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RESEARCH ARTICLE

UN Decade on Ecosystem Restoration

# Phylogenetic distance controls plant growth during early restoration of a semi-arid riparian forest

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## Abstract

1. Little attention has been paid to phylogenetic diversity during restoration initiatives. Because plant phylogenetic distance can be a surrogate for functional diversity, its consideration could foster the restoration of degraded areas.
2. This study investigates the influence of species richness and phylogenetic relatedness during early restoration of a riparian forest located between the Atlantic Forest and semi-arid ecosystems in NE Brazil. The restoration experiment was established along a perennial stream in Monte Alegre, RN, investigating the significance of species richness and phylogenetic diversity for sapling survival and growth of the restored communities.
3. We used phylogenetic information on 47 tree species naturally occurring at the study site. The resulting phylogenetic tree had a basal node with three major clades. To implement the experiment, three species from each clade were randomly selected, resulting in nine species (from five families). We defined five levels of diversity: (i) no planting, (ii) monoculture, (iii) three phylogenetically related species (same clade), (iv) three phylogenetically distant species (different clades) and (v) nine species. The experiment consisted of 96 (12 m × 10 m) plots established along the two margins of the stream. Overall, 1656 saplings (20–50 cm) were planted in September 2015 (184 per species). We tested whether the survival and growth of saplings are influenced by the number of species planted and phylogenetic distance among them.
4. We assessed plant mortality and growth during two consecutive years (2016 and 2017). Survival was lower but relative growth was higher for plants near the stream. After controlling for differences in initial size, plots with phylogenetically distant species produced significantly taller plants, but only when occurring near the stream. Diversity treatments did not influence plant survival, while initial size determined plant survival and growth.
5. Our findings show that greater phylogenetic distance led to increased plant growth, probably, because of the presence of functionally divergent species that

use resources in a complementary way. Therefore, plant phylogenetic relatedness should be considered during the design of restored communities to improve the outcomes of future restoration initiatives.

**KEYWORDS**
forest restoration, phylogenetic relatedness, phylogenetically informed restoration, plant survival, random partition design, relative growth, species richness

## 1 | INTRODUCTION

Restoration projects provide the opportunity for locally assessing how different aspects of plant diversity affect community assembly and the functioning of restored ecosystems (Hipp et al., 2015; 2018; Montoya et al., 2012). Such projects also offer the possibility of testing how the manipulation of diversity will influence plant performance and restoration outcomes (Hipp et al., 2018; Williams et al., 2021). Among the different facets of diversity, phylogenetic distance between species, that is the estimation of the amount of time in which a pair of species diverged from the most recent common ancestor (Vellend et al., 2010), is a promising component of restoration planning.

Phylogenetic distance can be considered as a surrogate for ecological differences, thus potentially correlating to the development of dissimilar functional traits across species with increasing phylogenetic distance (Cadotte, 2013; Cadotte et al., 2009; Díaz et al., 2013). This implies that such species would complementarily use resources with benefits for ecosystem functioning (Cadotte, 2013; Mazzochini et al., 2019), and increased species coexistence due to reduced competition for shared resources (HilleRisLambers et al., 2012; Maynard et al., 2017; Tilman, 1999; Verdú et al., 2012). Furthermore, positive plant–plant interactions are more frequent when phylogenetically distant species are co-occurring in the same community (Valiente-Banuet & Verdú, 2007; Verdú et al., 2012; but see Mayfield & Levine, 2010). This should increase survival of such species, especially when considering plants from harsh environments (Brooker et al., 2008; Carrión et al., 2017; Paterno, Siqueira Filho & Ganade, 2016). Therefore, the phylogenetic relatedness among species can be one of the aspects determining the outcomes of ecological succession during restoration of degraded areas (Verdú, Gómez-Aparicio & Valiente-Banuet, 2012; Winter, Devictor & Schweiger, 2013). However, the great disparity among studies investigating the effects of phylogenetic relations on species interactions (Anacker & Strauss, 2016), and the significance of environmental contingency (Pistón et al., 2015; Williams et al., 2021), impedes generalizations about the application of phylogenetic information during restoration.

Regardless of the ample evidence demonstrating the effects of species richness on the structuring of plant communities and functioning of ecosystems (Duffy et al., 2017; Tilman et al., 2014; Venail et al., 2015), the lack of consideration of other, more integrative, aspects of diversity (such as the phylogenetic relatedness among target species) during the design and implementation of restoration projects hinders the advancement of restoration research, and jeopardizes the development of new techniques or the delivery of better outcomes (Hipp et al., 2015; Verdú et al., 2012). By ignoring plant diversity beyond species richness, restoration projects also miss important evolutionary aspects that might have shaped community assembly (Staab et al., 2021). To better understand how these two facets of diversity affect survival, growth and other aspects of plant performance, such projects should be designed to account for effects of species numbers and its phylogenetic relatedness. In this context, the incorporation of study design and hypotheses testing the importance of phylogenetic diversity will contribute to improved restoration (Hipp et al., 2015). In spite of its promising implications to restoration initiatives, the incorporation of phylogenetic information during the planning and implementation of restored plant communities might also be hindered by the need of specific knowledge for its application by restoration practitioners (Hipp et al., 2015; Verdú et al., 2012).

Despite recent progress stimulated by the UN Decade on Ecosystem Restoration (Young & Schwartz, 2019), many restoration projects still lack the systematic inclusion of scientific evidence (Gómez-Aparicio, 2009; Hipp et al., 2015; Verdú et al., 2012), while this can be helpful for advancing restoration success (Perring et al., 2015), for upscaling (Perring et al., 2018) as well as to promote nature's contributions to people (Takahashi et al., 2022). This is particularly important for areas that comprise multiple uses, like riparian forests, with relatively fertile soils, mild climate and high water availability (Araújo, 2009; Bernhardt et al., 2005; Foley et al., 2005). Although being protected by legislation such as the Forest Law 12.651 (Brasil, 2012), these areas (in Brazil as in other parts of the world) are often degraded by deforestation, expansion of agriculture, urban development, river regulation and pollution (Foley et al., 2005). In semi-arid climates, restoration of riparian forests is also challenged by pulse dynamics drastically affecting soil conditions, that is from extremely dry to almost flooded soils (Collins et al., 2014; Williams et al., 2006). These dynamics can reduce plant establishment and survival, thus compromising restoration outcomes. However, the inclusion of communities with high diversity levels could buffer flooding impacts on plants (Wright et al., 2017), and thus increase ecosystem stability of riparian forests (Cadotte, Dinnage & Tilman, 2012; Tilman, Reich & Knops, 2006).

