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How to Bloom the Green Desert: *Eucalyptus* Plantations and Native Forests in Uruguay beyond Black and White Perspectives

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Abstract: The ongoing debate on the boon or bane of monocultural timber plantations demonstrates the need to develop alternative approaches that achieve forest productivity while conserving biodiversity. We assessed the diversity of tree species in native forests and in *Eucalyptus* plantations, and evaluated the potential use of native species to enhance plantation management. For this purpose, we established one-hectare permanent plots in nine native forests (riverine and park forests) and nine *Eucalyptus* plantations in the northwestern part of Uruguay. Forest inventories were carried out on 200 m² plots and regeneration was assessed along transects in 9 m² subplots. Riverine forests have the highest Shannon diversity index (2.5) followed by park forests (2.1) and *Eucalyptus* plantations (1.3). Tree density was high in riverine forests (1913/ha) and plantations (1315/ha), whereas park forests have lower tree density (796/ha). Regeneration density was high in riverine forests (39136/ha) and park forests (7500/ha); however, native species can regenerate in the understory of plantations (727/ha), and this underlines the possibility of developing a mixed species approach to reduce the negative impact of monocultures. Differences in the composition of plant communities were denoted between native forests and plantations, although native forests were similar in composition, even in the presence of exotic species. Native forests harbor specialist species that are absent from plantations, and therefore perform a decisive role in maintaining local biodiversity. Strategies to enhance species diversity and structural diversity within plantations or to establish mixed buffer strips containing native species at the edge of plantations are potential measures to enhance biodiversity and foster the integration of plantations into the local landscape.

Keywords: *Eucalyptus*; riverine forest; grassland afforestation; invasive species; multifunctional landscapes; park forest; species composition; species diversity

1. Introduction

Tree plantations are expanding around the world [1] for multiple purposes such as restoring degraded landscapes [2], conserving native tree species [3], satisfying timber and pulp demand [1], or carbon sequestration [4,5], among others. In the last decades, plantations increased from 1675 Mha in 1990 to 2779 Mha in 2015, which is equal to 7% of the global forest cover [1]. Despite the vast diversity of tree species, few fast-growing exotic species dominate plantations worldwide. Mainly, four genera (e.g., *Tectona*, *Eucalyptus*, *Pinus*, and *Acacia*) are used with intensive management operations, which are selected for their easy establishment and short-term higher productivity [6].

In Uruguay, small *Eucalyptus* plantations (<0.5 ha) were established to provide shelter and shade for livestock in the 1970s [7]. Subsequently, large-scale *Eucalyptus* plantations were promoted by

governmental policies, financial incentives, and investors' expectations [8,9], resulting in the expansion of the forest industry to meet the growing carbon market. The key laws that facilitated this process included the forestry law of 1987, the more flexible lease law of 1991, a law that facilitated land tenure by multiple owners (e.g., associations and companies), and the investment law, both of 1999 [10]. As a result, Uruguay has had the highest afforestation rate in South America; the total planted area increased over 500% from 201,000 hectares to 1,062,000 hectares between 1990–2015 [11]. Most plantations occur in the form of monocultures of fast-growing non-native *Eucalyptus* and *Pinus* species at the expense of grasslands [12]. In some cases, forestry companies lease their plantations for grazing to local farmers forming silvopastoral systems [13].

Today, *Eucalyptus* and *Pinus* plantations occupy 58% of the forest cover in Uruguay, and are located mainly in the north, northwest, and northeast of the country, while native forests cover 42% of the forest cover (recent statistics of the Food and Agriculture Organization of the United Nations, FAO 2015). Native forests are scattered within a matrix dominated by grasslands and crops, and range from savanna-like formations such as 'park forests' to riverine or gallery forests, creek forests, and hill forests. In total, 150 different native tree species have been reported for Uruguay, which represents a high diversity for a temperate grassland region [14,15]. While detailed inventory data are lacking for the majority of native forests, some of the tree species are hypothesized to have promising potential for the forest industry [16,17]. The limited information that is available on native species and their undeveloped or unstable market has promoted the use of well-known, fast-growing exotic tree species.

