

# Plant size dependent response of native tree regeneration to landscape and stand variables in loblolly pine plantations in the Atlantic Forest, Argentina

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## ABSTRACT

The interest in the conservation of biodiversity in productive ecosystems has increased considerably in recent years due to the continuing loss of natural vegetation. The effect of forest plantations on biodiversity is currently a relevant research topic since they are expanding worldwide. Native understory vegetation may maintain ecosystem processes and increase the availability of habitats, food and other resources for different animal groups. Native tree regeneration in plantations is affected by the planted species, stand age and density, and silvicultural practices, among others. Despite that some general trends have been identified, results from different studies are not always comparable, partially because not all sources of variation were considered simultaneously, the size of plants is different between studies, no different classes of plant sizes are compared, or the local flora determines specific responses to landscape and stand variables. In this work, we analyzed the relationship between native tree density, species richness and species composition in the understory of forest plantations and stand characteristics including stand age and density, canopy openness, proximity to native forests remnants and pre-planting land use history. The study was conducted in monoculture plantations of *Pinus taeda* in Misiones Province, Northeastern Argentina. In 35 stands, we estimated plant density and species richness for three plant size classes: seedlings (> 50 cm height and < 1 cm in diameter at breast height (DBH)), saplings (1–5 cm DBH) and small trees (5–10 cm DBH). Our results are in agreement with general trends previously reported in the study area and worldwide. We found that native trees in the plantations showed a strongly size-dependent response to stand and landscape variables. The composition and richness of the seedlings were primarily dependent on the native forest cover at a landscape scale while the species composition, richness, and density of saplings and small trees were mainly affected by stand age and density. Our results showed that the management of pine plantations should maintain the rotation for more than 20 years, a basal area below 30 m<sup>2</sup>·ha<sup>-1</sup> and a 25–30% of native forest cover at the landscape scale to increase the richness and density of the native trees in loblolly pine plantations of the Atlantic Forest.

## 1. Introduction

The interest in the conservation of biodiversity in productive ecosystems has increased considerably in recent years due to the continuing loss of natural vegetation and habitat reduction for animal and plant species (Estades et al., 2012; Simonetti et al., 2013). The effect of forest plantations on biodiversity is currently a relevant research topic since they are expanding worldwide. Biodiversity tends to increase when forest plantations are set in degraded environments (Hartmann et al., 2010; Lugo, 1997; Stephens and Wagner, 2007), but a clear loss

of biodiversity is observed when plantations replace native forests (Zurita, 2008). However, many native plant species can regenerate in tree plantations, leading to the formation of a diverse understory (Geldenhuys, 1997; Keenan et al., 1997; Lugo, 1997).

Native understory vegetation may maintain ecosystem processes and increase the availability of habitats, food and other resources for different animal groups. Therefore, plantations can act as corridors, rather than barriers, improving landscape connectivity, animal movement, and plant dispersion (Lindenmayer et al., 2003). Moreover, plant species contribute to the maintenance of a diverse soil biota enhancing

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the productivity in the long-term (De Deyn et al., 2008). In landscapes dominated by forest plantations, stands of different ages form a dynamic mosaic in which young stands increase their structural complexity until harvested. Improving understory density and diversity promotes an increase in the provision of ecological services throughout the growing cycle (Lindenmayer et al., 2003; Stephens and Wagner, 2007).

Previous studies worldwide showed that native tree regeneration in plantations is affected by the planted species, stand age and density, and silvicultural practices, among others. It has been observed an increase in regenerating native trees density and species richness with stand age (Geldenhuys, 1997; Keenan et al., 1997) as a consequence of increased chance for arrival, establishment and growth as well as due to changes in plantation structure. Habitat permeability for seed dispersers is higher in older than in younger stands (Vespa et al., 2014) which increase seed arrival. In addition, as a consequence of tree growth and silvicultural practices, there are changes in stand structure that strongly influence the understory structure throughout the growing cycle (Aubin et al., 2008; Dummel and Pinazo, 2013; Otto et al., 2012; Seiwa et al., 2012; Senbeta et al., 2002). Old stands show a higher species richness of native trees in the understory (Dummel and Pinazo, 2013; Onaindia and Mitxelena, 2009; Wang et al., 2004), and tend to be more similar to the surrounding native vegetation (Norton, 1998) than younger plantations. A reduction in the stand density planting density usually favors the understory development (Dummel and Pinazo, 2013; Onaindia and Mitxelena, 2009; Wang et al., 2004). At a similar age, stands with lower tree density exhibit a higher species richness than plantations stands with higher tree densities (Loumeto and Huttel, 1997; Seiwa et al., 2012).

Thinning affects the development of the understory by increasing the availability of resources as well as acting as a mechanical disturbance. Thinning can increase light availability and promote other environmental changes associated with the reduction in basal area (Arealo and Fernandez-Palacios, 2008; Trentini et al., 2017; Utsugi et al., 2006). The mechanical damage associated with thinning can also have a counteracting effect by increasing the mortality of native seedlings and saplings. The responses of tree species to the environmental changes promoted by thinning or tree growth throughout the growing cycle depend on plant size. Recruitment, growth and mortality rates are size-specific due to ontogenetic changes between life stages as well as different conditions of light availability associated with a vertical gradient (Brokaw and Busing, 2000; Lusk, 2004; Metcalf et al., 2009).

Land use history and landscape structure also affect the density and diversity of the native trees established in plantations. An intensive land-use history may result in plantations with a low seed bank expression and a low regrowth (Gachet et al., 2007). In these cases, the regeneration of understory plants is highly dependent on dispersion processes (Senbeta and Demel, 2001), so the presence of seed sources in the environment becomes essential (Ito et al., 2004). Management at the landscape scale should maintain or create a suitable configuration of native forest remnants to ensure the arrival of seeds to the understory of the plantations (Koh et al., 2015; Onaindia and Mitxelena, 2009). Also, maintaining the connectivity of forest remnants is extremely important to reduce degradation. Reduced seed dispersal has been recognized as an important mechanism for degradation of forest remnants, in the Atlantic Forest in Brazil (Cramer et al., 2007; Tabarelli et al., 2004).

Despite these general trends are recognized, results from different studies are not always comparable. This might be because not all sources of variation are simultaneously considered, for example, different plant sizes between studies, the different plant size classes were not compared, or because the local flora determined specific responses to landscape and stand variables. Thus, further local studies are needed to obtain specific information on silvicultural management and increase our general knowledge about plantations and biodiversity.