This study aims to advance the restoration of semi-arid riparian forests via the consideration of biodiversity–ecosystem functioning aspects during restoration design. As a suitable study case, we manipulated species richness and phylogenetic relatedness of plant species

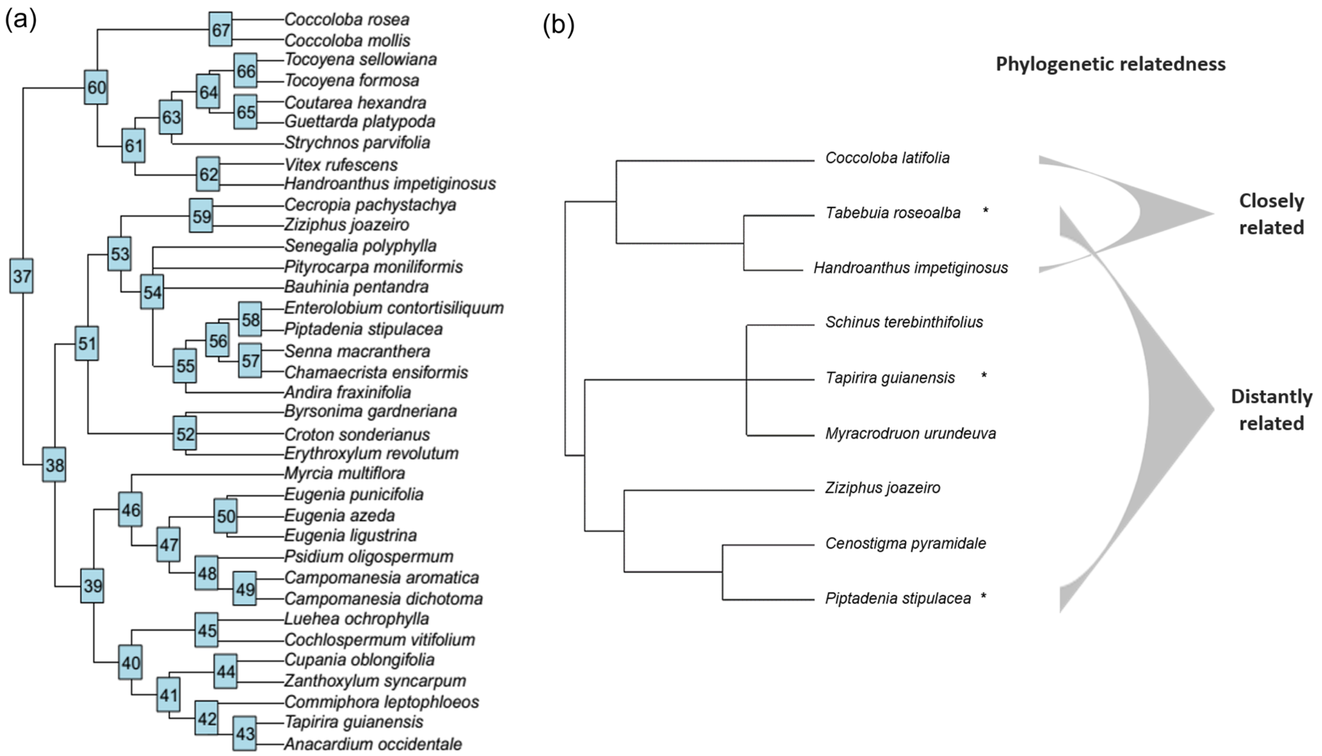

**FIGURE 1** Phylogenetic trees, implemented in R by the Grafen's method for branches length, for plant species native from Atlantic Forest and Caatinga (NE Brazil) and naturally occurring at the experimental site surroundings (a) and for the nine species randomly selected for composing our experimental communities (b)

during restoration of a riparian forest in NE Brazil, which is a region where plants are seasonally exposed to high temperatures and water stress. We tested the following hypotheses: (i) Increased distance to the stream reduces plant survival and growth due to lower water availability; (ii) Plant survival is higher in more diverse communities (i.e. higher number of species or greater phylogenetic distance) due to reduced competition at early establishment stages; and (iii) Plant growth is enhanced in communities with higher species richness or composed by phylogenetically distant species.

## 2 | MATERIALS AND METHODS

### 2.1 | Plant species selection and phylogenetic classification

In May 2015, we conducted a field survey in the study area located at Monte Alegre (NE Brazil) and its surroundings to identify native plant species that could be applied for the restoration of a degraded riparian forest. This area is at a transition zone between the Atlantic Forest and the tropical dry forests (Caatinga), known as the *Agreste Potiguar* (5°52′60″ S, 36°18′0″ W; Figures 1 and 2). Here, 47 woody species with potential use for restoration projects were identified that are native to the Atlantic Forest or the Caatinga of Rio Grande do Norte (Figure 1; Table S1).

A phylogenetic tree based on an angiosperm supertree (Zanne et al., 2014) was generated for the plant species identified during the field survey (Figure 1). The 47 species belonged to three main clades (the superasterids clade, and within the superrosids, the malvids and fabids clades). Nine species (three from each clade) were randomly selected for the experiment. However, since the commercial availability of species is an important constraint for restoration of degraded areas in NE Brazil, species selection was conducted separately for each clade, and repeated depending on availability from local producers. Plant species with regional provenance were acquired from two local producers and kept in a nursery (under natural light and temperature conditions) at the study site during 4 weeks for acclimatization until start of the experiment. All plants were 20–50 cm tall with 20–30 cm root length when transplanted to the experimental plots.

### 2.2 | Experimental design and monitoring

In July and August 2015, 96 plots (12 m × 10 m) were established within 800 m on both sides of a perennial stream in Monte Alegre (Figures 2 and S1). In each plot, 18 holes (c. 20 cm diameter and 50 cm depth) were prepared for receiving the saplings. Planting was done in a 2 m × 3 m grid, with six lines of holes receiving three plants in different distances from the stream (8, 10, 12, 14, 16 and 18 m, respectively). The experiment started in late September 2015 by transplanting 1656 saplings (184 per species and 18 per plot) from the nine plant species (Figure S1).

