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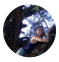
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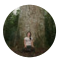
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RESEARCH ARTICLE

Eucalypt plantations for forest restoration in a fire-prone mosaic of grasslands and forests in northern Argentina

Rosario Montiel[1,2], Silvia C. Zaninovich[1], Natalia A. Bedrij[3], Ariel Insaurralde[3], Juan J. Verdoljak[4], José L. Fontana[1], Ma. Genoveva Gatti[3,5]

In ecosystems with grassland-forest boundaries, tree plantations could be used to promote forest restoration. In the Humid Chaco region of central South America, fire is one of the main disturbances that shapes the landscape. As eucalypt plantations are flammable, the contribution they can make to forest restoration is questionable. We planted saplings of five native tree species in three different environments (forests, grasslands, and eucalypt plantations) and assessed microclimatic conditions likely to influence sapling survival and growth. After 1 year, accidental fires that affected much of the study area allowed us to investigate the susceptibility of different environments to fire occurrence and post-fire sapling survival. We planted 600 saplings in four plots per environment. We evaluated fire occurrence in the study area for 2 years and ask whether this factor affects sapling survival. In grasslands, microclimatic conditions were more extreme than in plantations. Plantations and forests showed high pre-fire sapling survival but growth was almost double in plantations, similar to grasslands for most species. In the study area, fire frequency was similar in plantations and grasslands, whereas forests plots never burnt during the 2-year study period. Fire reduced sapling survival in plantations, but not in grasslands where survival was low and similar in burned and unburned plots. For top-killed plants, post-fire resprouting ability was species-specific. While more firm conclusions await future studies with even larger sample sizes, our results indicate that fire management may be necessary in order to use eucalypt plantations as nurses in this fire-prone ecosystem.

Key words: **burn severity, Humid Chaco, microclimatic conditions, normalized burn ratio, sapling survival**

Implications for Practice

- Under eucalypt plantations, high temperatures and low humidity levels are more moderate than in grasslands and planted tree saplings survived and grew well.
- Pre-fire sapling survival rates were high under plantations and low in grasslands. However, fire occurrence leads to low survival in both environments.
- Post-fire resprouting of top-killed saplings varied among species, and *Handroanthus heptaphyllus* showed the highest ability.

Introduction

Ecological restoration is a promising tool to mitigate human impact on ecosystems and to improve human well-being (Holl 2017). Several studies highlight the potential of non-native tree plantations for large-scale natural forest restoration (Parrotta et al. 1997; Brancalion et al. 2020) by promoting establishment of native woody species in their understory (Barret & Tressens 1996; Brockerhoff et al. 2013; Pryde et al. 2015; Wu et al. 2015). However, the high flammability of some of the most widely used species in tree plantations (e.g. *Eucalyptus* spp. and *Pinus* spp.; Oliveira et al. 2000; Fernandes et al. 2011) raises concerns about their roles as nurse plants for natural forest restoration in fire-prone ecosystems.

Fire shapes vegetation where grassland-forest boundaries occur (Chuvieco 2009) and affects biogeochemical cycles, local climate, and other variables (Crutzen & Andrea 1990; Hoffmann et al. 2003). Natural processes and human-use of fire to manage grasslands generate mosaics in the Humid Chaco region of

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[1]Laboratorio de Ecología, Departamento de Biología, Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste (FaCENA-UNNE), Av. Libertad 5470, Corrientes, Argentina
[2]Address correspondence to M. R. Montiel, email mdrmontielg@gmail.com
[3]Instituto de Biología Subtropical, Universidad Nacional de Misiones-CONICET, Puerto Iguazú, Misiones, Argentina
[4]Estación Experimental Agropecuaria del Instituto Nacional de Tecnología Agropecuaria Colonia Benítez (EEA-INTA Colonia Benítez), Marcos Briolini 750, Chaco, Argentina
[5]Facultad de Ciencias Forestales, Universidad Nacional de Misiones, Bertoni 124, 3380 Eldorado, Misiones, Argentina

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northern Argentina and southern Paraguay (South America) where fire is used as a tool for rangeland management and vegetation clearing (Kunst et al. 2003; Irigoin 2018). In this region, biomass accumulates during summer–autumn and typically burns in late winter and early spring ("fire season") when atmospheric conditions include steady warm winds from the N/NE and air temperatures of 30–35°C. Normally, fires end when heavy rains begin in late spring (NMS 2019). The Chaco is one of the regions most affected by fires in Argentina (Di Bella et al. 2011), with Corrientes Province having the highest incidence. In 2017, most of the fires recorded in this province were anthropogenic and due to negligence (Irigoin 2018).

Despite the fires, Humid Chaco has favorable environmental conditions for high-yield tree plantations, especially of non-native *Eucalyptus* spp. (Barret & Tressens 1996). For example, in Corrientes, eucalypt plantations covered 107,457 ha in 2009 (CFI 2015) and the government plans for plantations to cover more than 250,000 ha by 2025 (Braier 2010), at the expense of natural ecosystems, mainly grasslands (NESDS 2018). While these plantations suppress grass growth (Lima 1996), their understories are quickly colonized by native woody species (Barret & Tressens 1996). This phenomenon, known as the "nurse" effect (Brancalion et al. 2020), fosters recruitment of woody species (Carnevale & Montagnini 2002) mainly by moderating stressful environmental conditions (Zahawi & Augspurger 2006).

Some scientists consider that only native tree species should be used in forest restoration projects, whereas others hold that fast-growing non-native species also can serve as nurse plants (Ashton et al. 1997; Lamb et al. 2005; Catterall 2016). Studies in Atlantic forest indicate that plantations provide conditions suitable for regeneration of natural forest species. These plantations could act as nurses, playing the role pioneer species may have under natural conditions (Da Silva et al. 1995). Also in Atlantic forest, Brancalion et al. (2020) suggested that many of the negative effects attributed to eucalypts depend on features of the production system, landscape structure, soil, and climate in which they are grown, rather than the effects of eucalypts per se. They proposed that exotic eucalypts can be allies of tropical forest restoration, and their use and investment opportunities should be considered within the portfolio of options supported by public and private funding and policies. However, as eucalypts are extremely flammable (Wilson 1992), planting them in fire-prone areas could increase the likelihood and spread of fire (Fernandes et al. 2011). In this context, we ask if these plantations provide adequate environments for promoting forest restoration in the Humid Chaco so that they can be used where forest cover has been lost.