The subtropical forests in northeastern (NE) Argentina correspond

to the southern portion of the Atlantic Forest extending along the Atlantic coast of Brazil and southeastern Paraguay. Approximately 93% of the original cover of the Atlantic Forest has been lost due to human activities. During the last three decades, the area of forest plantations in Argentina, mostly of *Pinus taeda*, had a five-fold increase (Izquierdo and Clark, 2012). Specific information is undoubtedly needed to optimize a cost-benefit relationship for adopting management decisions. In this work, we analyzed the relationship between the species composition, richness, and abundance of native trees in the understory and stand characteristics including stand age and density, canopy openness, proximity to native forests remnants and pre-planting land use history. We expect that (1) aging will have a positive effect at lower stand densities and close proximity to native forests, (2) the intense land use history and the proximity to the native forest will affect the composition of tree species by influencing the species establishment differentially from the soil propagule bank or through seed dispersal, and (3) factors related to the soil propagule bank and to seed dispersal (i.e., land use history and proximity to the native forest) will more strongly affect small plants while those related to growth conditions (i.e., stand density and canopy openness) will affect especially larger plants.

## 2. Materials and methods

### 2.1. Study area

The study was conducted in monoculture plantations of *Pinus taeda* belonging to small and medium forest companies with distinctive management conditions, land use history and site quality, located in Misiones Province, Northeastern Argentina (Fig. 1). Thirty-five stands of different age and plantation density were selected for sampling. The pine plantations were located mainly on red soils (Ultisols, Kandudults) (Soil Survey Staff, 1992) and corresponded to the first, second or third production cycle on lands from both agricultural crops and native forest clearcuts. The annual rainfall in the study area is about 2000 mm, evenly distributed throughout the year, and an average annual temperature of 21.8 °C with a monthly mean amplitude of approximately 10.8 °C (Cabrerá, 1976).

### 2.2. Sampling design

In each stand, we established one sampling unit which consisted of four circular plots located in the corners of a 30 m side square. Circular plots of different areas were used for trees (300 m<sup>2</sup>), saplings (100 m<sup>2</sup>) and seedlings (25 m<sup>2</sup>). Sampling units were established at least 20 m far from the stand edge. The center of each plot was georeferenced using a global positioning system (GPS). The geographical coordinates were projected into plane coordinates for spatial analysis.

### 2.3. Tree regeneration

We estimated the species richness and density of three size classes: seedlings (> 50 cm height and < 1 cm in diameter at breast height (DBH)), saplings (1–5 cm DBH) and small trees (5–10 cm DBH). We considered trees those greater than 10 cm DBH at adult stage.

### 2.4. Canopy cover and stand structure

In the center of each circular plot, we took a hemispheric photo at 1.3 m height using a Nikon Coolpix 950 camera with a Nikkor 8 mm lens on a self-level platform (Delta-T Devices, Cambridge, UK). Photos were analyzed with the software Gap Light Analyzer to estimate: a) the fraction of total solar radiation transmitted (FRT, %), b) the canopy openness (CO, %), and c) the leaf area index (LAI). The diameter at breast height (DBH) of the *Pinus taeda* trees was measured in each of the 300 m<sup>2</sup> plot and the stand basal area (BA), density (individuals per hectare) and mean quadratic diameter of pines (pmqd) was calculated.

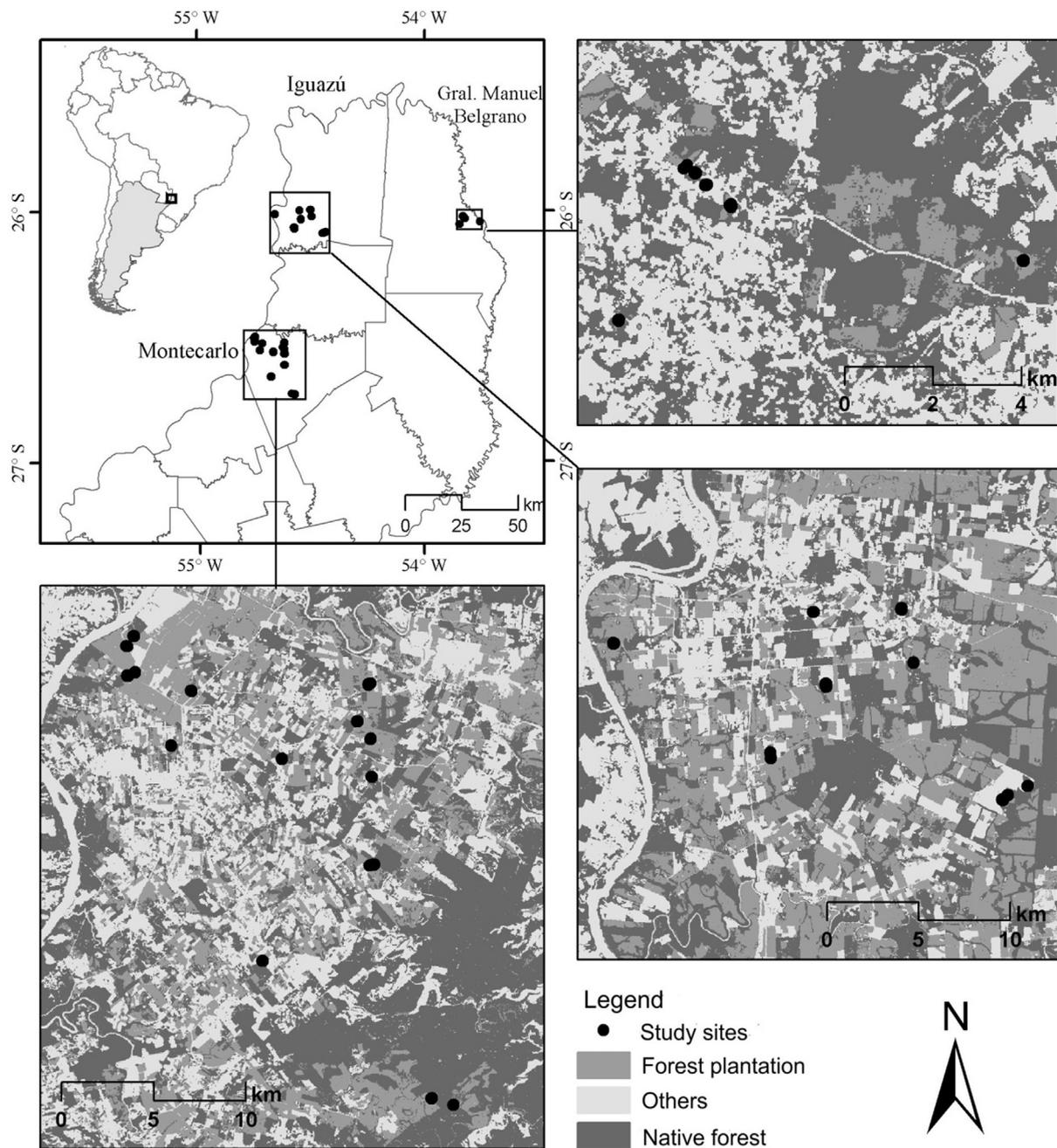


Fig. 1. Location of the study sites and land use/cover classes in Misiones Province, Northeastern Argentina.