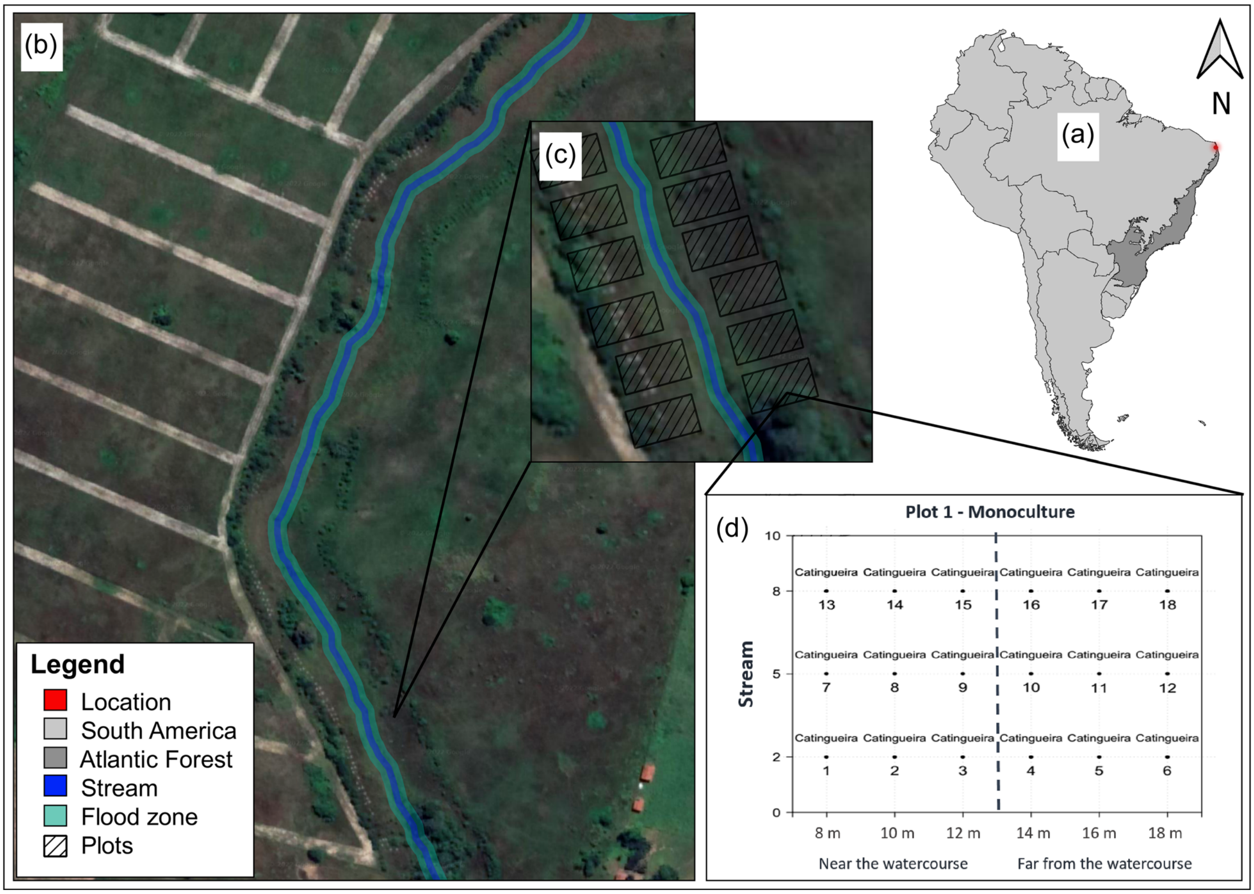

**FIGURE 2** Riparian forest restoration experiment implemented in Monte Alegre (NE Brazil). The figure depicts a map of South America presenting the extension of the Atlantic Forest domain in the Brazilian territory and indicating the position of the study site (a). The riparian forest restoration experiment was established along an 800-m section of a perennial stream (b) in a private property located at a transition zone between Atlantic Forest and Caatinga (5°52′60″ S, 36°18′0″ W). After definition of a flooding zone with 8 m width, 96 experimental plots (12 m × 10 m) were distributed along both margins of the stream (c) and were planted with 18 saplings each in a 2 m × 3 m grid (d), except for the control treatment to which no saplings were allocated (i.e. no planting).

We used a random partition design (Bruelheide et al., 2014) restricted to the plant species used for the construction of our phylogenetic tree, where the randomization was conducted for the plant species composing each branch of our phylogenetic tree (Figure 1). The experiment included five levels of diversity: (i) no planting (zero species, i.e. control [C] treatment); (ii) monoculture; (iii) three closely related plant species (belonging to the same branch); (iv) three distantly related species (one species from a different branch) and (v) nine species (with three species per branch). Control, monoculture, closely and distantly related species treatments were replicated four times. Polyculture treatment (all nine species used in the experiment planted together) was replicated nine times, resulting in a total of 96 experimental plots (Table S2). In total, the experiment comprised 22 community compositions (Table S3). Besides the nine monocultures and the polyculture, we used three compositions of phylogenetically ‘related communities a–c’ and nine phylogenetically ‘distant communities a–i’; see Table S3 for details of the experimental communities.

Plant survival and height (cm) were monitored during the first 2 years of the experiment, that is in April, June and October 2016, and in September 2017. Using height measurements, we calculated relative plant growth, that is a ratio between the most contemporary size measurement ($t_1$) and the measure of size collected in the previous monitoring ($t_0$), and community mean growth, that is average height of all individuals planted in experimental plots. In November 2015, there were 157 dead plants in eight species, that is 78 individuals of *Tapirira guianensis*, 23 *Piptadenia stipulacea*, 20 *Schinus terebinthifolius*, 13 *Handroanthus impetiginosus*, 11 *Tabebuia roseoalba*, nine *Cenostigma pyramidale*, two *Myracrodruon urundeuva* and one *Ziziphus joazeiro*, representing approximately 9.5% of mortality 1 month after the experiment was implemented; species nomenclature follows APG IV (Angiosperm Phylogeny Group et al., 2016). Those individuals were replaced in early December by plants from the same sources, that is kept in a nursery at the study site. Therefore, height in December 2015 (instead of September 2015) was considered as the initial size for all plants.

## 2.3 | Statistical analysis

Prior to analysing the data, we re-classified the distances into two categories based on personal observations of stream flooding at the field site. Plants at 8, 10 and 12 m were considered near to the stream (i.e. more permanently affected by stream pulse or flooding dynamics), while plants at 14, 16 and 18 m were considered far from the stream (i.e. having less access to water, but also suffering less from flooding; Figure S1). Afterward, we tested the relationships between plant survival and distance to the stream ('near' vs. 'far'), species richness, phylogenetic relatedness and time with a generalized mixed-effects model (GLMM) with binomial error. This model controlled for plot number nested within the specific margin of the stream (E or W) and species composition as random intercepts. Models assessing plant survival were structured as follows: *glmm(plant survival ~ plants initial size + diversity treatments * distance from the stream + plant diversity * time + (1|margin/plot) + (1|species), family = binomial)*. GLMMs with Gaussian error structure and random intercepts were used to test the effects of distance to the stream, species richness, phylogenetic relatedness and time on plant growth (calculated as height $t_n/t_0$). To control for differences in plant size and its potential effects along the experiment, we used the initial size (log-transformed values) as a covariate in the models assessing survival and growth. These models tested for the individual effects of predictors (distance to the stream, species richness, phylogenetic relatedness and time) and for the interaction between diversity treatments, that is species richness or phylogenetic relatedness, and distance to the stream or time (as a categorical variable represented by the month and year in which measurements were taken). Three-way interactions were not considered. Models assessing plant growth were structured as follows: *glmm(plant growth ~ plants initial size + plant diversity * distance from the stream + diversity treatments * time + (1|margin/plot) + (1|species))*.