In a restoration experiment in Argentinean Humid Chaco, we evaluated the interaction of contrasting environments (grasslands, forests, and eucalypt plantations) and species on the survival and growth of planted saplings of five native tree species. One year after saplings were planted, unexpected and accidental fires that affected the study area allowed us the opportunity to also assess the relative likelihood of fires in these three environments and the ability of saplings of the five species to resprout after being top-killed by fire. We ask if eucalypt plantations moderate microclimatic conditions and promote native tree establishment and growth through their nurse effect and if environments show different fire occurrence. We expected better sapling survival and growth in the plantations than in grasslands. We also expected higher fire occurrence in grasslands than in forests, with intermediate occurrence in plantations as their structure and biomass allow fire to come into the understory from adjoining grasslands (Agee et al. 1973; Braun 2006). Finally, we ask how fire affects sapling survival in different environments and if the planted species differ in resprouting likelihoods. Based on the observation that shade-tolerant species typically store abundant resources in their roots to allow them to resprout after aerial damage, we expected they are more likely to resprout than light-demanding species (Myers & Kitajima 2007; Poorter & Kitajima 2007).

Methods

Study Site

We carried out field studies over the course of 3 years in Humid Chaco region on lands of the National Institute of Agricultural Technology (INTA; 27°40′27.14″S; 58°45′3.30″W) and the Cabaña Los Orígenes Ranch (27°44′7.86″S; 58°45′50.99″W), in Corrientes Province, northern Argentina (Fig. 1). The climate in the area is subtropical humid (Carnevalli 1994), with a mean annual rainfall of 1,200 mm concentrated in the spring–summer season when temperatures can be over 31°C. The mean temperature in July (the coldest month) is 15.2°C with occasional frosts and in January (the hottest month) it is 27.2°C and the mean annual temperature is 21.5°C (data collection: 1982–2012, www.climate-data.org, 2016). The most widely distributed soils are sandy Alfisols with some Entisols, Mollisols, and Inceptisols (Santa Cruz et al. 2018). The relief consists of undulated sandy hills, decreasing from the Paraná River alluvial fan apex to its base, with E–W or NE–SW direction (Contreras et al. 2018). Topography is the main physical factor generating vegetation heterogeneity in the region (Marino & Pensiero 2003) but its effects are greatly influenced by fire. So, both elements configure this landscape.

Vegetation in the Humid Chaco region is composed of native forest patches surrounded by natural grasslands in which different productive uses, such as tree plantations and cattle ranching, occur. In forest patches, the dominant species are *Handroanthus heptaphyllus* (Bignoniaceae), *Enterolobium contortisiliquum* (Fabaceae), *Ocotea diospyrifolia* (Lauraceae), *Eugenia myrcianthes* (Myrtaceae), *Myracroduon balansae* (Anacardiaceae), among others. Forest edges are surrounded by shrubs dominated by *Chrysophyllum marginatum* (Sapotaceae) and *Annona emarginata* (Annonaceae) with an herbaceous stratum in which the rosette succulents *Aechmea distichanta* and *Bromelia serra* (Bromeliaceae) are dominant (Fontana 2018). Grasslands are natural but have been managed for thousands of years by indigenous people who used fire to promote gathering and hunting as well as to generate open habitats (Coltorti et al. 2010) as in other regions around the world (Kirch 2005). In these natural and human managed grasslands, the native grasses *Andropogon lateralis*, *Axonopus compressus*, *Elionurus muticus*, and *Sorghastrum nutans* (Poaceae) are the dominant species (Fontana 2018). Eucalypt plantations are generally established on low fertility soils that

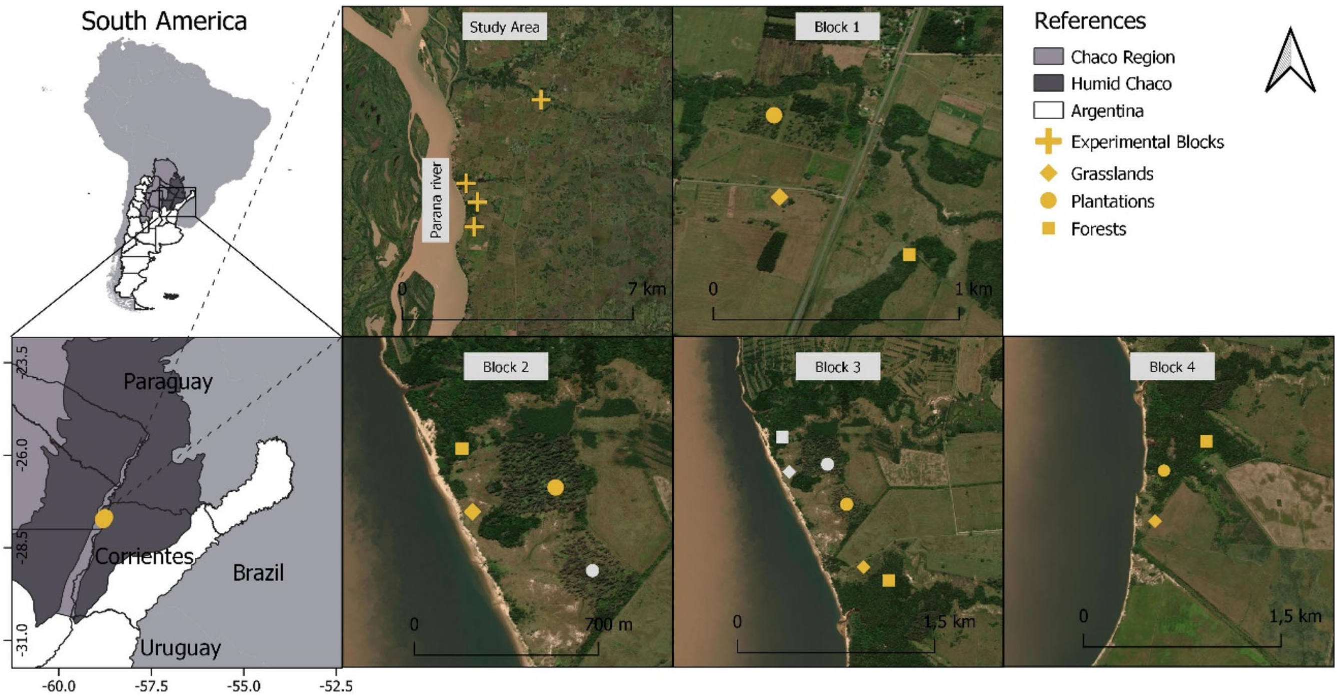

Figure 1. Location of the study area and the four experimental blocks in Argentinean humid Chaco of NW Corrientes Province. In yellow are indicated plots belonging to the same block.