### 2.5. Land use history and native forest remnants

The type of land use history or vegetation cover before plantation establishment was also assessed. Three land use categories were identified: agriculture, forestry and native forest. Data were reported by property owners and corroborated by Landsat images but the date of the beginning of land use changes was not determined. At the landscape scale, the influence of remnant forests on sapling density and richness was studied. The Landsat satellite image was classified using a supervised procedure (Richards and Jia, 1999) and then converted from raster to vector format to calculate the area of native forest (aNF) within a radius of 150, 300, 600, 1200, and 2400 m from the central sampling point of each stand (Koh et al., 2015). In addition, the distance from the center point of each plantation to the nearest patch of native forest (dNF) was calculated. This procedure was performed considering different neighboring native forest patches of 1, 2, 5, 10,

25, 50, 100 and 300 ha of minimum size (Lion et al., 2014).

### 2.6. Data analyses

Multiple linear regressions were performed to study the relationship between plant density and species richness using variables of stand (AGE, BA, density, pmqd, FRT %, CO %, LAI) and landscape (aNF, dNF), and land-use history. Because available sampling sites did not follow a balanced combination of the effects that we were evaluating, we used exploratory analysis to avoid spurious results as recommended by Zuur et al. (2010). Automatic procedures were not used for model selection due to the high rates of type I error that its application entails when a large number of variables are considered (Mundry and Nunn, 2009). Therefore, we made a selection of variables based on descriptive procedures and guided by theoretical assumptions related to the problem and the hypothesis to be tested. Firstly, stand level variables (BA, age,

**Table 1**

Multiple regressions for species richness (R) and native trees density (D) on stand variables, landscape variables and previous land use/cover in *Pinus taeda* plantations in Misiones, Argentina. AGE: stand age, BA: pine basal area, MSD pine mean square diameter (cm). TTR%: total transmitted radiation (%). CO%: canopy openness (%). LAI: leaf area index, NF 300: native forest cover in a 300 m radius circular area around each sample unit, NP: distance to the nearest patch of native forest. F PLU: forestry as previous land cover. NF PLU: native forest as previous land cover (UPF and UPNF were compared to agricultural as previous land use). \*\*\*:  $P < 0.001$ , \*\*:  $P < 0.01$ , \*:  $P < 0.05$ , .:  $P < 0.1$ , NS: not significant.

Models	Independent variables	Dependent variables					
		D seedlings	R seedlings	D saplings	R saplings	D small trees	R small trees
Only stand variables	AGE	-0.29	0.83	6.53***	6.13***	9.50***	12.49***
	BA	-0.27	0.36	-3.17**	-2.24*	-1.94.	-1.08
	Pine density	NS	NS	NS	NS	NS	NS
	MSD	NS	NS	NS	NS	NS	NS
	FRT %	NS	NS	NS	NS	NS	NS
	CO %	NS	NS	NS	NS	NS	NS
	LAI	NS	NS	NS	NS	NS	NS
	R <sup>2</sup>	-0.05	-0.02	0.55***	0.51***	0.72***	0.82***
Stand + landscape variables	AGE	0.25	1.71.	6.32***	6.23***	10.31***	13.58***
	BA	-1.13	-0.97	-3.01**	-2.53*	-2.87**	-2.18*
	aNF	1.90.	2.86**	0.51	1.16	2.25*	2.46*
	dNF	NS	NS	NS	NS	NS	NS
	R <sup>2</sup>	0.02	0.16*	0.54***	0.51***	0.75***	0.85***
	Stand + landscape variables + land use	AGE	-0.02	1.89.	5.44***	5.54***	8.73***
BA		-1.08	-0.85	-2.90**	-2.48*	-3.02**	-2.27*
aNF		1.76.	3.28**	0.51	1.28	1.61	2.019.
UPF		0.53	1.90.	0.54	1.32	-0.99	-0.1
UPNF		1.06	0.81	0.81	1.59	1.16	1.93.
R2		-0.001	0.20*	0.52***	0.53***	0.76***	0.86***

pmqd, % FRT, % CO, LAI) were considered, and those that were significant or whose effect was of interest to test were retained. In case of collinearity, variables with a higher “t” value were retained in the model. Once variables related to stand structure were selected, landscape variables were considered. Two different approaches were used: the effect of the area of native forest at different distances from the sampling unit (aNF) (Koh et al., 2015), and the distance to the closest native forest patches with different areas (dBN). These variables were incorporated separately into the model containing the stand level variables previously selected and the species richness as the dependent variable for each plant size class (seedlings, saplings, and small trees). The “t” value that reflected the contribution of the variable (aBN or dBN) in the respective models, was used as criteria for selecting the most appropriate radius or patch size when calculating aBN and dBN. The selection was done by plotting the “t” value in the respective models against radius or patch size. Radius used in the final models were those that for different size classes showed values close to the significance level of the variable within the model. When the contribution of the different radius was similar, values closest to the distances in which dispersion processes begin to be limiting (i.e., 150–300 m according to Hewitt and Kellman, 2002) were prioritized. Similarly, we plotted “t” values representing the contribution of the distance to the nearest native forest patch against patch size (area). For similar contributions, we retained the patch size for which fewer forest patches were the same nearest neighbor of different forest plantation stands. This lack of independence was observed when increasing the minimum patch size. The effect of land use history was included in the model together with the landscape effect. Different values were assigned to different land uses or land covers after plantation establishment: 0 = agriculture, 1 = pine plantation and 2 = native forest. Agriculture was then used as the reference group against which the other levels were compared. After model fitting, plots of predicted vs. observed values were used to visually evaluate the linearity of the relationship.

A spatial trend analysis was conducted to investigate the existence of non-random distribution of residues between plant richness and density and the stand and landscape scale variables in the models. A non-random spatial distribution of unexplained variation for these

models might indicate that some positions in the studied region exhibited consistently higher or lower richness or density than predicted. Spatial coordinates (x and y) and its product and square values ( $x, y, x^2, y^2$ ) were used as independent variables to detect spatial linear trends, interactions or maximum values located at intermediate positions in the studied area.

To evaluate the relationship between the species composition and the variables at the stand scale, the landscape scale, and the land use history, we used similar analyses to those performed for the richness and density. A Principal Component Analysis (PCA) was performed based on the covariance matrix calculated from a rectangular matrix of stands  $\times$  species. Species frequencies were calculated on the basis of their presence/absence in the four plots of each sampling unit. Thus, species frequency ranged from 0 to 4, meeting equal units and similar variances required for the PCA. In a previous exploratory analysis, we found a near-linear or monotonic distribution of species frequencies along floristic gradients, which constitutes appropriate data for the PCA (Ter Braak and Prentice, 2004). The first three axes of the PCA were used as different dependent variables in the multiple regression analysis.

Logistic regressions were used to evaluate the effect of the stand scale (stand age and canopy openness) and of the surrounding native forest area, on the number of zoochoric/ non-zoochoric, and anemochoric/ non-anemochoric species.

