.5195	genus	18.18	Safar et al., 2022	Z00	Safar et al., 2022	0.9	Safar et al., 2022
139	Ocotea confertiflora	Lauraceae	0.5195	genus	14.79	Safar et al., 2022	Z00	Safar et al., 2022	0.91	Safar et al., 2022
140	Ocotea indecora	Lauraceae	0.5195	genus	19.06	Try	Z00	Safar et al., 2022	0.98	Safar et al., 2022

141	Ocotea longifolia	Lauraceae	0.5195	genus	20	Try	Z00	Safar et al., 2022	1.5	Safar et al., 2022
142	Ocotea notata	Lauraceae	0.5195	genus	5	REFLORA	Z00	Safar et al., 2022	0.6	Brotto et al., 2013
143	Parapiptadenia pterosperma	Fabaceae	0.7400	genus	20	Try	nzoo	Safar et al., 2022	1.4	Safar et al., 2022
144	Pera glabrata	Peraceae	0.6655	genus	24.7	Try	Z00	Safar et al., 2022	0.2	Safar et al., 2022
145	Pera parvifolia	Peraceae	0.6655	genus	10	IPÊ	Z00	Safar et al., 2022	0.2	Safar et al., 2022
146	Persea	Lauraceae	0.4508	genus	20	Try	Z00	Barbosa et al., 2016	5	Lorenzi, 2021
147	Persea americana	Lauraceae	0.4508	genus	20	Try	Z00	Barbosa et al., 2016	5	Lorenzi, 2021
148	Piper cernuum	PIPÊraceae	0.3300	genus	6	BDC	Z00	Try	0.08	Lobato et al., 2005
149	Piptadenia gonoacantha	Fabaceae	0.7467	genus	20	Lorenzi, 2021	nzoo	Try	1	REFLORA
150	Piptadenia paniculata	Fabaceae	0.7467	genus	34.2	Try	nzoo	Try	1.15	Safar et al., 2022
151	Plathymenia reticulata	Fabaceae	0.4850	genus	40	REFLORA	nzoo	Try	1.2	REFLORA
152	Platypodium elegans	Fabaceae	0.7500	genus	41.25	Try	nzoo	Try	1.5	REFLORA
153	Pleroma estrellense	Melastomataceae	0.5604	family	10	REFLORA	nzoo	REFLORA	1	REFLORA
154	Pleroma fissinervia	Melastomataceae	0.5604	family	8	REFLORA	nzoo	REFLORA	1	REFLORA
155	Pourouma guianensis	Urticaceae	0.3905	genus	28.75	Try	Z00	Barbosa et al., 2016	0.89	Safar et al., 2022
156	Pouteria gardneri	Sapotaceae	0.7583	genus	12	REFLORA	Z00	Try	1.2	REFLORA
157	Protium heptaphyllum	Burseraceae	0.5543	genus	20	Try	Z00	Try	1.5	REFLORA
158	Pseudobombax grandiflorum	Malvaceae	0.2925	genus	25	Lorenzi, 2021	nzoo	Try	3	REFLORA
159	Pseudopiptadenia contorta	Fabaceae	0.6449	genus	19.87	Safar et al., 2022	nzoo	Try	0.79	Safar et al., 2022
160	Psidium guajava	Myrtaceae	0.6845	genus	25	Try	Z00	Try	0.5	REFLORA
161	Psidium myrtoides	Myrtaceae	0.6845	genus	20	REFLORA	Z00	Try	0.5	REFLORA
162	Psychotria carthagenensis	Rubiaceae	0.5200	genus	13.26	Safar et al., 2022	Z00	Try	0.43	Safar et al., 2022
163	Psychotria pedunculosa	Rubiaceae	0.5200	genus	5	REFLORA	Z00	Barbosa et al., 2016	0.4	FFESP
164	Psychotria vellosiana	Rubiaceae	0.5500	genus	6	IPÊ	Z00	Barbosa et al., 2016	0.3	FFESP