characteristically support grasslands (Aparicio et al. 2005) and managed in short cycles to produce poles, or in long cycles for higher-quality wood (Torres Cayman 2017). Tree saplings of *Cordia americana* (Boraginaceae), *Holocalyx balansae* (Fabaceae) and *H. heptaphyllus* are frequent in plantation understories (Barret & Tressens 1996), with some natural regeneration of eucalypts as well.

In the study area, fire is frequently used to improve forage quality for cattle (Armúa et al. 2004). Although fire management is regulated by law, it is widely used without prescriptions, authorization, or adequate control and, as a result, fire frequently escapes and burns through plantations, grasslands, and, less often, forests. For example, in 2017, 74% of Argentina's non-native tree plantations affected by fire were located in the Province of Corrientes, 69% of which occurred in eucalypt plantations (Irigoin 2018). Although there is a gap in published information about the fire occurrence in eucalypt plantations in the study area, prior to the burns in this study, no fire scars on adult trees were evident, as compared to otherwise similar plantations in southern Brazil where farmers use low-intensity prescribed fires for plantation management (Soares 1990). Plantation managers in the study area neither install fire breaks nor use prescribed fire.

Experimental Design

We used a randomized complete block design with four blocks separated by more than 500 m (Fig. 1). Within each block, we established an experimental plot (10 × 15 m; Autumn: May–June 2016) which we surrounded with fences to exclude cattle in each of the three environments (treatments), separated from each other by 100–400 m. The three environments per block were: (1) natural grasslands dominated by *E. muticus* and *S. nutans* (Poaceae) (hereafter "grasslands"); (2) coppiced monospecific *Eucalyptus globulus* and *E. grandis* (Myrtaceae) plantations ("plantations") of around 30 years old since the last clear-cut harvest; and (3) natural forest patches, dominated by *M. balansae* and *Schinopsis balansae* ("forests"). We selected five native tree species from the inventories of the Humid Chaco region to cover a range from shade-tolerant to light-demanding (Table S1). We collected seeds from at least five different mother plants per species and planted them in trays in a shade house. Once germinated, seedlings were transferred to 2 L individual pots. After 120–150 days, in the rainy season of the first year of study (spring: Sep–Nov 2016) the plants were hardened off outside the shade house for 3 weeks. Then, we transplanted into the field 10 saplings (30 cm tall on average) per species in each plot at more than one-meter spacing (a total 5 species with 120 saplings per species, 600 saplings). See Supplement S1 for further information about transplantation.

Sapling Measurements

We monitored sapling (1) survival and (2) growth, by measuring with a caliper the diameter at the base of the stem (above any irregularities) at 3 months' intervals for 1 year (in all seasons), until non-prescribed human-ignited fires occurred. Growth rate (G) was calculated as the relative increment of size over a time interval:

$$G = \left(\frac{D_2 - D_1}{D_1}\right) / (t_2 - t_1) \quad (1)$$

where D_1 and D_2 are the stem diameters at times t_1 and t_2, the beginning of the experiment (sapling's plantation; spring: Sep–Oct 2016) and the last measurement before fire occurrence (winter/spring: Aug–Oct 2017), respectively. As the dates of the last measurement varied depending on when fire occurred at a given site, after calculating G, we multiplied it by a common time interval (11 months) to obtain a comparable relative growth rate across species.

These unplanned fires allowed us to describe fire events in the different environments (see below) as well as to measure sapling response to this disturbance to contrast data between different species and environments. For the burned environments (grasslands and plantations), we also calculated (3) post-fire survival per species 2 months after burning, examining if each sapling was or not top-killed and, in the first case, if it had resprouted or died.

Microclimatic Conditions

During the first summer and winter of the study (2016–2017) we recorded air temperature and relative humidity placing data loggers (HOBO U23-002; Onset Corporation, U.S.A.) 25 cm aboveground in all the environments under study. Records were made every 5 minutes, for between 40 and 70 days per plot in each season. From the obtained data, we calculated the mean temperature averaging the values between the hottest time slot in summer and the coldest time slot in winter (10–15 and 00–07 hour, respectively). We also calculated the minimum daily relative humidity per environment, for both seasons. High temperatures and low humidity levels represent limiting factors for sapling survival (Barajas-Guzmán & Barradas 2011).

Fire Events

Fire occurrence in the study area was monitored for 2 years, and the frequency and burn severity of the recorded fires were characterized by environment. We calculated fire frequency (Fi, Equation (2); Curt 2018) as the number of plots of each environment that experience fires (ni) during the time the work lasted ($a = 2$ years).

$$\mathrm{Fi} = (1/a) \sum \mathrm{ni} \quad (2)$$

Table 1. Categories of burn severity (since the United States geographical service; https://burnseverity.cr.usgs.gov/).

dNBR	*Burn severity*
−0.1 to 0.1	Unburned/none
0.1–0.27	Low
0.27–0.44	Moderate
0.44–0.66	Moderate–high
>0.66	High

To evaluate burn severity, an innovative approach was developed following USGS (https://www.mtbs.gov/) and the methodology explained by Anaya et al. (2018) taking the advantage that we had real field data. We calculated the normalized burn ratio (NBR, Equation (3)), an index that allows the detection of disturbances caused by fire events based on the differences between the reflectance values of near infrared and short wave infrared bands. This NBR can be calculated from any sensor that operates at these wavelengths (Landsat, Sentinel, MODIS, CBERS, etc.). On this occasion, we adapted it for the sensor Sentinel 2A MSI: MultiSpectral Instrument, Level-1C of the European Space Agency (ESA, https://sentinel.esa.int/), taking advantage of its higher spatial resolution (20 m) above other sensors. With the calculated NBR values, the effect of burning was determined (dNRB, Equation (4)). Higher dNBR values indicate a higher burn severity, according to different categories (Table 1).

$$\mathrm{NBR} = (\mathrm{NIR} - \mathrm{SWIR}) / (\mathrm{NIR} + \mathrm{SWIR}) \quad (3)$$

$$\mathrm{dNBR} = \mathrm{PreNBR} - \mathrm{PostNBR} \quad (4)$$

where NIR is the near-infrared band and SWIR is the short-wave infrared band; dNBR is the difference between pre (PreNBR) and post (PostNBR) fire NBR.