Additionally, we calculated community mean growth as the mean absolute growth of all individuals alive (height $t_n - t_{n-1}$); $t_{n-1}$ represents the time point immediately before $t_n$ for all experimental communities (with each community stratified according to distance to the stream) and is used as a proxy for community biomass production. We then fitted a similar GLMM model to assess the effects of distance to the stream, diversity treatments (i.e. species richness and phylogenetic relatedness) and time on community mean growth. In this case, random intercepts were plot number nested within the margin of the stream (E or W) and community types. Mean initial size (calculated as the averaged initial size of all individuals composing the experimental communities) was the covariate used in the models assessing community mean growth. Models assessing community mean growth were structured as follows: *glmm(community mean growth ~ mean initial size + diversity treatments * distance from the stream + diversity treatments * time + (1|margin/plot) + (1|community types))*.

Values of plant height and relative growth were log-transformed (log10), while community mean growth values were standardized by the most negative value, that is by adding 22.85, so all negative values would be ≥0, and, then, log-transformed [log(*x*+1)] to fulfil the assumptions of the analysis (normality of residuals and homogeneity of variances). Species richness values were also log-transformed before running the GLMMs. As a consequence of the experimental design, models testing the effects of phylogenetic relatedness on plant survival and growth considered only communities composed of three species of trees: those being phylogenetically distant or phylogenetically related (Figure 1; Table S2).

All models were implemented using the R package glmmTMB in R (Brooks et al., 2017). Significance was determined through a Wald Test (type 3) calculated with the function *Anova* of the car package (version 3) in R (Fox & Weisberg, 2019). Statistical analyses were calculated using R Statistical Computing version 3.6.3 (R Core Team, 2020).

## 3 | RESULTS

### 3.1 | Effects of diversity and distance to the stream on plant survival

Overall plant survival was 86%, 86% and 83% across levels of species richness (for one, three and nine species, respectively) and varied from 87% to 85% for phylogenetically close and distant communities, respectively (Figure 3). Still, survival probability was not influenced by the diversity treatments (species richness: $\chi^2 = 0.25$, df = 1, $p = 0.6$; phylogenetic relatedness: $\chi^2 = 0.005$, df = 1, $p = 1.0$; Figure 3a,b). In turn, individual survival was significantly reduced for plants located near the stream ($\chi^2 = 8.85$, df = 1, $p \leq 0.01$). However, this effect was only observed when testing for the effects of species richness, mainly due to including the monoculture treatments in the analysis (Figure 3a). When fitting the model for the effects of phylogenetic diversity (which used only plots composed of three species of plants), the distance to the stream marginally increased plant survival ($\chi^2 = 3.15$, df = 1, $p = 0.08$; Figure 3b). Additionally, plant survival was also significantly reduced with time ($\chi^2 = 340.9$, df = 3, $p \leq 0.001$ for the model testing species richness effects; and $\chi^2 = 266.1$, df = 3, $p \leq 0.001$ when testing for phylogenetic relatedness effects). Survival probability was almost 100% in April 2016, 96% in June 2016 and 85% in October 2016. In September 2017, 2 years after the experiment started, we registered 1003 alive plants resulting in 61% survival (Figure 4). We also observed plant survival to strongly vary among plant species and community composition (Appendix S2; Figures S2 and S4).

### 3.2 | Effects of diversity and distance to the stream on plant growth

Mean plant height in September 2017 was 57.2 ± 3.3 cm (±SE) for monocultures, 62.3 ± 2.9 cm for three-species communities, and 66.1 ± 8.3 cm for nine-species communities. In turn, mean height in September 2017 was approximately. 28% higher in phylogenetically distant in comparison to phylogenetically related communities (66.1 ± 3.7 cm height for phylogenetically distant and 51.6 ± 4.2 cm for close communities).

Plant height and relative growth were positively affected by species richness in interaction with the distance to the stream ($\chi^2 = 3.13$, df = 1, $p = 0.08$; Figure 5a,c), while community mean growth was not ($\chi^2 = 0.53$, df = 1, $p = 0.5$; Figure 6a), being significantly influenced by the individual effect of time ($\chi^2 = 25.2$, df = 3, $p \leq 0.001$). Still, the

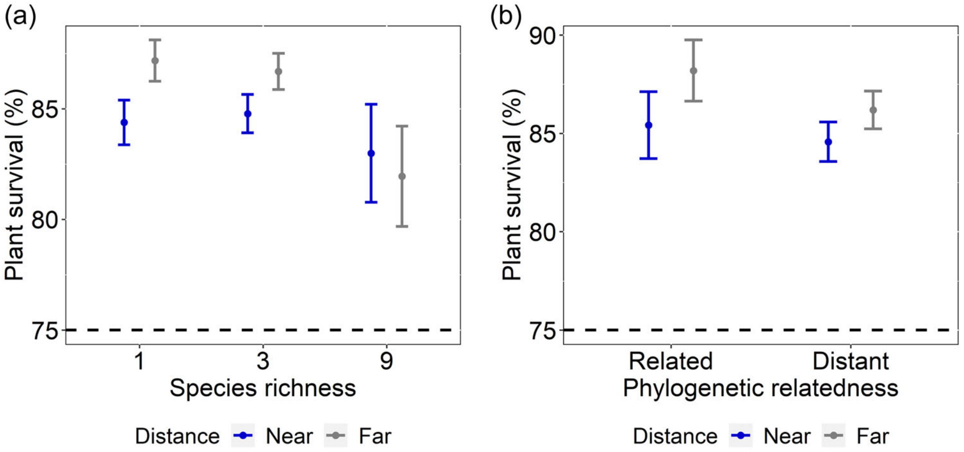

**FIGURE 3** Effects of distance to the stream, species richness (a) and phylogenetic relatedness (b) on plant survival in a restoration experiment on riparian forest in NE Brazil (means ± SE). Survival probability was positively affected by distance to the stream (mainly in monoculture communities), while diversity treatments had no effects.