165	Pterocarpus rohrii	Fabaceae	0.4997	genus	50	Try	nzoo	Try	0.45	Safar et al., 2022
166	Pterygota brasiliensis	Malvaceae	0.5900	genus	30	Safar et al., 2022	nzoo	Safar et al., 2022	1.3	Safar et al., 2022
167	Rauvolfia grandiflora	Apocynaceae	0.5048	genus	25	Lorenzi, 2021	Z00	Lorenzi, 2021	3	Lorenzi, 2021
168	Roupala montana	Proteaceae	0.7967	genus	35	Try	nzoo	Try	1.1	Safar et al., 2022
169	Rubiaceae	Rubiaceae	0.5604	family	6	Safar et al., 2022	nzoo	Safar et al., 2022	0.1	Safar et al., 2022
170	Sapium glandulosum	Euphorbiaceae	0.4309	genus	33.81	Try	Z00	Try	0.6	Safar et al., 2022
171	Schoepfia brasiliensis	Schoepfiaceae	0.5604	SouthAmerica	19.73	Safar et al., 2022	Z00	Try	0.3	Safar et al., 2022
172	Senefeldera verticillata	Euphorbiaceae	0.7800	genus	16.5	Safar et al., 2022	nzoo	Safar et al., 2022	1	Safar et al., 2022
173	Senegalia polyphylla	Fabaceae	0.5604	family	17	Safar et al., 2022	nzoo	Try	0.6	Safar et al., 2022
174	Senna macranthera	Fabaceae	0.5555	genus	11.5	Try	nzoo	Barbosa et al., 2016	0.3	Pozitano & Rocha, 2011
175	Senna multijuga	Fabaceae	0.5555	genus	15	Try	nzoo	Barbosa et al., 2016	0.7	Dantas & Silva, 2013
176	Serjania erecta	Sapindaceae	0.5604	family	2	REFLORA	nzoo	Try	0.8	Silva et al., 2013
177	Simarouba amara	Simaroubaceae	0.3942	genus	32.5	Try	Z00	Try	0.8	Safar et al., 2022
178	Siparuna guianensis	Siparunaceae	0.6618	genus	10	REFLORA	Z00	Safar et al., 2022	0.4	Valentini et al., 2008
179	Sloanea sinemariensis	Elaeocarpaceae	0.7860	genus	30	Try	Z00	Safar et al., 2022	0.48	Safar et al., 2022
180	Solanum	Solanaceae	0.2800	genus	9	Safar et al., 2022	Z00	Try	0.5	REFLORA
181	Solanum castaneum	Solanaceae	0.2800	genus	3	Miranda, 2015	Z00	Barbosa et al., 2016	0.5	REFLORA
182	Solanum leucodendron	Solanaceae	0.2800	genus	20	Lafetá, 2002	ZOO	Barbosa et al., 2016	0.5	REFLORA
183	Solanum melissarum	Solanaceae	0.2800	genus	4	REFLORA	Z00	Barbosa et al., 2016	0.5	REFLORA
184	Solanum pseudoquina	Solanaceae	0.2800	genus	13.6	Try	Z00	Try	0.33	Safar et al., 2022
185	Sorocea guilleminiana	Moraceae	0.5775	genus	20	Try	Z00	Try	0.88	Safar et al., 2022
186	2		0.5 (0.4	£	21.22	Sofer at al 2022	2200	Terry	0.12	Sofer at al 2022
-	Sparattosperma leucanthum	Bignoniaceae	0.5604	Tamity	21.52	Salar et al., 2022	lizoo	119	0.15	Salar et al., 2022
187	Sparattosperma leucanthum Spondias macrocarpa	Anacardiaceae	0.3945	genus	<u>17.86</u>	Safar et al., 2022 Safar et al., 2022	Z00	Barbosa et al., 2016	1.77	Safar et al., 2022 Safar et al., 2022