For all these procedures, we used satellite images with an adequate level of pre-processing (corrected and calculated in reflectance values, with low or no cloudiness [<10%]), processed through the Google Earth Engine (GEE) platform (https://code.earthengine.google.com), for the fire seasons: Aug–Oct 2017 and Aug–Oct 2018. As the NBR is calculated by the comparison between an image of a given moment and a reference situation (e.g. a pre-fire image), to decrease the noise of short term environmental changes (e.g. rain events), and to comprehend a more representative reference situation, we created compounds of monthly images working with the median of images from a period (since 1–3 months before the fire events). This procedure is successfully applied for monitoring land cover changes and transitions in open projects as MapBiomas (https://mapbiomas.org/en/project). These composite images were used to calculate NBR and dNBR (Equations (3) and (4)). The resulting dNBR map represented burn severity in the study area. In the Supporting information, we provide the GEE code that we have created for these purposes and more detailed information about calculations (Supplement S2).

Statistical Analysis

We used linear mixed models: (1) to evaluate how air temperature and RH change among environments (treatments) in contrasting seasons; and (2) to evaluate the effect of environments on sapling growth for 11 months prior to the fires. Models were fitted with normal distribution and model's structure included block as a random effect. For modeling of microclimate data, we tested different temporal autocorrelation (Zuur et al. 2009; Gałecki & Burzykowski 2013) using the functions corAR1 and corCAR1 of the nlme package (Pinheiro et al. 2020) to capture this component within models. The structure corAR1 was the best one for all models to correct the residuals autocorrelation. To evaluate the assumption of no temporal autocorrelation of models' residuals, we used correlograms calculated with acf function (R Core Team 2019). For diameter growth analyses, fixed effects were parameterized with the factors species and environments with their interactions. We used Wald's chi-square to verify the effect of each factor (Bolker et al. 2009), and Tukey's pairwise contrasts to compare means of microclimatic and growth variables between environments.

Generalized linear mixed models were used to evaluate the effect of species, environments, and fire on sapling survival probability. Models were fitted using a binomial distribution with sapling survival (alive or dead) as a response variable. Due to constraints in the experimental design, we performed analyses of sapling survival probability in three different parts. (1) The effect of the environment on the survival was evaluated in all environments (plantations, grasslands, and forests) throughout 11 months before the fire event. Models were parameterized with species and environment as predictors with interactions between them in the fixed effect, and the block factor was used in random effect structure. Then, after the fire events, we tested (2) the effect of fire and environment in overall sapling survival using data from burned and unburned plots only in environments that recorded fires (plantations and grasslands). Models were parameterized by fire (burned and unburned) and environment predictors with interaction between them; due to the scarcity of data, it was not possible to included species as fixed factors. In this instance, the blocks and species were used in random effect structure. Although only five species are a value that could be considered at the limit of the levels that a group could contain (Gelman & Hill 2007), we compared the significance of the random effect adjusting models incorporating and discarding it. Then, we selected the most parsimonious model based on Akaike's information criterion (Zuur et al. 2009). The model finally selected included the random effect, indicating that adding species as a random effect contributed to increasing the goodness of fit of the statistical model. The value of the variance captured by "species" was 0.3625 ($\pm$0.6021). Finally, we tested (3) the effect of species on post-fire survival considering only saplings in burned plots. Models were parameterized by species and environment predictors in the fixed effect, it was not possible to include the interaction between them, due to the scarcity of data. The block factor was used in random effect structure.

For (2) and (3) survival was estimated considering the last pre-fire survival records and the measurements made 2 months after the fire. We used a Tukey contrast test to pairwise compare survival means between environments, species, and fire. All the