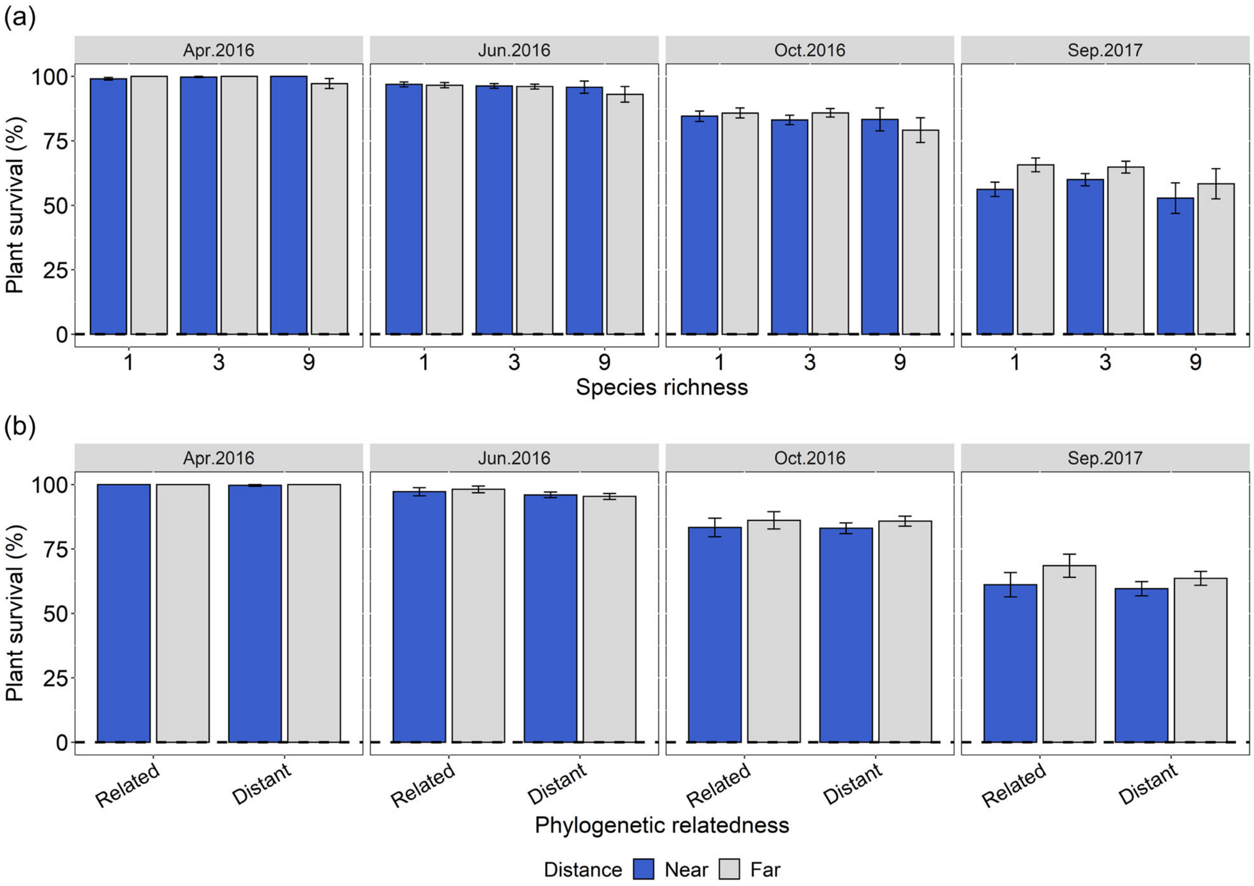

**FIGURE 4** Plant survival affected by the distance to the stream, species richness and phylogenetic relatedness over time during early restoration of a riparian forest in NE Brazil. Barplots show the mean values (±SE) for plant survival according to the effects of species richness (a) and phylogenetic relatedness (b) as monitored in April, June and October 2016, and in September 2017. Survival was close to 100% in April 2016 and decreased to approximately. 60% in September 2017, indicating a significant effect of time on plant survival. Dead plants were not continuously replaced during the experiment.