189 5	Swartzia linharensis	Fabaceae	0.8407	family	25	Safar et al., 2022	ZOO	Safar et al., 2022	1.7	Safar et al., 2022
190 \$	Swartzia myrtifolia	Fabaceae	0.8407	family	15.66	Safar et al., 2022	Z00	Safar et al., 2022	0.86	Safar et al., 2022
191 \$	Swartzia simplex	Fabaceae	0.8407	family	35	Try	Z00	Safar et al., 2022	0.92	Safar et al., 2022
192 \$	Syagrus pseudococos	Arecaceae	0.5604	family	6.75	Try	Z00	Try	1.91	Safar et al., 2022
193 \$	Syzygium cumini	Myrtaceae	0.7000	genus	15	Try	Z00	Try	1.5	REFLORA
194 \$	Syzygium jambos	Myrtaceae	0.7000	genus	15	Try	Z00	Try	2.5	REFLORA
195	Tachigali pilgeriana	Fabaceae	0.5834	genus	17.17	Safar et al., 2022	nzoo	Safar et al., 2022	1.55	Safar et al., 2022
196	Tachigali vulgaris	Fabaceae	0.5834	genus	13	Safar et al., 2022	nzoo	Try	1.5	Abreu et al, 2017
197 7	Tapirira guianensis	Anacardiaceae	0.3750	genus	35	Try	Z00	Try	0.7	Safar et al., 2022
198 7	Thyrsodium spruceanum	Anacardiaceae	0.5950	genus	14	Safar et al., 2022	Z00	Safar et al., 2022	1.26	Safar et al., 2022
199 7	Trema micrantha	Cannabaceae	0.2750	genus	39	Try	Z00	Try	0.3	Carvalho, 2003
200	Trembleya parviflora	Melastomataceae	0.5604	family	1.7	Try	nzoo	Try	0.5	Renato et al., 2015
201	Trichilia hirta	Meliaceae	0.6512	genus	38	Try	Z00	Try	0.6	REFLORA
202 7	Trichilia pallens	Meliaceae	0.6512	genus	20	Safar et al., 2022	Z00	Safar et al., 2022	0.61	Safar et al., 2022
203	Vernonanthura discolor	Asteraceae	0.5400	SouthAmerica	22.8	Try	nzoo	Try	0.3	Grzybowski et al., 2016
204	Vernonanthura divaricata	Asteraceae	0.5400	SouthAmerica	18	IPÊ	nzoo	Try	0.3	Grzybowski et al., 2016
205	Virola bicuhyba	Myristicaceae	0.4784	genus	28.5	Try	Z00	Try	2.7	Carvalho, 2003
206	Vismia brasiliensis	Hypericaceae	0.4637	genus	10	REFLORA	Z00	Try	0.2	Mourão & Beltrati, 2001
207	Vismia guianensis	Hypericaceae	0.4637	genus	13.1	Safar et al., 2022	Z00	Safar et al., 2022	0.11	Safar et al., 2022
208	Vismia martiana	Hypericaceae	0.4637	genus	13.33	Safar et al., 2022	Z00	Try	0.2	Mourão & Beltrati, 2001
209	Vitex polygama	Lamiaceae	0.5558	genus	12	Lorenzi, 2021	Z00	Try	1	Embrapa
210	Vochysia	Vochysiaceae	0.4441	genus	24	Safar et al., 2022	nzoo	Safar et al., 2022	0.57	Safar et al., 2022
211 2	Xylopia frutescens	Annonaceae	0.5790	genus	19	Try	ZOO	Try	0.5	Safar et al., 2022
212 2	Xylopia sericea	Annonaceae	0.5790	genus	27.5	Try	Z00	Try	0.5	REFLORA
213 2	Zanthoxylum acuminatum	Rutaceae	0.5860	genus	20	REFLORA	ZOO	Try	0.3	FFESP
214 2	Zanthoxylum rhoifolium	Rutaceae	0.5860	genus	17.54	Try	Z00	Safar et al., 2022	0.3	Safar et al., 2022
215 2	Zeyheria tuberculosa	Bignoniaceae	0.7700	genus	23	Lorenzi, 2021	nzoo	Try	6.2	Embrapa