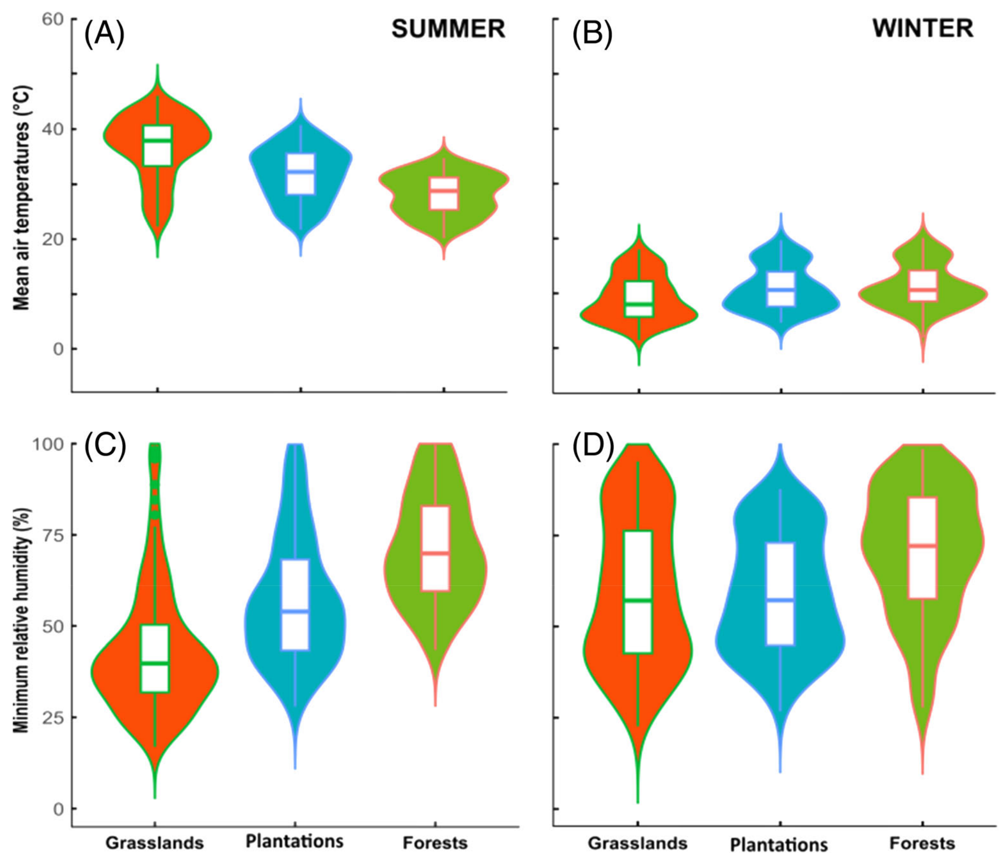

Figure 2. Air temperature (°C) and relative air humidity (%) recorded during the summer (left) and winter (right) grouped by environment (treatment): grasslands (orange), plantations (light blue) and forests (green), in Argentinean humid Chaco. box plot shows distributions of individual data, median, first quartile below the median, and third quartile above it.

analyses were conducted in R v.3.6.0 (R Core Team 2019). We used the package lme4 (Bates et al. 2014), car (Fox & Weisberg 2019), and lsmeans (Lenth 2016) to estimate the means and confidence intervals.

Results

Microclimatic Conditions

Air temperature varied among environments (Fig. 2). In summer, during the hottest hours, forests showed the lowest temperatures ($p < 0.001$) whereas temperatures in plantations were intermediate ($p < 0.001$) and in grasslands, they showed the highest values ($p < 0.001$) sometimes reaching more than 40°C (Fig. 2A). In relation to the minimum relative humidity, the three environments also showed differences (Fig. 2C): forests showed the highest ($p < 0.001$), plantations intermediate ($p < 0.001$), and grasslands the lowest values ($p < 0.001$). In winter, during the coldest hours, the temperature was lower in grasslands than in plantations and forests ($p < 0.01$), with no differences between the last two (Fig. 2B). The minimum relative humidity was higher than 50% in the three environments. There was no difference between grasslands and plantations, but in forests it was 10% higher ($p < 0.001$; Fig. 2D).

Pre-Fire Sapling Survival

After 11 months, the effect of the environment on sapling survival was species-specific ($\chi^2_{(8)} = 27$, $p < 0.001$; Fig. 3). Two of the five species (the high-light demanding *Enterolobium contortisiliquum* and *Schinopsis balansae*) did not show differences in survival between the three environments; two other species (the shade-tolerant *Gleditsia amorphoides*: $p < 0.01$; and the mid-shade tolerant *Peltophorum dubium:* $p < 0.05$) survived more in forests than in grasslands and showed intermediate values in plantations. The last shade-tolerant species included in our study, *Handroanthus heptaphyllus*, showed lower survival in plantations than in grasslands and forests ($p < 0.05$).

As observed for survival, after 11 months the effect of environment on sapling growth was also species-specific ($\chi^2_{(8)} = 39.6$, $p < 0.001$; Fig. 4). Two of the five species (*E. contortisiliquum* and *P. dubium*) showed higher growth rates in grasslands and plantations than in forests ($p < 0.05$). The other three species (*S. balansae*, *H. heptaphyllus*, and *G. amorphoides*) showed similar growth rates between the three environments ($p < 0.05$).

Fire Frequency and Burn Severity

The fire frequency (Fi) observed during the 2 years study was higher in plantations, where all the plots burned (Fi = 2). Grasslands plots suffered an intermediate frequency with three of the four plots burned (Fi = 1.5), and Forest plots experienced no fire events (Fi = 0) (Table 2). On the other hand, burn severity tended to be higher in plantations where three of the four burned plots experienced at least moderate severity, than in grasslands where two of the three burned plots showed low severity (Table 2). Moreover, the burn severity classification in the study area along the fire seasons on 2017 and 2018 showed that the environment that experienced high severity burnings were