### 3. Results

The age of the stands ranged between 7 and 54 years. The ranges of pine density and basal area were 242–1567 trees.ha<sup>-1</sup> and 15–43 m<sup>2</sup>.ha<sup>-1</sup>, respectively. A total of 114 species belonging to 36 botanical families (Appendix A) were registered (seedlings: 79, saplings: 93, and small trees: 63 species). The most abundant species were *Lonchocarpus campestris*, *Matayba elaeagnoides*, *Tabernaemontana catharinensis*, *Nectandra lanceolata* and *Trema micrantha*.

The effect of stand variables on native tree density and richness was dependent on plant size. Stand age exhibited a strong positive effect on sapling and small tree density and species richness but only a marginal or null effect on seedlings (Table 1). Sapling and small tree density and

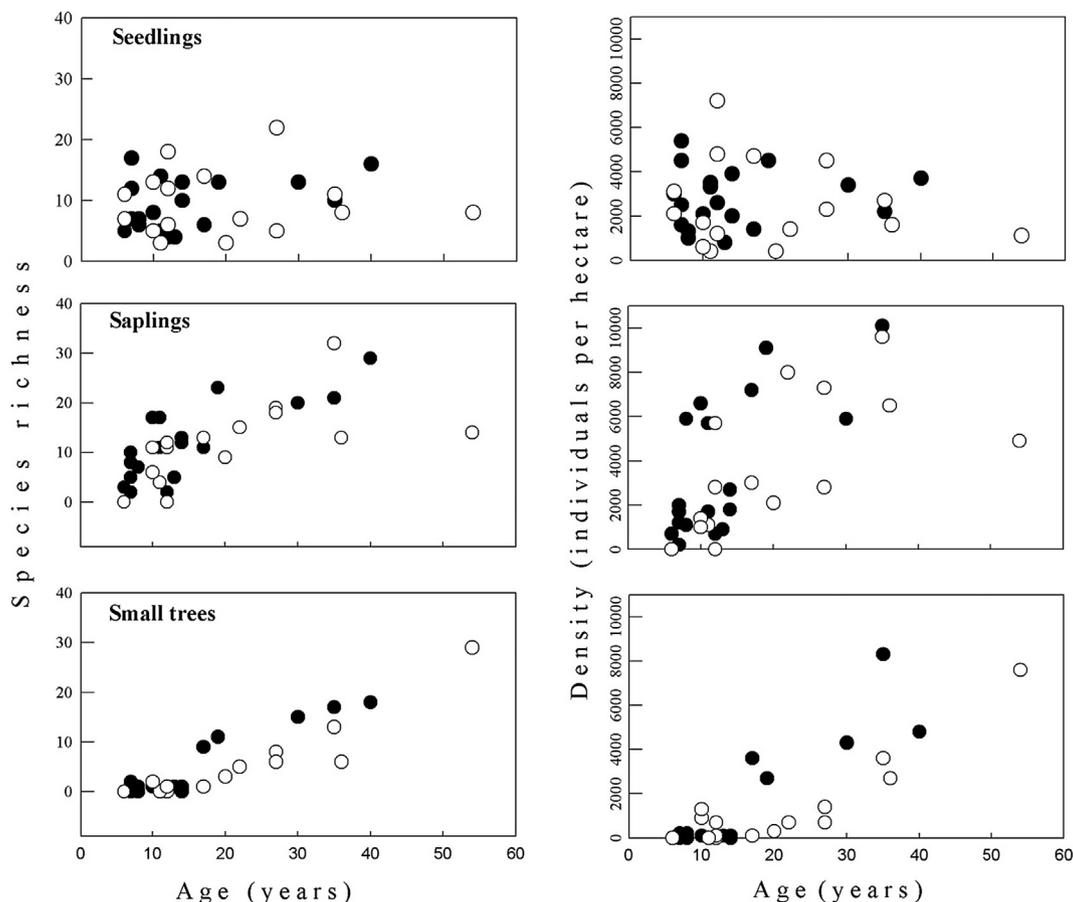


Fig. 2. Species richness (left) and abundance (right) per plant size class as a function of stand age in *Pinus taeda* plantations in the North of Misiones, Argentina. Filled points: plantations with basal lower than  $29 \text{ m}^2 \cdot \text{ha}^{-1}$ , empty points: plantations with a basal area higher than or equal to  $29 \text{ m}^2 \cdot \text{ha}^{-1}$ .

species richness in stands older than 20 years were greater than in younger stands by approximately 2-fold (Fig. 2). Basal area negatively affected sapling and small tree density and richness but had no effect on seedlings. The absolute correlation coefficients between independent variables were below 0.6 except between square mean diameter and density ( $r = -0.77$ ). However, neither of these variables were retained even when they entered separately in the model. In all cases, plots of predicted vs. observed values indicated linearity and no outliers were detected.

The cover of native forests surrounding each sampling unit clearly exhibited a positive effect on seedling richness at every radius although its effect on small tree richness was only evident at a 300 m and 600 m radius (Fig. 3). No effect was found on sapling richness. The negative

effect of the distance to the nearest patch of native forest on seedling richness was significant at every minimum patch size (Fig. 2). A maximum “t” value was observed at 1 ha, and therefore we considered to be an appropriate minimum patch size. This effect was only significant on small tree richness at a minimum patch size of 2 ha. No significant effect of the distance to the nearest patch of native forest was observed on sapling richness.

After the selection of 300 m radius and 1 ha minimum patch size, we included both variables together in models obtained for stand variables. The surrounding native forest cover was retained as a predictor of species richness at the landscape scale since the distance to the nearest native forest patch was not significant. The effect of the surrounding native forest cover was significant only for seedling richness.

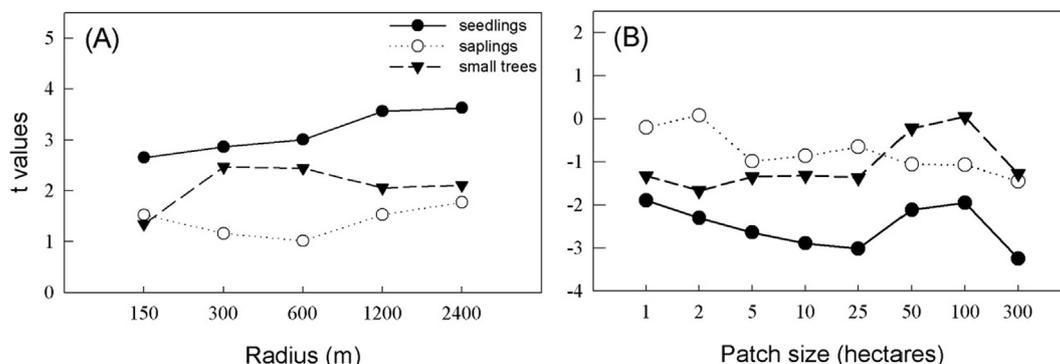


Fig. 3. “t” values from multiple regression models for native forest cover at different radius around sample unit (A), and the distance to different native forest patch size (B), on native tree species richness in *Pinus taeda* plantations in the North of Misiones, Argentina.