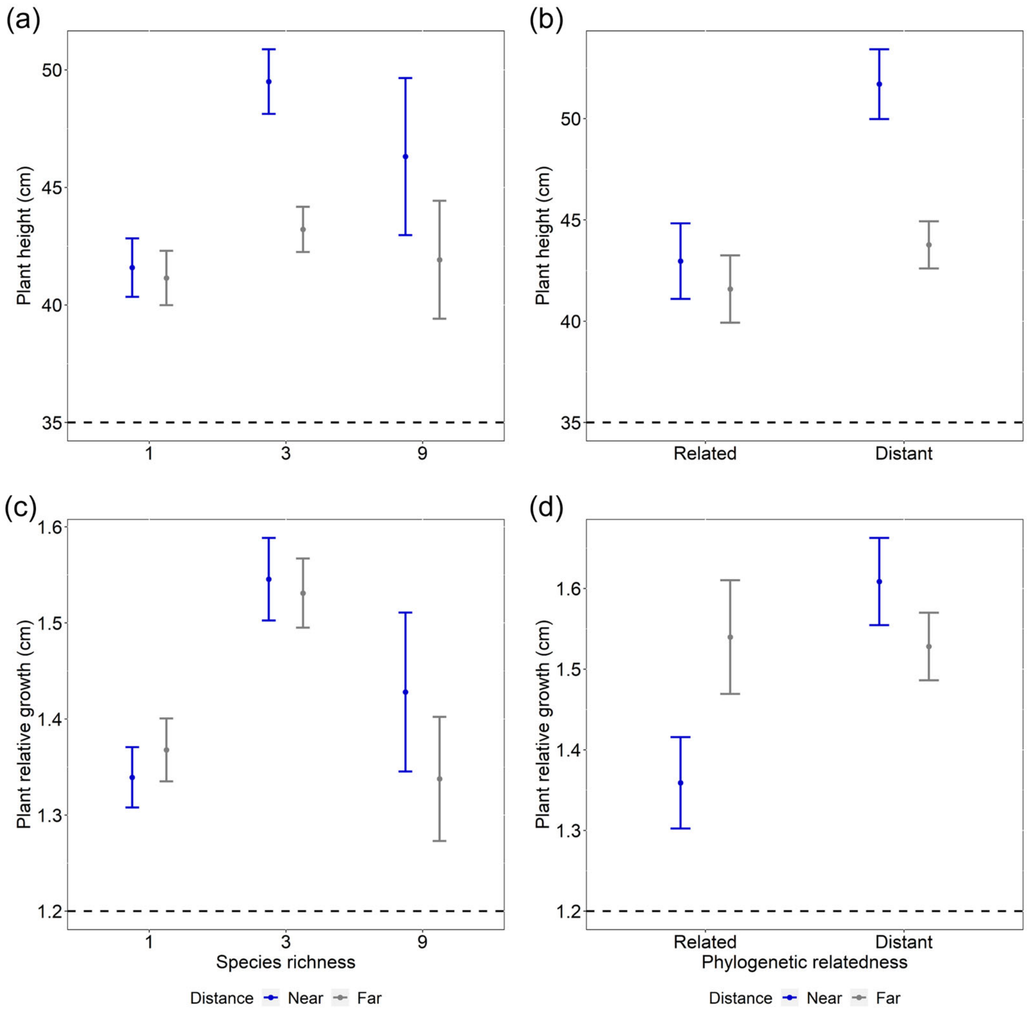

**FIGURE 5** Effects of the distance to the stream, species richness and phylogenetic relatedness on plant height (a and b) and on plant relative growth (c and d). Plots show mean values (±SE) for plant growth along the restoration experiment. Plant height and relative growth were significantly affected by the interaction between phylogenetic relatedness and distance to the stream, but with a contrasting pattern. While plant height increased with phylogenetic distance close to the stream, relative growth decreased for phylogenetically related communities near the stream. Species richness (in interaction with the distance to the stream) produced only marginal effects.

marginal positive effects of the interaction between species richness and distance to the stream on plant growth (i.e. height and relative growth) can only be seen for the three-species plots as a parabolic relationship (Figure 5a,c). Furthermore, we observed plant height and relative growth ($\chi^2 = 7.08$, df = 3, $p = 0.07$) to be marginally positively influenced by the species richness in interaction with time, indicating that diversity effects on plant growth might increase with time. Finally, species richness and distance to the stream (by itself) did not influence plant height nor relative growth ($\chi^2 = 0.28$, df = 1, $p = 0.6$; $\chi^2 = 0.55$, df = 1, $p = 0.4$ for richness and distance from the stream, respectively).

Plant height and relative growth significantly increased with phylogenetic relatedness in interaction with the distance to the stream, and this differed from species richness (Figure 5b,d). Therefore, plants from phylogenetically distant communities were larger when growing near the stream ($\chi^2 = 6.4$, df = 1, $p \leq 0.05$). No significant effects were observed for the interaction between phylogenetic relatedness and time ($\chi^2 = 2.07$, df = 3, $p = 0.5$); however, plant height and relative growth were significantly influenced by the distance to the stream ($\chi^2 = 7.62$, df = 1, $p \leq 0.01$) and time, when considered individually ($\chi^2 = 13.1$, df = 3, $p \leq 0.01$). Again, community mean growth did not respond to the interaction between phylogenetic relatedness and distance to the stream ($\chi^2 = 0.006$, df = 1, $p = 0.9$), nor to the interaction between phylogenetic relatedness and time ($\chi^2 = 2.07$, df = 3, $p = 0.5$), but was significantly influenced by time alone ($\chi^2 = 9.41$, df = 3, $p \leq 0.05$; Figure 6b). Finally, plant growth also varied strongly among plant species and communities (Appendix S2; Figures S3, S5 and S6).

### 3.3 | Initial size affects plant survival and growth

Plant initial size had strong effects when evaluating survival probability according to species richness ($\chi^2 = 62.7$, df = 1, $p \leq 0.001$; Figure 7a) and phylogenetic relatedness ($\chi^2 = 21.6$, df = 1, $p \leq 0.001$; Figure 7b). The same effects of initial size were observed when

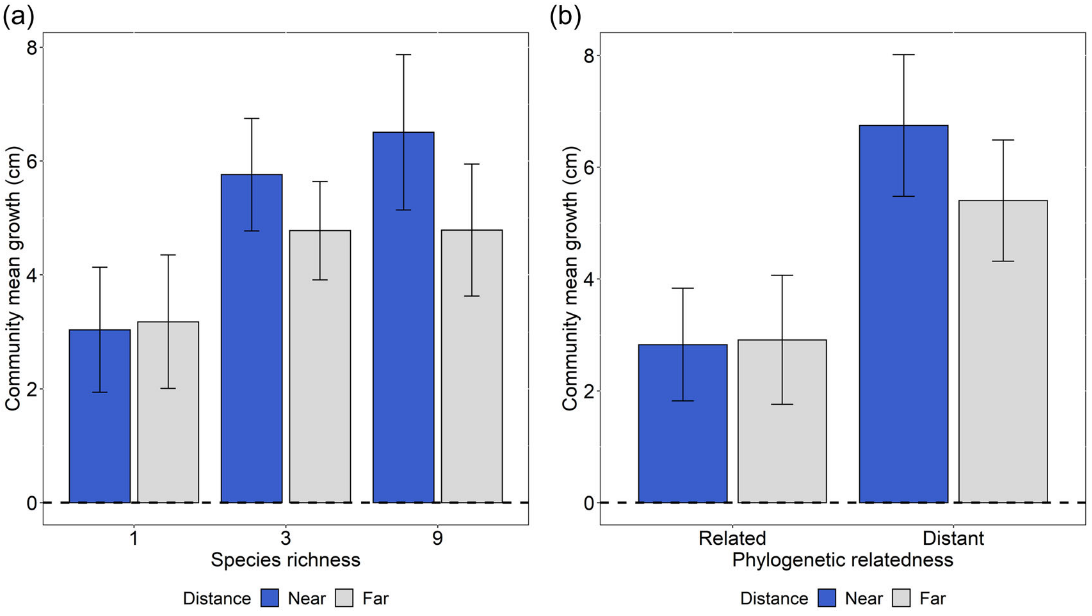

**FIGURE 6** Effects of the distance to the stream, species richness and phylogenetic relatedness on community mean growth. Barplots show mean values (±SE) for the community mean growth according to levels of species richness (a) and phylogenetic relatedness (b) of the experimental communities. Although a positive trend was observed for community mean growth in response to increasing species richness or the phylogenetic distance of plant communities (especially when occurring near the stream), no statistical differences were observed across treatments.

evaluating plant growth against species richness ($\chi^2 = 753.1$, df = 1, $p \leq 0.001$; Figure 7c) and phylogenetic relatedness ($\chi^2 = 222.2$, df = 1, $p \leq 0.001$; Figure 7d). As observed above, effects of initial size were stronger over plant growth in comparison to plant survival.