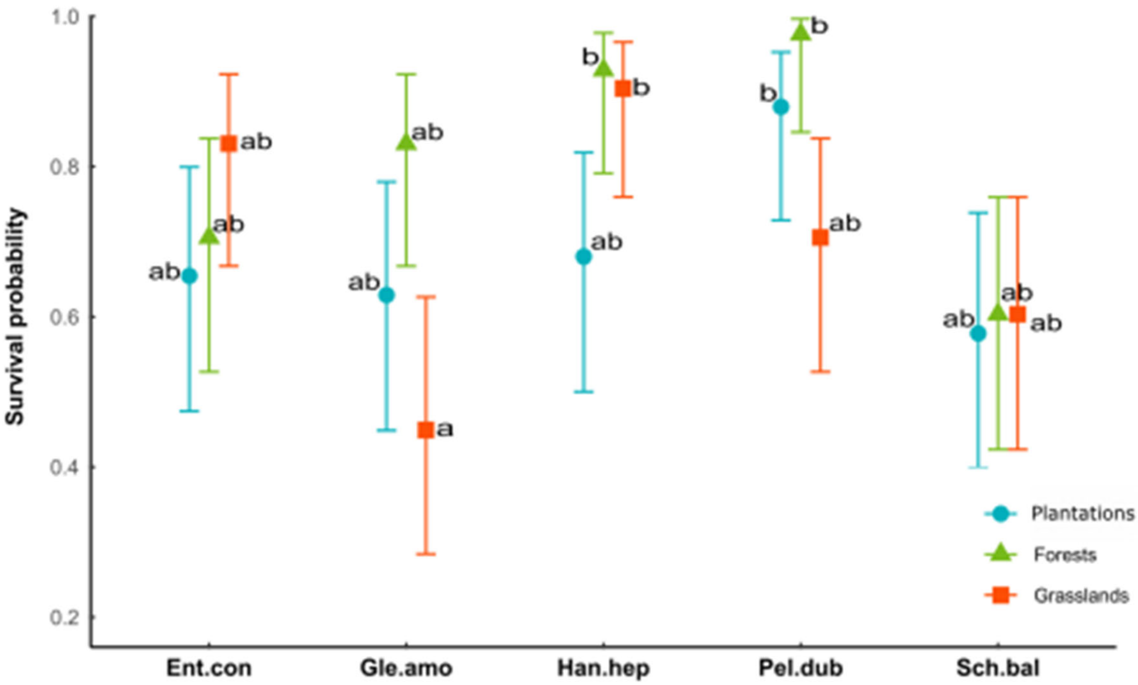

Figure 3. Sapling survival probabilities (estimated means and ± 95% CI) of five tree species in grasslands, plantations, and forests after 11 months of growth in Argentinean Humid Chaco. The species are *Enterolobium contortisiliquum* (Ent.con), *Gleditsia amorphoides* (Gle.amo), *Handroanthus heptaphyllus* (Han.hep), *Peltophorum dubium* (Pel.dub) and *Schinopsis balansae* (Sch.bal). Different letters indicate statistical differences ($p < 0.05$).

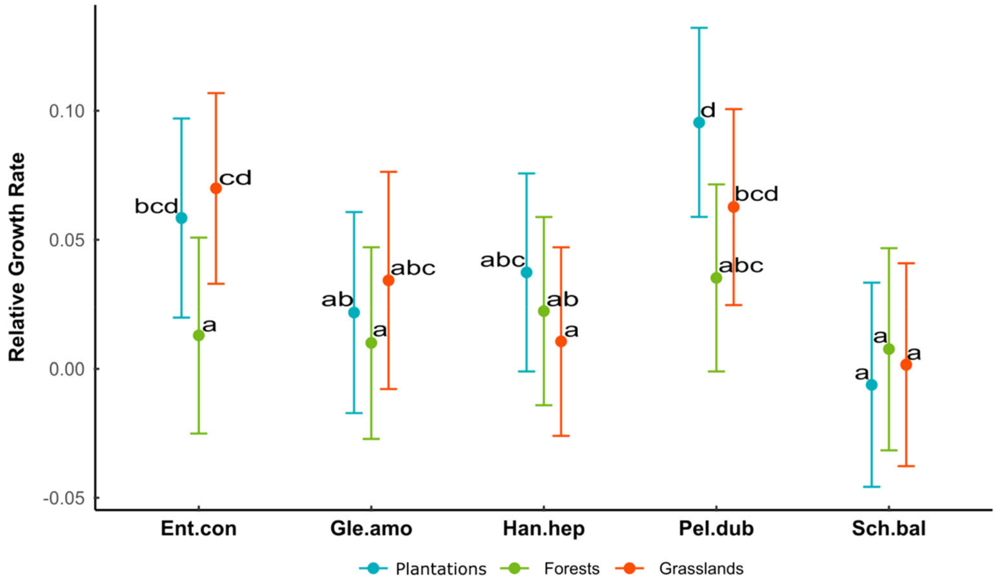

Figure 4. Relative growth rates (dimensionless variable mm/mm, estimated means and ± 95% CI) of saplings stem diameter for 11 months for five tree species planted in grasslands, plantations, and forests in Argentinean Humid Chaco. See Figure 3 for species abbreviations. Different letters indicate statistical differences ($p < 0.05$).

Table 2. Burn severity and fire frequency (Fii), and total percentage of burnings of each environment under study, during the time the work lasted (2017–2018).

Study plots	*Environment*	*Burn severity in 2017*	*Burn severity in 2018*
Fi in grasslands: 1.5; percentage of burning 75%			
Plot 1	Grasslands	Not burned	Not burned
Plot 2	Grasslands	Low	Not burned
Plot 3	Grasslands	Not burned	Moderate–high
Plot 4	Grasslands	Low	Not burned
Fi in plantations: 2; percentage of burning 100%			
Plot 5	Plantations	Not burned	Moderate–high
Plot 6	Plantations	Low	Not burned
Plot 7	Plantations	Moderate	Not burned
Plot 8	Plantations	Moderate	Not burned
Fi in forests: 0; percentage of burning 0%			
Plot 9	Forests	Not burned	Not burned
Plot 10	Forests	Not burned	Not burned
Plot 11	Forests	Not burned	Not burned
Plot 12	Forests	Not burned	Not burned

plantations and grasslands, despite some areas had moderate severity, mainly showed a low burn severity (Fig. 5).

Fire Effect on Sapling Survival

In plantations, fire reduced average sapling survival by more than 80%, being higher than 90% in unburned plots and less than 20% in the burned ones ($p = 0.007$; Fig. 6). By contrast, in grasslands average survival was low and similar between burned and unburned plots ($p = 0.517$; <50%; Fig. 6). Moreover, saplings in unburned grasslands showed a high variation in survival as it changed widely between species (Fig. S1). In burned plots, there were no differences in sapling survival between environments ($p = 0.360$; Fig. 6).

Finally, post-fire sapling survival was species-specific ($\chi^2_{(4)} = 11.61$, $p < 0.05$). *Handroanthus heptaphyllus* was the species that showed the highest post-fire survival and *G. amorphoides* the lowest. The other three species showed intermediate survival probabilities (Fig. 7).