**Table 2**

Spatial analysis of the residuals from models for plant density and species richness on stand variables, landscape and previous land use/cover per plant size class in *Pinus taeda* plantations in Misiones, Argentina. Y: latitude, X: longitude. \*\*:  $P < 0.01$ , \*:  $P < 0.05$ , .:  $P < 0.1$ .

Plant size	VD	Ord.	X	Y	x <sup>2</sup>	y <sup>2</sup>	Xy	r <sup>2</sup>	M
Seedlings	Residuals richness	2.2E+5	3.3E-3	-6.55E-2	-2E-9	2.65E-9	3.74E-9	-0.065	0.711
	Residuals density	-6.16E+7	1.1E+1	5.26	-3.44E-7	9.77E-8	-8.95E-7	-0.043	0.616
Saplings	Residuals richness	6.63E+5*	-1.41E-2	-0.172*	-4.85E-9	5.75E-9*	1.22E-8	0.219	0.030
	Residuals density	2.16E+8	-6.28	-54.29	-7.99E-7	2.48E-6*	2.56E-6	5.77E-2	0.248
Small trees	Residuals richness	5.69E+4	4.0E-3	-2.03E-2	-1.31E-9	2.87E-10	2.18E-9	-0.123	0.933
	Residuals density	4.60E+7	-2.45	-1.04E+1	-3.68E-7	1.47E-7	1.12E-6	-0.149	0.987

Residuals from models did not fit to spatial variables in most cases (Table 2). These results indicated that the deviations of the observed values from the predicted richness and density were independent of the spatial location of the stands. Only a weak spatial trend was observed for the model fitted to sapling richness. Stands located in the NW (Fig. 1) exhibited higher richness and density than predicted. Due to the general lack of spatial trends and the weak relationship found for saplings, we accepted spatial independence.

For all three size classes, changes in species composition represented by PCA axis 1 were associated with stand age (Table 3). At the seedling stage, species responded positively or negatively to stand age whereas null or positive responses were observed at sapling and small tree stages (Table 4). The basal area affected the species composition of saplings and small trees while the effect of the surrounding native forest cover was only observed on seedlings. The species composition in stands with native forest as previous land use differed from stands that were subjected to agricultural management.

Logistic regressions indicated that dispersal mode was associated with stand age and canopy openness. The number of zoochoric species increased with increasing stand age ( $z = 2.51$ ,  $P < 0.05$ ) and canopy openness ( $z = 2.33$ ,  $P < 0.05$ ) while an inverse trend was observed for anemochoric species (stand age:  $z = -2.14$ ,  $P < 0.05$ , canopy openness  $z = -2.24$ ,  $P < 0.05$ ). No significant effects of the surrounding native forest cover were found.

**Table 3**

Multiple regressions of principal components (pc) on stand variables, landscape and previous land use/cover per plant size class in *Pinus taeda* plantations in Misiones, Argentina. Age: stand age (years). AB: pine basal area ( $m^2 \cdot ha^{-1}$ ). Density: pine density ( $ind \cdot ha^{-1}$ ). DCM: pine mean square diameter (cm). TTR%: total transmitted radiation (%). CO%: canopy openness (%). LAI: leaf area index. NF 300: native forest cover in a 300 m radius circular area around each sample unit. dNF: distance to the nearest native forest patch. UPF: forestry as previous land use. UPNF: native forest as previous land use. \*\*:  $P < 0.01$ , \*:  $P < 0.05$ , .:  $P < 0.1$ , NS: not significant.

Models	Independents variables	Dependents variables								
		Seedlings			Saplings			Small trees		
		pc 1	pc 2	pc3	pc1	pc 2	pc 3	pc 1	pc 2	pc 3
Only stand variables	AGE	0.003	-0.001	0.002	0.01***	-0.001	-0.003	0.001***	0.003	-0.0001
	BA	0.005	-0.004	0.004	-0.01**	0.006	-0.0005	-0.003	-0.01*	-0.004
	Density	NS	NS	NS	NS	NS	NS	NS	NS	NS
	DCM	NS	NS	NS	NS	NS	NS	NS	NS	NS
	TTR%	NS	NS	NS	NS	NS	NS	NS	NS	NS
	CO%	NS	NS	NS	NS	NS	NS	NS	NS	NS
	SLA	NS	NS	NS	NS	NS	NS	NS	NS	NS
Stand + landscape variables	R <sup>2</sup>	0.05	-0.03	-0.01	0.48	-0.02	-0.01	0.69	0.1	-0.04
	AGE	0.003	-0.004	0.001	0.01***	-0.001	-0.003	0.01***	0.004	0.0009
	BA	0.005	0.005	0.005	-0.01*	0.005	0.0006	-0.005	-0.01*	-0.007
	aNF	-0.01	-0.68**	-0.1	0.06	0.03	-0.07	0.16	0.09	0.19
	dBN	NS	NS	NS	NS	NS	NS	NS	NS	NS
	R2	0.02	0.24	-0.03	0.46	-0.05	-0.04	0.71	0.08	-0.04
	AGE	0.006*	-0.003	0.0005	0.01***	-0.003	-0.002	0.01***	0.004	0.003
Stand + landscape variables + land use	BA	0.005	0.005	0.005	-0.01*	0.005	0.0008	-0.005	-0.01*	-0.007
	aNF	0.06	-0.6**	-0.17	0.03	0.01	-0.03	0.12	0.09	0.19
	UPNF	-0.17*	-0.14*	-0.0003	0.11*	0.13	-0.09	0.06	0.002	-0.2**
	UPF	0.003	-0.08	-0.08	0.02	0.03	0.01	-0.01	-0.0004	-0.09
	R2	0.15	0.31	-0.06	0.51	-0.01	-0.05	0.72	0.01	0.13

**Table 4**

Principal component (pc) analysis scores of selected species on three first axis. Comparatively high absolute scores are highlighted. Stand, landscape and land use history variables related to each axis and the sign of the relationship are indicated. Successional status after Das Chagas e Silva and Soares-Silva (2000). SS: successional status: C, climax; I, initial secondary; P, pioneer; T, late secondary. NF 300: native forest proportion 300 around the sample unit, NF PLC: stands covered by native forest immediately before plantation.