Legend: BDC: Biblioteca Digital de Ciências, University of Campinas; Embrapa: Empresa Brasileira de Pesquisa Agropecuária; FFESP: Flora Fanerogâmica do Estado de São Paulo; IPÊ: Instituto de Pesquisas Ecológicas; REFLORA: REFLORA Programme; Try: TRY Plant Trait Database.

SUPPLEMENTARY MATERIAL

Abandoned Eucalyptus plantations can be used as catalysts for natural regeneration

Matheus C. Santos¹, Jeanpierre R. Mirano², Nathália V. H. Safar³, Luiz Fernando S. Magnago^{2*}

¹ Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Universidade Estadual de Santa Cruz, Ilhéus, Bahia, Brazil; ² Centro de Formação em Ciências e Tecnologias Agroflorestais, Universidade Federal do Sul da Bahia, Ilhéus, Bahia, Brazil; ³ Departamento de Botânica, Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil.

* Corresponding author. E-mail: <u>luiz_fsm@hotmail.com</u>.

This Supplementary Material includes:

Figure S1. Phylogenetic tree of tree species sampled in mixed and native treatments, in the Atlantic Forest. The scale of this phylogenetic tree is in millions of years.

Figure S2. Linear regression between phylogenetic diversity and structure indices and species richness.

Figure S3. Plots of models of basal area of native species (BA) in relation to Mean Nearest Taxon Distance (MNTD) with outliers, in mixed and native treatments of natural regeneration in the Atlantic Forest. The red line represents the fitted curve and the gray areas are the 95% confidence intervals.

Table S1. Mean and standard deviation of phylogenetic metrics for mixed and native treatments. PD, MPD, and MNTD are expressed in millions of years. sesPD, NRI, and NTI are expressed in units of standard deviation.

Table S2. Values of diversity indices and phylogenetic structure in mixed and native treatments.



Figure S1. Phylogenetic tree of tree species sampled in mixed and native treatments, in the Atlantic Forest. The scale of this phylogenetic tree is in millions of years.



Figure S2. Linear regression between phylogenetic diversity and structure indices and species richness.



Figure S3. Plots of models of basal area of native species (BA) in relation to Mean Nearest Taxon Distance (MNTD) with outliers, in mixed and native treatments of natural regeneration in the Atlantic Forest. The red line represents the fitted curve and the gray areas are the 95% confidence intervals.

r										
Phylogenetic metric	Treat	Student's t-test								
indices	Mixed	Native	t	P-value						
PD	1436.02 ± 438.93	1534.29 ± 555.60	-0.692	0.49						
MPD	235.10 ± 8.27	235.89 ± 9.25	-0.313	0.75						
MNTD	135.98 ± 29.51	140.44 ± 34.88	а	0.78						
sesPD	-0.55 ± 1.02	$\textbf{-0.39} \pm 1.15$	-0.503	0.61						
NRI	0.23 ± 1.04	0.12 ± 1.26	0.334	0.74						
NTI	0.75 ± 1.10	0.49 ± 1.03	0.800	0.42						

Table S1. Mean and standard deviation of phylogenetic metrics for mixed and native treatments. PD, MPD, and MNTD are expressed in millions of years. sesPD, NRI, and NTI are expressed in units of standard deviation.

^a The data were not normal (Mann-Whitney U test: W = 312). Legend: PD: Phylogenetic Diversity; MPD: Mean Pairwaise Distance; MNTD: Mean Nearest taxon distance; sesPD: standardized effect size of PD; NRI: Net Relatedness Index; NTI: Nearest Taxon Index.