Although plantations are being established at a high rate in Uruguay, the use of exotic species has sparked much controversy regarding their impact on local ecosystems. For example, plantations are 'green deserts' or valuable habitats for indigenous flora and fauna [18,19], or whether *Eucalyptus* can be a useful tool for restoring degraded land [20]. Nowadays, *Eucalyptus* plantations are progressively replacing *Pinus*. Current afforestation practices may reduce species richness and alter the composition of grassland vegetation in Uruguay [21]. Yet, studies on the impact of *Eucalyptus* plantations in Uruguay are scarce, and the overall impact of plantations on local ecosystems is largely unknown.

Worldwide, studies have shown that the use of native species in forestry projects facilitates processes that are associated with natural ecosystems such as native understory development or biodiversity enrichment [18]. Native species meet better local cultural needs [22] and provide a greater range of goods and services (i.e., 'multi-use species') than exotic species [22,23]. Additionally, native species are considered to provide longer-term benefits and be more stable in the face of disturbances in our changing world [24].

In this work, we evaluated three typical understudied forest types (i.e., park forests, riverine forests, and *Eucalyptus* plantations) in the northwestern part of Uruguay regarding (1) forest structure and regeneration, (2) forest composition and diversity, (3) the importance value index, and (4) the potential use of native species. We assessed the value of native forests and plantations in promoting diversity at the landscape scale and explored how the ecological properties of natural forests can be used to better manage plantations. Our study provides novel evidence for an existing landscape element of the northwestern part of Uruguay and the relationship between native forests and *Eucalyptus* plantations beyond polarized comparisons.

2. Materials and Methods

2.1. Study Area

With an area of about 176,215 km², Uruguay is located in the temperate zone of South America. The mean annual temperature ranges from 16 °C in the south to 20 °C in the north, and the annual rainfall average is approximately 1500 mm in the north and 1000 mm in the south. The Pampas and Campos of Uruguay and neighboring Argentina and Brazil are one of the world's species richest grasslands [9]. Grasslands cover over 70% of the Uruguayan territory, while native forests cover approximately 4% of Uruguay [15]. The FAO estimates that 6% of the land area is afforested with

Eucalyptus and pine plantations [11]. Uruguayan native forests have been traditionally used to extract timber and firewood. They are classified according to their physiognomy and topographic location into riverine or gallery forests along rivers, park forests, or transition zones between riverine forest and grasslands, creek forest in the rocky parts of the mountains, and hill forests on steep slopes [14]. Native forests are protected by law, and logging is only allowed for local use or under a management plan. These measures have led to an increase of native forest cover across Uruguay over the last decade.

Our study region in the northwestern part of Uruguay (Figure 1a) has sandy soils with high forestry potential, and is consequently one of the areas where plantations are concentrated. Our sample plots are located within the administrative borders of the Uruguayan departments of Paysandú, Soriano, Río Negro, and Durazno. Park forests (Figure 1c) are intermediate stands between a wooded range and a dense (riverine) forest located in low and plain areas, and are often associated with alkaline soils. They form an open canopy of disperse trees growing in a dense herbaceous vegetation that is composed mainly of grasses. Grazing is a key factor for the park forest formation and strongly reduces the occurrence of tree seedlings [14,25]. Riverine forest (Figure 1d) comprises vegetation strips ranging from 100 to several hundred meters of width along rivers and streams on poorly drained soils. It forms a dense canopy that is composed of shrubs and trees [14,26]. Forest plantations are monospecific *Eucalyptus grandis* and *E. dunnii* stands (Figure 1e) of five to eight years of age. *Eucalyptus* stands have been intensively cultivated in this region, mostly for the paper industry. The plantation density is generally 1300 trees per hectare. After the seedlings are planted, almost no management is used until clear-cutting, apart from the application of insecticides when needed. Stands are harvested after 10 years.