## 4 | DISCUSSION

We presented results for the first 2 years of a long-term restoration experiment in a riparian forest in NE Brazil. Despite the small species pool included in the study, our findings reveal that the planting of phylogenetically distant species can produce positive outcomes for the restoration of a semi-arid riparian forest. However, not all of our expectations were confirmed. For example, despite the relatively high overall survival probability (61%) in comparison to what is observed in other parts of NE Brazil (c. 35% survival; Sales et al., 2019), plants survived less when located near the stream, possibly indicating that flooding affects plants adapted to semi-arid conditions more negatively than does water scarcity. However, this relationship was only detected when testing plant survival against the richness of species planted, mainly because of the influence of monocultures that might have reflected individual species performance as affected by, for example, functional traits. Also, we observed that mortality was particularly high for three species, that is *H. impetiginosus*, *T. guianensis* and *T. roseoalba*. Incidentally, these species had the smallest plants when the experiment was implemented. Thus, plant initial size affects plant establishment and survival during the restoration of degraded areas and, ultimately, restoration outcome. Finally, we found that plant mortality increased with time, possibly due to cumulative effects of environmental harshness representing the main filter during early community assembly in such systems (Maia et al., 2020; Méndez-Toribio et al., 2020). Furthermore, dead plants were not continuously replaced during the restoration experiment.

Some of our results should be considered in future restoration research and applications: First, the interaction between phylogenetic relatedness and distance to the stream resulted in faster plant growth, while marginally positive effects were observed for species richness in interaction with distance to the stream. This indicates that diversity effects on plant biomass are stronger when natural resources are abundant. Furthermore, it is possible that the differential effects observed when comparing phylogenetic relatedness and species richness as affecting plant growth might be related to the number of species comprising both diversity treatments. Because species richness reached up to nine species (whereas phylogenetic relatedness was only manipulated in communities composed by three species of trees), competition exerted by dominant species might have played a stronger role during early assembly of the restored communities. Second, increases in plant growth were associated with particular communities. Hence, the inclusion of phylogenetic aspects in restoration experiments allows for the identification of species combinations that would maximize growth, thus fostering restoration in the long term. Third, we observed that the significant effect of phylogenetic relatedness (and the marginal effect of species richness) affects plant growth at the individual but not at the community level. This indicates that broad-scale measures for the evaluation of restoration outcomes require more time to show the positive influence of diversity.

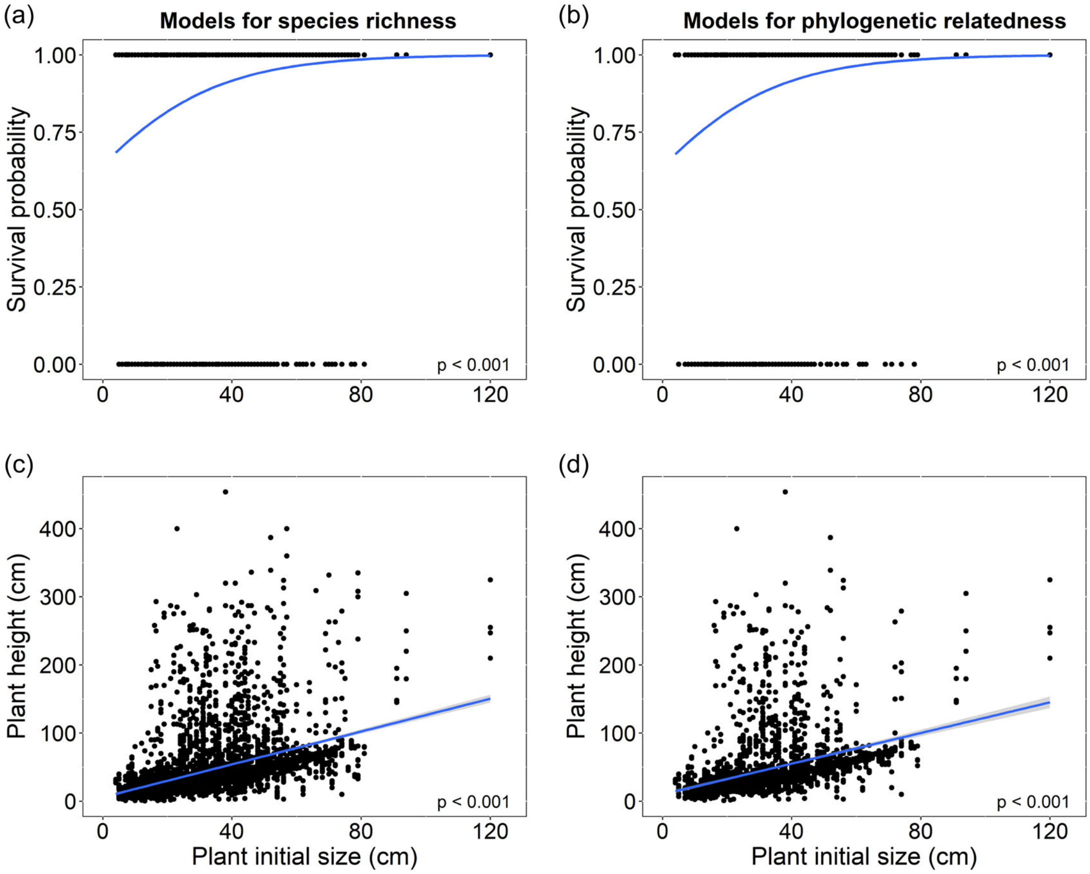

**FIGURE 7** Effects of plant initial size on the survival probability (a, b) and height (c, d) of plants used during the restoration experiment implemented in a riparian forest in NE Brazil. Plots depict the relationship observed via the generalized linear mixed-effects models (GLMMs) calculated for the effects of species richness (a, c) and phylogenetic relatedness (b, d) on plant survival (model with binomial error structure) and height (model with Gaussian error structure), including plant initial size as a covariate. Marginal $R^2$ for models assessing survival probability are 0.36 for species richness and 0.72 for phylogenetic relatedness, whereas for models evaluating plant height marginal $R^2 = 0.18$ (species richness) and $R^2 = 0.11$ (phylogenetic relatedness).

### 4.1 | Diversity, pulse dynamics and plant survival in restored riparian forests

One previous study found that species diversity is important for increasing plant survival during restoration of tropical forests in Malaysia (Tuck et al., 2016). In these areas, where logging and agricultural activities reduced tropical forest coverage and threatened species diversity and population viability, the authors argue that so-called *enrichment planting* (i.e. multispecies mixtures inside semi-natural fragments) facilitates forest regeneration by overcoming recruitment limitations. This technique can increase establishment and survival of endangered species via insurance effects, thus contributing to restoration success (Tuck et al., 2016). In fact, various studies described the potential benefits of species diversity for plant survival and the consequences to species coexistence and community structure. The mechanisms responsible for this positive relationship can include reduction of competitive and an increase of facilitative interactions and, also, the dilution of herbivory effects (Lambers et al., 2004; Srivastava et al., 2012; Tilman, 1999; Verdú, Gómez-Aparicio & Valiente-Banuet, 2012).