Variables	Species	EC	Seedlings			saplings			small trees		
			pc1	pc2	pc3	pc1	pc2	pc3	pc1	pc2	pc3
	<i>Trema micrantha</i>	P	<b>0.56</b>	−0.14	−0.35	0.34	−0.23	0.47	0.28	0.32	0.71
	<i>Cecropia pachystachya</i>	P	−0.08	−0.31	−0.24	<b>0.48</b>	− <b>0.38</b>	0.33	0.37	0.32	<b>0.61</b>
	<i>Solanum granulolum – leprosum</i>	P	−0.12	0.21	−0.39	0.26	− <b>0.49</b>	−0.38	0.30	<b>0.61</b>	−0.32
	<i>Nectandra lanceolata</i>	T	<b>0.62</b>	−0.22	−0.19	0.36	− <b>0.55</b>	−0.15	<b>0.85</b>	<b>0.32</b>	0.07
	<i>Prunus brasiliensis</i>	I	0.15	0.01	0.29	0.20	− <b>0.50</b>	−0.28	<b>0.79</b>	0.12	0.02
	<i>Ocotea puberula</i>	T	0.23	−0.27	0.36	<b>0.59</b>	−0.38	0.16	0.35	<b>0.79</b>	− <b>0.37</b>
	<i>Ilex paraguariensis</i>	T				<b>0.63</b>	−0.18	0.19	<b>0.85</b>	0.11	0.46
	<i>Cabralea canjerana</i>	I	<b>0.77</b>	− <b>0.39</b>	0.11	0.14	0.05	0.09	<b>0.69</b>	−0.19	−0.02
	<i>Balfourodendron riedelianum</i>	T	−0.27	− <b>0.55</b>	−0.17	<b>0.57</b>	0.39	0.32	0.22	<b>0.31</b>	−0.03
	<i>Cedrela fissilis</i>	T	0.26	−0.02	0.10	−0.06	−0.04	0.38	0.30	<b>0.78</b>	−0.27
	<i>Chrysophyllum gonocarpum</i>	T	<b>0.66</b>	− <b>0.32</b>	0.36	<b>0.62</b>	0.28	0.59			
	<i>Cordia americana</i>	T	0.10	− <b>0.68</b>	−0.12	0.09	<b>0.57</b>	−0.13	<b>0.71</b>	− <b>0.46</b>	−0.10
	<i>Allophylus edulis</i>	I	−0.30	−0.16	−0.23	<b>0.86</b>	−0.21	−0.24	<b>0.71</b>	− <b>0.29</b>	− <b>0.49</b>
	<i>Cupania vernalis</i>	T	−0.01	− <b>0.40</b>	0.22	<b>0.50</b>	0.28	−0.37			
	<i>Lonchocarpus campestris</i>	I	− <b>0.34</b>	−0.33	−0.21	0.36	0.21	0.21			
	<i>Mataiba eleagnoides</i>	T	0.18	− <b>0.42</b>	0.12	0.35	−0.12	−0.60	<b>0.87</b>	−0.19	−0.10
	<i>Nectandra megapotamica</i>	T	−0.02	− <b>0.56</b>	0.40	<b>0.48</b>	<b>0.62</b>	−0.15	0.47	− <b>0.31</b>	− <b>0.39</b>
	<i>Ruprechtia laxiflora</i>	I				0.32	<b>0.64</b>	−0.33	0.44	− <b>0.40</b>	−0.14
	<i>Parapiptadenia rigida</i>	T	− <b>0.35</b>	− <b>0.49</b>	−0.31	0.24	<b>0.65</b>	−0.24	<b>0.57</b>	−0.20	<b>0.52</b>
	<i>Holocailix balansae</i>	C	−0.30	−0.29	−0.03	0.43	−0.09	0.71			
	<i>Campomanesia xanthocarpa</i>	T	−0.23	−0.02	−0.37	0.48	<b>0.44</b>	−0.24			
	<i>Trichilia catigua</i>	C	0.04	− <b>0.55</b>	0.25						
	<i>Eugenia uniflora</i>	T	− <b>0.39</b>	− <b>0.42</b>	0.14						
Stand age			−			+			+		
Basal area						−				−	
NF 300				−							
NF PLC			−	−		+	+				−

richness of native plants is positively related to stand age (Gachet et al., 2007; Geldenhuys, 1997; Keenan et al., 1997; Loumeto and Huttel, 1997; Norton, 1998; Onaindia and Mitxelena, 2009; Selwyn and Ganesan, 2009; Wang et al., 2004) and negatively related to stand density (Chen and Cao, 2014; Loumeto and Huttel, 1997). We found that in the study area, such trend was strongly dependent on plant size. Seedling richness was clearly affected by the availability of seed sources in the vicinity of the plantations. The native forest cover in a 300 m radius surrounding the sampling units was a better predictor of seedling richness than measures based on the distance to the nearest patch of native forest. It has been observed that in the studied area (Vespa et al., 2014) as well as in other forests (Carlo et al., 2013; Hewitt and Kellman, 2002), only a very small proportion of seeds is dispersed further than 300 m. Igarashi et al. (2016) found that the species richness in a cedar plantation in Japan was correlated with the proportion of native forest within a radius of 300 m for seedlings (plants similar in size to those here called seedlings), and within a radius of 100 m for saplings (plants similar in size to those here called saplings). These authors also found that stand age positively affected sapling species richness but no such effect was observed for seedlings. Then, the establishment of small plants might occur under a variety of conditions independently of stand age and basal area but depending on the availability of seed sources. Conversely, the survival and growth depend on time (stand age) and favorable conditions which in our study might be associated with low basal area. Similar conclusions were attained by Poorter et al. (2005) in a study on tree regeneration in a tropical forest where shade-tolerant, as well as shade-intolerant species, germinated under a wide range of environmental conditions and a selection process occurred when individuals were growing towards the canopy.

Land use history only had a marginal effect on plant density and species richness. Igarashi et al. (2016) found that second-rotation cedar plantations exhibited a lower seedling and sapling species richness than the first rotation plantations. We found a greater seedling species richness in stands established on sites that were previously used for pine

production than in those used for agriculture, although a stronger effect was observed on species composition, especially of smaller plants. The species composition of all plant sizes was mainly affected by stand age, however, the effect of other variables was dependent on plant size. Early-successional trees prevailed in young stands and the frequency of late-successional ones tended to increase with stand age. Other forest plantations in the study area (Dummel and Pinazo, 2013) as well as in other parts of the world (Nagaike, 2012; Senbeta et al., 2002) showed the same trend. A remarkable size-dependent response of species composition was that seedlings were affected by the cover of native forest at the landscape scale, while larger size classes (i.e. saplings and small trees) were affected by stand basal area. These trends were similar to those found for plant density and species richness. At the seedling stage, the light-demanding and early-successional species, either short-lived (*Trema micrantha*) or long-lived (*Nectandra lanceolata* and *Cabralea canjerana*), were the most frequent in young stands whereas, in old stands, the most frequent were shade-tolerant and middle-to-late-successional species, such as *Lonchocarpus campestris*, *Parapiptadenia rigida* and *Eugenia uniflora*. Thus, the change in seedling species composition associated with stand age involved a species turnover with no trends in species richness. Long-lived early successional as well as late successional species increased in frequency with increasing native forest cover at the landscape scale. For the largest plant size class (i.e., small trees), long-lived early successional as well as late-successional species increased in frequency with stand age, promoting an overall increase in species richness. As an independent gradient, species which increased in frequency with decreasing basal area were mainly long-lived early successional and, to some extent, short-lived ones. The land use effect was more evident on the species composition than on plant density or species richness. The stands that were on sites covered by native forest immediately before the plantation establishment, exhibited higher frequencies of long-lived early successional species than stands on agricultural sites. Species composition trends were similar to that found by Dummel and Pinazo (2013) for the

studied area and by Senbeta et al. (2012) for forest plantations in Ethiopia. Native woody species in plantations were found to be predominantly animal dispersed (Geldenhuys, 1997; Keenan et al., 1997). In our study area, Dummel and Pinazo (2013) also found that the frequency of zoochoric species tend to increase with stand age whereas they observed an opposite trend for anemochoric species. Our results only showed an increasing trend in the frequency of zoochoric species with stand age but no effect of the native forest cover was found at the landscape scale. Quantitative data on dispersal traits are needed to better understand the incidence of the seed source availability on the species composition established in forest plantations.