Discussion

Our study shows that although eucalypt plantations can provide a suitable environment for native woody sapling recruitment in the Humid Chaco, that benefit for forest restoration is lost when they burn. For most of the species under study, the plantations showed a survival probability as high as forests and a high growth rate, similar to grasslands. Fire decreased survival for

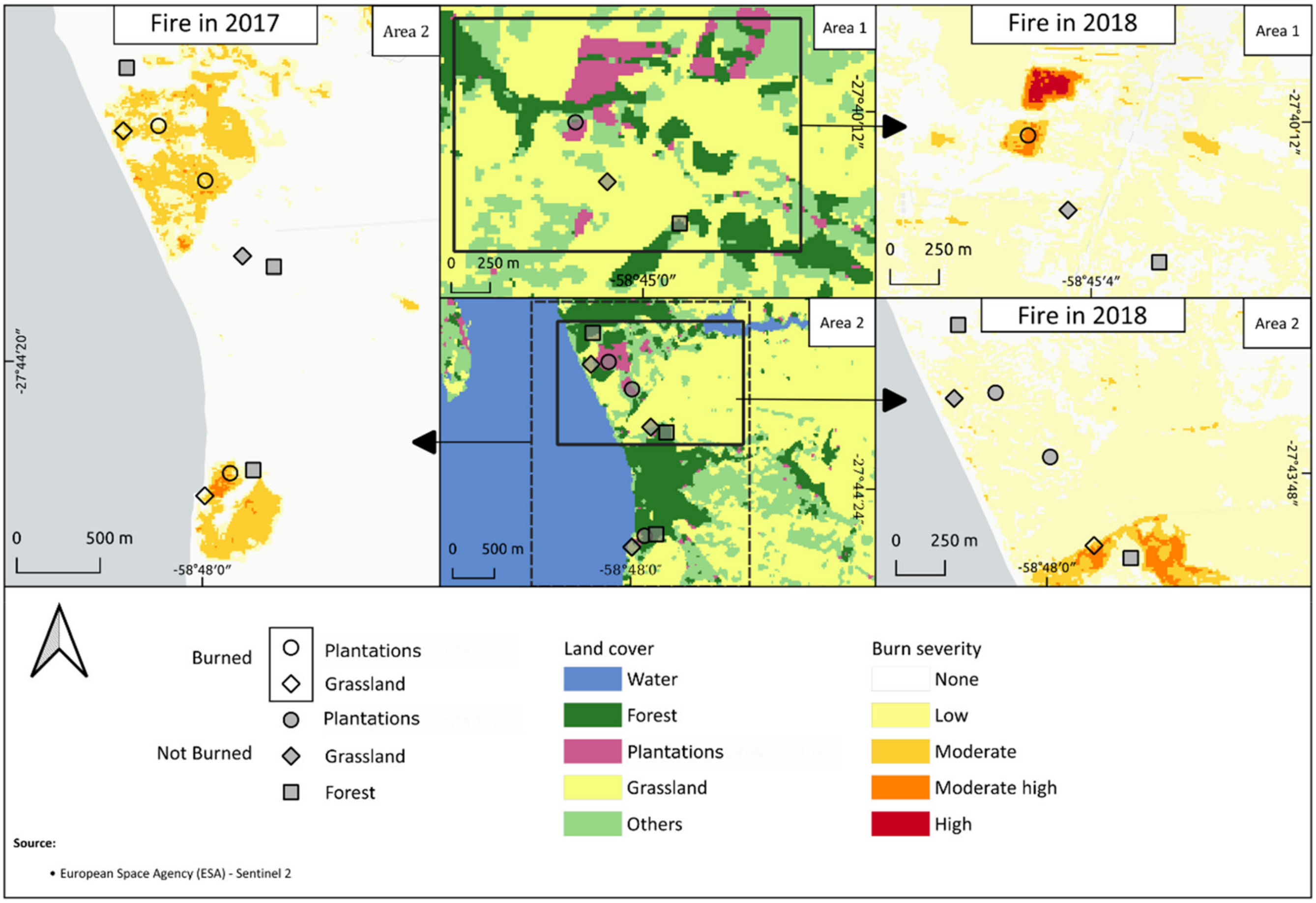

Figure 5. Burned area and estimated fire severities in the study plots in 2017 and 2018 in the study area in Humid Chaco region, Corrientes Province, Argentina. Middle panel shows the land cover of two burn areas (area 1 and area 2) of the experimental plots. Left and right panels show burn severity in 2017 and 2018, respectively. Rhombuses, circles and squares indicate experimental plots located under different environments (grasslands, plantations, and forests, respectively), burned and not burned during the study period.

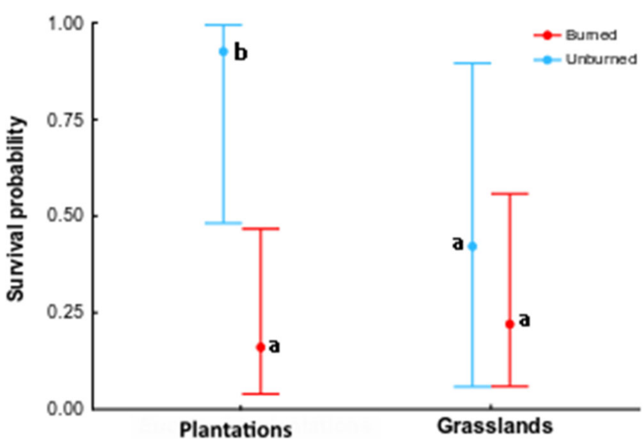

Figure 6. Fire effects (estimated means and ± 95% CI) on planted sapling survival in grasslands and plantations in Argentinean Humid Chaco ($\chi^2_{(1)} = 17.32$, $p < 0.001$). Survivors included both plants that were not top-killed by fires and those that resprouted. Different letters indicate statistical differences ($p < 0.05$).

most of the studied species, but the effect was species-specific. Our results suggest that in a fire-prone ecosystem as the Humid Chaco, eucalypt plantations can be allies for forest restoration but fires should be excluded. During our study, forest patches never burnt indicating that fire avoidance would be possible in the area.

Several studies show that tree plantations can provide a nurse effect and may be an effective instrument in the rehabilitation of degraded sites, catalyzing the restoration of native vegetation under their canopies (Geldenhuys 1997; Parrotta et al. 1997; Feyera 1998). As we expected, eucalypts exerted a nurse effect on tree sapling development in the Humid Chaco. Under their canopy, extreme environmental conditions observed in grasslands, such as temperatures above 40°C, were attenuated. Before the fires, sapling survival was high and similar between forest and plantations, which also experienced similar microclimatic conditions, compared with grasslands. Although shade limits plant growth, it can also be beneficial in hot environments reducing leaf temperatures, transpiration, and photoinhibition. The canopy of eucalypts is dense enough to reduce the excess