Here, we tested whether species richness and phylogenetic relatedness increase survival probability of plants used for the restoration of a riparian forest in NE Brazil. This was expected because recent findings indicate that plant communities can recover better after a flood when they have higher levels of species diversity (Wright et al., 2017). Contrarily to our expectations, plant survival was not affected by plant diversity. However, such results might be due to the relatively short observation period of our study rather than to an absence of diversity effects. Furthermore, we can argue that species diversity, ultimately, has more importance for community dynamics, ecosystem stability and resilience than for immediate or local evaluations of plant survival probability (Foster et al., 2004; Tuck et al., 2016; Wright et al., 2017). Therefore, long-term monitoring is paramount for assessing plant community dynamics and the success of restoration projects.

Moreover, we expected higher survival in plants close to the stream, while actually the opposite pattern was found. It seems that survival here is reflecting individual species characteristics instead of diversity effects on plant establishment. Because riparian forests are exposed to strong pulse dynamics, the ability to grow fast and reach resource patches in the soil would confer an advantage for such species during initial stages of succession (Chesson et al., 2004; Collins et al., 2014; Williams et al., 2006). Therefore, we can argue that fast-growing species will have higher survival during restoration of a riparian forest. Besides, plant size when transplanted to the field (i.e. initial size) and, also, the conditions in which plants were produced might have an important role for survival (Charles et al., 2018; Gardiner et al., 2019; Jacobs et al., 2020). In fact, this factor could have caused the low survival rates found for three species in our experiment, that is *H. impetiginosus*, *T. guianensis* and *T. roseoalba*. All individuals of such species were smaller than plants of other species (minus 20–50 cm stem height, and minus 30 cm root length), and as they were produced under greenhouse conditions (under shade and with high water availability) with insufficient time for acclimatization to the harsh field conditions. Additionally, in the case of *T. guianensis*, high plant mortality can also be related to the species poor responses to the habitat conditions of the areas to be restored or undergoing restoration. *Tapirira guianensis* is an evergreen species commonly found along river margins, thus preferably occurring where soil water and air humidity are not limiting factors.

### 4.2 | Phylogenetic relatedness effects on plant growth of restored communities

Plant interactions can determine ecological succession with different starting communities (HilleRisLambers et al., 2012). Such influence is equally important when considering plant community dynamics in restored or regenerating systems (Gómez-Aparicio, 2009; Tuck et al., 2016). Therefore, the inclusion of positive interactions among plants contributed to ‘nurse-based restoration’ (Castillo, Verdú & Valiente-Banuet, 2010; Gómez-Aparicio, 2009; Verdú, Gómez-Aparicio & Valiente-Banuet, 2012).

Here, we assessed the effects of phylogenetic relatedness on plant growth and community mean growth during restoration of a riparian forest in NE Brazil. We found phylogenetic relatedness to significantly increase plant growth (when plants occurred near the stream), but not community mean growth. Such significant interaction indicates that the positive relationship between diversity and productivity is stronger when environmental conditions are favourable. These findings are in accordance with previous studies showing that creating phylogenetically distant communities can enhance plant performance while restoring a degraded area due to increased plant–plant positive interactions, thus contributing to improved restoration outcomes (Castillo, Verdú & Valiente-Banuet, 2010; Verdú et al., 2012). Nonetheless, scientific evidence when assessing the effects of phylogenetic relations on species interactions and coexistence is still unresolved (Pistón et al., 2015). While some studies showed that increased phylogenetic distance might favour plant–plant positive interactions (Castillo, Verdú & Valiente-Banuet, 2010; Verdú et al., 2012), others found unimportant effects (Cahill et al., 2008; Pistón et al., 2015), or increased negative interactions among plant species (Anacker & Strauss, 2016), especially under stressful environmental conditions (Williams et al., 2021). Here, we tested how the species richness and phylogenetic relatedness of planted trees would influence plant survival and growth during restoration of a semi-arid riparian forest in NE Brazil. Because of the small species pool considered in our study and the strong filter imposed by the environmental harshness observed in our study system (i.e. frequently high temperatures and water stress), findings might differ when testing different sets of species or having other type of environmental stress.

The differential effects of community composition on plant growth (and survival) suggest that other species combinations should be tested to identify plant compositions that will maximize the effects of positive interactions on restoration (Cadotte, 2013; Verdú et al., 2012). Additionally, our results did not account for the effects arising from the imbalance of abundance among clades (IAC). This measure can be calculated as the deviation of abundances at internal nodes from a null distribution (Cadotte et al., 2010). High values of IAC indicate that some clade, family, or genus is disproportionately represented in the phylogenetic tree in comparison to others (Cadotte, 2013). Such values can be associated with strong selection effects, indicating that this measure accounts for the effects of closely related species (Cadotte, 2013). The phylogenetic tree in our experiment included nine species belonging to five families (Anacardiaceae, Bignoniaceae, Fabaceae, Polygonaceae and Rhamnaceae). Anacardiaceae plants dominated our experimental design (three species), therefore controlling for IAC would allow us to separate the effects of phylogenetic relatedness from those of the dominant family in our experiment. The aspects related to the influence of more abundant species or dominant clades should be considered in future initiatives of establishing phylogenetically oriented restoration projects in order to disentangle phylogenetic diversity from identity effects (Hipp et al., 2018; Staab et al., 2021).

## 5 | CONCLUSION

Because phylogenetic relatedness can positively affect growth and, potentially, plant performance, the inclusion of phylogenetic information in restoration projects can have an important contribution to advance such initiatives. The relatively cheap and easy application of such an approach, that is simply plotting a phylogenetic tree and selecting distantly related species for the composition of restored communities (which can be easily accomplished by the inclusion of a list with the species names in an online tool such as the *PhyloT v2*; https://phylot.biobyte.de/), makes it a promising strategy for restoring degraded areas in semiarid environments. Therefore, we recommend the use of phylogenetically distant communities in order to maximize cost-effective restoration activities.

## AUTHOR CONTRIBUTIONS

Leoandro H. Teixeira and Guilherme G. Mazzochini designed the research. Leonardo H. Teixeira, Guilherme G. Mazzochini and Gislene

Ganade implemented the experiment. Leoandro H. Teixeira and Guilherme G. Mazzochini monitored the experiment. Johannes Kollmann and Gislene Ganade financially supported field activities. Leonardo H. Teixeira analysed the data and led the writing of the manuscript. All authors revised the manuscript and agreed on the submitted version.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

All data associated with this study are archived in the Technical University of Munich repository, mediaTUM: https://doi.org/10.14459/2022mp1687209 (Teixeria et al., 2022).

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## PEER REVIEW

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supporting information

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