## 5. Conclusions

General patterns are in agreement with previous results in the study area and other parts of the world. Our results indicate that these responses are size-dependent: seedling species richness and composition primarily depend on native forest cover at the landscape scale while sapling and small tree plant density, species richness and species

composition are mainly affected by stand age and density. According to these results, management practices should consider to maintain the rotation age longer than 20 years, the basal area below  $30 \text{ m}^2 \cdot \text{ha}^{-1}$  and a 25–30% of native forest cover at the landscape scale to increase native tree density and species richness in loblolly pine plantations in the Atlantic Forest.

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## Appendix A. Tree species complete list in the sampled stands of *Pinus taeda* plantations in Northern Misiones, Argentina.

Species	Family	Common name
<i>Actinostemon concolor</i> (Spreng.) Müll. Arg.	Euphorbiaceae	Laranjeira
<i>Aegiphila brachiata</i> Vell.	Lamiaceae	Pelotero
<i>Albizia niopoides</i> (Spruce ex Benth.) Burkart	Fabaceae	Anchico blanco
<i>Alchornea sidifolia</i> Müll. Arg.	Euphorbiaceae	Mora blanca
<i>Alchornea glandulosa</i> Poepp. ssp. iricurana (Casar.) Secco	Euphorbiaceae	Mora blanca
<i>Alchornea triplinervia</i> (Spreng.) Müll. Arg.	Euphorbiaceae	Mora blanca
<i>Allophylus edulis</i> (A. St.-Hil., A. Juss. & Cambess.) Hieron. ex Niederl.	Sapindaceae	Cocú
<i>Allophylus guaraniticus</i> (A. St.-Hil.) Radlk.	Sapindaceae	Cocú-ra
<i>Aloysia virgata</i> (Ruiz & Pav.) Pers. var. <i>virgata</i>	Verbenaceae	Palo lija
<i>Annona rugulosa</i> (Schltdl.) H. Rainer	Annonaceae	Araticú
<i>Apuleia leiocarpa</i> (Vogel) J.F. Macbr.	Fabaceae	Grapia
<i>Araucaria angustifolia</i> (Bertol.) Kuntze	Araucariaceae	Pino Paraná
<i>Aspidosperma australe</i> Müll. Arg.	Apocynaceae	Guatambú amarillo
<i>Ateleia glazioviana</i> Baill.	Fabaceae	Timbó de campo
<i>Bauhinia forficata</i> Link ssp. <i>pruinosa</i> (Vogel) Fortunato & Wunderlin	Fabaceae	Pata de buey
<i>Balfourodendron riedelianum</i> (Engl.) Engl.	Rutaceae	Guatambú blanco
<i>Banara parviflora</i> (A. Gray) Benth.	Salicaceae	Pitumba
<i>Banara tomentosa</i> Clos	Salicaceae	Guazatumba hoja grande
<i>Bastardiopsis densiflora</i> (Hook. & Arn.) Hassl.	Malvaceae	Loro blanco
<i>Brunfelsia australis</i> Benth.	Solanaceae	Jazmín del Paraguay
<i>Cabralea canjerana</i> (Vell.) Mart.	Meliaceae	Cancharana
<i>Calliandra foliolosa</i> Benth.	Fabaceae	Plumerillo
<i>Campomanesia xanthocarpa</i> O. Berg var. <i>xanthocarpa</i>	Myrtaceae	Guabirá
<i>Casearia sylvestris</i> Sw. var. <i>sylvestris</i>	Salicaceae	Burro caá
<i>Casearia decandra</i> Jacq.	Salicaceae	Guazatumba
<i>Casearia lasiophylla</i> Eichler	Salicaceae	Espeto
<i>Cecropia pachystachya</i> Trécul	Cecropiaceae	Ambay
<i>Cedrela fissilis</i> Vell.	Meliaceae	Cedro
<i>Celtis iguanaea</i> (Jacq.) Sarg.	Celtidaceae	Tala
<i>Cestrum laevigatum</i> Schltdl.	Solanaceae	Bola de venado
<i>Chrysophyllum gonocarpum</i> (Mart. & Eichler) Engl.	Sapotaceae	Aguay
<i>Chrysophyllum marginatum</i> (Hook. & Arn.) Radlk. ssp. <i>marginatum</i>	Sapotaceae	Basuriña
<i>Cinnamomum amoenum</i> (Ness & Mart.) Kosterm.	Lauraceae	Canela
<i>Citronella paniculata</i> (Mart.) R.A. Howard	Cardiopteridaceae	Yerbón
<i>Citrus aurantium</i> L.	Rutaceae	Apepú
<i>Cordia americana</i> (L.) Gottschling & J.S. Mill.	Boraginaceae	Guayubira
<i>Cordia ecalyculata</i> Vell.	Boraginaceae	Colita
<i>Cordia trichotoma</i> (Vell.) Arráb. ex Steud.	Boraginaceae	Loro negro
<i>Cupania vernalis</i> Cambess.	Sapindaceae	Camboata colorado
<i>Dendropanax cuneatus</i> (DC.) Decne. & Planch.	Araliaceae	Omburá
<i>Diatenopteryx sorbifolia</i> Radlk.	Sapindaceae	María preta