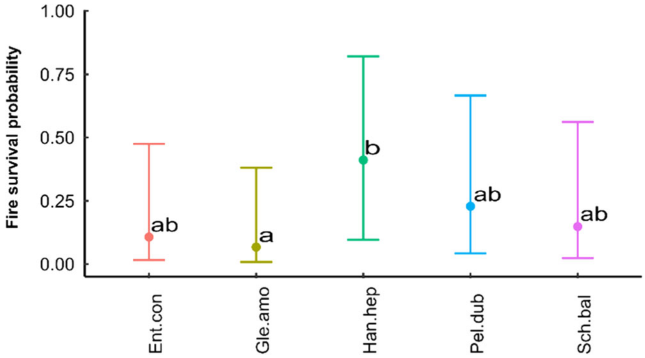

Figure 7. Post-fire survival probabilities (mean ± 95% CI) of planted saplings of five native tree species in Argentinean Humid Chaco. Plants considered to have "survived" either were not top-killed or resprouted. See Figure 3 for species references. Different letters indicate significant differences ($p < 0.05$).

of solar radiation during the sapling establishment stage contributing to their high survival and growth rates (Sakai et al. 2009). So, higher survival rates in plantations than in grasslands, but similar to forests, could be influenced by the effect of canopy ameliorating stressful environmental conditions. But also, reduced belowground competition with grasses could explain this high sapling survival in plantations. Sapling survival in grasslands can be reduced because their root systems explore the same soil layer than grasses, which develop high density root systems (Pärtel & Wilson 2002). On the other hand, a higher growth in plantations than in forests, and similar to grasslands, could be related with higher radiation levels reaching saplings because of a more open canopy in plantations compared with forests (Calviño-Cancela et al. 2012).

The fire frequency and burn severity recorded in this study were high and similar to that of fire-prone eucalypt savannas of Australia (Russell-Smith et al. 2020). We observed that fire affected grasslands, plantations, and forests differentially, although more extensive studies are needed to establish the fire regime of these environments in the Humid Chaco. Fires spread in grasslands and reached neighboring plantations, resulting in a higher severity. The type of the most abundant fuel biomass in each environment would explain the different fire severity. The calorific value of the grasslands under study is 3,920 kcal/kg compared with 4,790 kcal/kg of the plantations (Quirino et al. 2005; Kunst 2011). On the contrary, during our 2-year study period, fires were not observed entering natural forests. Local people express that fires never cross the forest edge because the bromeliad species *Aechmea distichantha* in the understory could play an important role as "firewalls." This bromeliad forms dense colonies in the understory and forest edges of *Schinopsis balansae* forests in the Chaco region (Lewis et al. 1997; Barberis & Lewis 2005). As it is a tank-formed plant that storages water (Benzing 2000), its fleshy leaves arranged in a very dense rosette (Cavallero et al. 2009), it is likely to have a role suppressing the passage of fire into forest patches. However, as these plants are spiny and not palatable, they are usually removed from cattle ranching areas (Delvalle et al. 2012) and are not present between grasslands and plantations. On the other hand, no practices are actively implemented to prevent fire spread into plantations in small farms beyond preventive burns to decrease fuel biomass (Toppazzini et al. 2013). Thus, the absence of natural barriers and protective measures may allow fires to spread from grasslands into plantation understories.

Despite burn severity was different between burned environments, survival was very low in all the burned sites. An explanation could be that, as the sapling stage is the more susceptible to fires (Kunst et al. 2003), the lowest burn severity was high enough to top-kill most of them; and as we used the same species in both environments, fires affected them similarly. But, some species tended to survive more by resprouting after the fire event, indicating that the survival probability could be species-specific. This species-specific response can be related to the species ability to allocate resources, as non-structural carbohydrates, belowground (Clarke & Knox 2009) which allow them to overcome periods of negative net carbon balance, that is when suddenly shaded (Myers & Kitajima 2007). Carbon investment in storage organs is an advantageous strategy in habitats with frequent stress and disturbance (Iwasa & Kubo 1997). In this context, shade-tolerant plants could be better resprouters, but with only five species it was not possible to test this idea in our study. A more extended study considering more species is necessary to know if this response can be related with other species functional attributes.

In the anthropogenic grassland–forest transition system of the Argentinean Humid Chaco where fire plays a predominant role (Kunst 2011), eucalypt plantations would not be a way to catalyze and facilitate the restoration of forests as long as fire use in the area is uncontrolled or plantations are unprotected against fire. Our study suggests that these plantations tend to experience the same fire occurrence as the surrounding grasslands, however longer and extensive studies are needed. A possible alternative could be to experience with *Aechmea* spp. curtains. Also, the use of some native tree species as *Handroanthus heptaphyllus* and *Peltophorum dubium* could increase survival probabilities of planted saplings if fire occurs. The literature highly recommends using *Enterolobium contortisiliquum* in restoration projects (Max et al. 2004; Lacerda & Figueiredo 2009; Marcuzzo et al. 2020) but it was one of the species with the lowest post-fire performance. This two-year study has allowed determining that fire may be the main constraint for woody sapling recruitment in plantations in the region. Our study on burn severity is innovative and shows a high sensitivity detecting differences at small spatial scales, so it may become a new standard for future studies. However, as it is the first time it is implemented, it should be used carefully until more extensive studies validate it. In order to promote its application, we provide the GEE codes in the supplementary information.

Restoration interventions, in eucalypt plantations, grasslands, or any other human-modified environment will likely fail if restoration sites are not protected from human-mediated disturbances. Although this work provides evidence about eucalypt plantations as nurses for forest restoration in the Humid Chaco, conserving the mosaic-like forest-grassland habitats where different plant communities coexist, deserves special attention

(Veldman et al. 2015; László et al. 2018). The results of this work should be carefully implemented and be used only where specific needs of forest restoration are identified, as in degraded forests or reduced forest remnants, or for enhancing forest corridors or riparian forests.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Light requirement and ecological description of tree species under study.
Figure S1. Sapling mortality probability (estimated means and 95% CI) one month after transplanting in different environments (Grasslands, Plantations, and Forests) in Argentinean Humid Chaco.
Figure S2. Sapling survival in burned and unburned sites of environments that experienced fires (Plantations and Grasslands) for five native tree species of Argentinean Humid Chaco.
Supplement S1. Additional information about saplings' transplantation.
Supplement S2. Extra information about NBR calculations

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