Transect	Treatment	SR	PD	MPD	MNTD	sesPD	pd.obs.p	NRI	NTI
1	Mixed	6	586.662	236.445	127.402	-1.438	0.082	0.092	2.103
2	Mixed	9	842.729	219.120	160.614	-1.300	0.115	1.758	0.618
3	Mixed	13	1134.418	225.303	131.564	-1.509	0.068	1.520	1.145
4	Mixed	18	1558.575	237.083	120.202	-0.865	0.193	0.023	1.134
5	Mixed	11	986.326	222.715	134.862	-1.444	0.079	1.714	1.272
6	Mixed	11	1281.748	246.586	219.597	1.764	0.978	-1.071	-1.830
7	Native	10	1110.426	241.151	198.621	0.859	0.799	-0.434	-0.843
8	Mixed	15	1372.634	242.185	129.944	-0.618	0.262	-0.691	1.061
9	Native	4	436.472	218.765	181.981	-0.906	0.172	0.930	0.791
10	Native	6	638.169	227.038	176.974	-0.576	0.260	0.791	0.586
11	Native	16	1327.441	226.808	122.449	-1.572	0.075	1.621	1.262
12	Native	13	1069.893	229.486	103.374	-2.110	0.023	1.106	2.293
13	Native	18	1687.563	243.232	139.786	0.202	0.562	-0.992	0.205
14	Native	12	1314.705	239.970	194.272	1.214	0.901	-0.323	-1.173
15	Native	20	1784.872	234.636	139.162	-0.137	0.438	0.488	-0.031
16	Native	12	1180.059	241.789	145.888	-0.176	0.420	-0.563	0.728
17	Native	20	1675.553	231.005	123.721	-0.989	0.159	1.195	0.876
18	Mixed	14	1449.002	243.369	169.934	0.838	0.791	-0.883	-0.594
19	Mixed	19	1793.399	238.373	146.778	0.486	0.664	-0.184	-0.257
20	Mixed	23	1845.954	237.755	93.511	-1.126	0.148	-0.081	2.195
21	Mixed	19	1517.623	235.237	92.320	-1.682	0.043	0.393	2.488
22	Mixed	13	1132.563	223.669	127.205	-1.463	0.072	1.704	1.379
23	Native	16	1271.343	227.710	91.145	-2.147	0.025	1.498	2.655
24	Native	19	1413.743	230.333	85.215	-2.412	0.016	1.182	2.858
25	Native	20	1833.220	235.326	141.729	0.254	0.598	0.334	-0.192
26	Mixed	18	1586 952	235 456	129 465	-0.578	0.282	0.260	0.656
27	Mixed	14	1308 406	234 494	147 674	-0.493	0.320	0.330	0.395
28	Native	27	2294 825	236 329	128 907	0.223	0.520	0.220	-0.332
29	Native	37	2668 021	230.327	93 084	-0.924	0.182	-1.021	1 240
30	Mixed	17	1583 126	247 869	129 035	0.038	0.482	-1 739	0.864
31	Mixed	24	2197 984	238.968	141 151	0.028	0.829	-0.272	-0 573
32	Native	19	1696 460	239 248	119 833	-0.323	0.359	-0.296	1.032
33	Native	19	1726 471	237 513	134 578	-0.029	0.339	-0.031	0.360
34	Native	17	1523 515	228 977	135 294	-0.555	0.475	1 366	0.380
35	Native	27	2254 402	239 498	114 820	0.030	0.505	-0.489	0.557
36	Native	19	1800.001	244 879	141 612	0.576	0.202	-1 288	-0.010
37	Mixed	29	2234 281	232.115	110 552	-0.975	0.161	1 178	0.694
38	Native	21	1926 568	242 102	138 169	0.452	0.663	-0.917	-0.115
39	Native	11	1264 257	251 273	207 613	1 568	0.005	-1 629	-1 384
40	Native	9	812 372	212 086	146 179	-1.832	0.049	2570	1 145
40	Native	10	971 997	278 434	158 905	-0.814	0.211	0.961	0.500
42	Native	16	1514 645	220.434	141 438	-0.014	0.211	-1 213	0.300
43	Native	11	1170 749	245.660	181.092	0.592	0.475	-0.958	-0.447
44	Native	24	1896 924	231 373	112 170	-1.224	0.115	1 140	1 040
45	Native	16	1254 341	231.373	106 750	-2 361	0.020	1 488	2 023
46	Native	22	1966 193	243 162	139 991	0.185	0.562	-1.083	-0.283
40	Native	12	1064 522	243.102	120 172	-1 397	0.002	0 566	1 / 30
48	Native	33	2736 877	235.522	118 455	0 793	0.788	-2 268	-0.200
40	Native	21	1785 570	232 076	130 477	-0.685	0.768	0.931	0.200
-+ <i>2</i> 50	Native	$\frac{21}{20}$	1493 563	232.070	109 927	-0.085	0.240	2 740	1 437
51	Nativo	5	631 130	253 800	244 885	1 000	0.000	_1 08/	_1 130
52	Native	27	2503.590	233.800	137.816	1.735	0.968	-2.077	-0.828

Table S2. Values of diversity indices and phylogenetic structure in mixed and native treatments.

Legend: SR: Species richness; PD: Phylogenetic Diversity; MPD: Mean Pairwaise Distance; MNTD: Mean Nearest taxon distance; sesPD: standardized effect size of PD; NRI: Net Relatedness Index; NTI: Nearest Taxon Index.