<i>Endlicheria paniculata</i> (Spreng.) J.F. Macbr.	Lauraceae	Laurel petiso	
<i>Enterolobium contortisiliquum</i> (Vell.) Morong	Fabaceae	Timbó colorado	
<i>Eriobotrya japonica</i> (Thunb.) Lindl.	Rosaceae	Nispero	
<i>Eugenia burkartiana</i> (D. Legrand) D. Legrand	Myrtaceae	Typycha arroyo	
<i>Eugenia hyemalis</i> Cambess. var. <i>marginata</i> (O. Berg) D. Legrand	Myrtaceae	–	
<i>Eugenia pyriformis</i> Cambess. var. <i>pyriformis</i>	Myrtaceae	Ubajai chico	
<i>Eugenia uniflora</i> L.	Myrtaceae	Pitanga	
<i>Euterpe edulis</i> Mart.	Arecaceae	Palmito	
<i>Ficus luschnathiana</i> (Miq.) Miq.	Moraceae	Higuera	
<i>Gleditsia amorphoides</i> (Griseb.) Taub. var. <i>amorphoides</i>	Fabaceae	Espina corona	
<i>Guarea kunthiana</i> A. Juss.	Meliaceae	Carayá bola	
<i>Guarea macrophylla</i> Vahl ssp. <i>spiciflora</i> (A. Juss.) T.D. Penn.	Meliaceae	Cedrillo	
<i>Helietta apiculata</i> Benth.	Rutaceae	Canela de venado	
<i>Heliocarpus popayanensis</i> Kunth	Tiliaceae	Afata	
<i>Holocalyx balansae</i> Micheli	Fabaceae	Alecrin	
<i>Hovenia dulcis</i> Thunb.	Rhamnaceae	Hovenia	
<i>Ilex brevicuspis</i> Reissek	Aquifoliaceae	Cauna	
<i>Ilex paraguariensis</i> A. St.-Hil. var. <i>paraguariensis</i>	Aquifoliaceae	Yerba mate	
<i>Inga affinis</i> DC.	Fabaceae	Ingá colorado	
<i>Inga marginata</i> Willd.	Fabaceae	Ingá chico	
<i>Jacaranda micrantha</i> Cham.	Bignoniaceae	Caroba	
<i>Lonchocarpus campestris</i> Mart. ex Benth.	Fabaceae	Rabo itá	
<i>Lonchocarpus muehlbergianus</i> Hassl.	Fabaceae	Rabo molle	
<i>Lonchocarpus nitidus</i> (Vogel) Benth.	Fabaceae	Rabo abá	
<i>Luehea divaricata</i> Mart.	Tiliaceae	Zoita	
<i>Machaerium paraguariense</i> Hassl.	Fabaceae	Isapui pará	
<i>Machaerium stipitatum</i> (DC.) Vogel	Fabaceae	Isapui morotí	
<i>Maclura tinctoria</i> (L.) Steud. ssp. <i>tinctoria</i>	Moraceae	Mora amarilla	
<i>Matayba elaeagnoides</i> Radlk.	Sapindaceae	Camboata blanco	
<i>Melia azedarach</i> L.	Meliaceae	Paraiso	
<i>Miconia pusilliflora</i> (DC.) Naudin	Melastomataceae	Caá tirí	
<i>Morus alba</i> L.	Moraceae	Mora	
<i>Myrocarpus frondosus</i> Allemão	Fabaceae	Incienso	
<i>Myrsine balansae</i> (Mez) Otegui	Myrsinaceae	Pororoca	
<i>Myrsine parvula</i> (Mez) Otegui	Myrsinaceae	Resinoso	
<i>Nectandra lanceolata</i> Nees & Mart. ex Nees	Lauraceae	Laurel amarillo	
<i>Nectandra megapotamica</i> (Spreng.)	Lauraceae	Laurel negro	
<i>Ocotea diospyrifolia</i> (Meisn.) Mez	Lauraceae	Laurel ayuí	
<i>Ocotea puberula</i> (Rich.) Nees	Lauraceae	Laurel guaica	
<i>Ocotea pulchella</i> (Nees) Mez	ocopul	Lauraceae	Canela layana
<i>Parapiptadenia rigida</i> (Benth.) Brenan	parrig	Fabaceae	Anchico colorado
<i>Peltophorum dubium</i> (Spreng.) Taub.	peldub	Fabaceae	Cañafístola
<i>Pilocarpus pennatifolius</i> Lem.	pilpen	Rutaceae	Jaborandí
<i>Prunus brasiliensis</i> (Cham. & Schltdl.) D. Dietr.	prubra	Rosaceae	Persiguero
<i>Psidium guajava</i> L.	psigua	Myrtaceae	Guayaba
<i>Randia armata</i> (Sw.) DC. var. <i>Armata</i>	ranarm	Rubiaceae	Ñuatí curuzú
<i>Annona emarginata</i> (Schltdl.) H. Rainer	annema	Annonaceae	Araticú
<i>Annona neosalicifolia</i> H. Rainer	annneo	Annonaceae	Araticú
<i>Rudgea jasminoides</i> (Cham.) Müll. Arg. ssp. <i>jasminoides</i>	rudjas	Rubiaceae	Jasmín de monte
<i>Ruprechtia laxiflora</i> Meisn.	ruplax	Polygonaceae	Marmelero
<i>Sapium glandulosum</i> (L.) Morong	sapglg	Euphorbiaceae	Curupí caí
<i>Sapium haematospermum</i> Müll. Arg.	saphae	Euphorbiaceae	Curupí
<i>Schinus terebinthifolius</i> Raddi	schter	Anacardiaceae	Mollecito
<i>Sebastiania brasiliensis</i> Spreng.	sebbra	Euphorbiaceae	Palo leche
<i>Sebastiania commersoniana</i> (Baill.) L.B. Sm. & Downs	sebcom	Euphorbiaceae	Blanquillo
<i>Symplocos uniflora</i> (Pohl) Benth.	symuni	Symplocaceae	Leña de papel
<i>Solanum granulolum-leprosum</i> Dunal	solgra	Solanaceae	Fumo bravo
<i>Solanum pseudoquina</i> A. St.-Hil.	solpse	Solanaceae	Bola de venado
<i>Sorocea bonplandii</i> (Baill.) W.C.Burger, Lanj. & Wess.Boer	sorbon	Moraceae	Ñandipa
<i>Styrax leprosus</i> Hook. & Arn.	stylep	Styracaceae	Carne de vaca
<i>Strychnos brasiliensis</i> (Spreng.) Mart.	strbra	Loganiaceae	Espolón de gallo
<i>Syagrus romanzoffiana</i> (Cham.) Glassman	syarom	Arecaceae	Pindó
<i>Tabernaemontana catharinensis</i> A. DC.	tabcat	Apocynaceae	Horquetero
<i>Trema micrantha</i> (L.) Blume	tremic	Celtidaceae	Palo polvora
<i>Trichilia catigua</i> A. Juss.	tricat	Meliaceae	Catigua
<i>Trichilia elegans</i> A. Juss.	triele	Meliaceae	Catigua chico

*Vassobia breviflora* (Sendtn.) Hunz.  
*Vitex megapotamica* (Spreng.) Moldenke  
*Xylosma tweediana* (Clos) Eichler  
*Zanthoxylum fagara* (L.) Sarg.  
*Zanthoxylum petiolare* A. St.-Hil. & Tul.  
*Zanthoxylum rhoifolium* Lam.

vasbre	Solanaceae	Fruta de paloma
vitmge	Lamiaceae	Tarumá
xyltwe	Salicaceae	Azucará
zanfag	Rutaceae	Curaturá
zanpet	Rutaceae	Naranjillo
zanrho	Rutaceae	Mamica

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