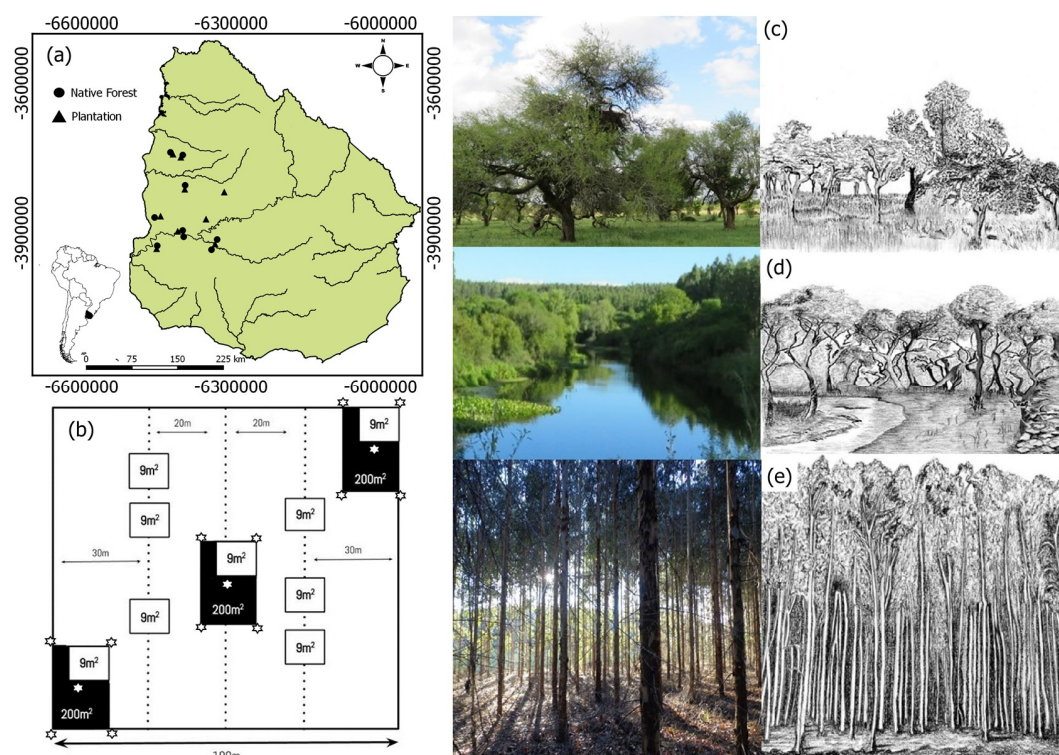


Figure 1. Map of the study area with: (a) the study sites in the northwestern part of Uruguay (black dots: native forests and black triangles: *Eucalyptus* plantations); (b) sampling design composed of permanent plots (100 × 100 m²), inventory plots for trees (20 × 10 m²), regeneration subplots (3 × 3 m²) and measurement points of LAI (leaf area index) showed in asterisks. Examples for forest-type structures; (c) park forest characterized by disperse trees growing in a dense herbaceous cover, the figure shows *Vachellia caven* “espinillo” (Department of Paysandú); (d) riverine or gallery forest, forming a narrow dense vegetation strip of shrubs and trees along the river (Department of Río Negro); (e) *Eucalyptus grandis* plantation (Department of Durazno); Coordinate system UTM zone 21 S.

2.2. Field Inventory Design

Forest inventories were undertaken between December 2015 and February 2016. We used the FAO forest definition where forests are defined as having at least 10% of the canopy coverage with trees higher than 5 m and a stand area of more than 0.5 ha [21,26]. We established nine permanent plots of one hectare in *Eucalyptus* plantations and nine permanent plots in native forests (four in park forests and five in riverine forests) (Figure 1a). Since the woody flora of Uruguay tends to be short in height with several slim trunks, and thus does not completely fit in common tree or shrub definitions, we categorized tree and tree-like plants as terrestrial or hemiepiphyte plants that are perennial and erect, with one or a few well-defined stems [15]. Tree assessment was undertaken in three $20 \times 10 \text{ m}^2$ plots that were systematically distributed in the corners and center of the permanent plot (Figure 1b). Tree attributes such as species name, diameter at breast height (DBH), and height were recorded in all of the individual or multi-stem living trees having $\text{DBH} \geq 2.5 \text{ cm}$ at 1.3 m. Regeneration assessment (individuals with $<2.5 \text{ cm}$ diameter and height $<1 \text{ m}$) was evaluated in nine $3 \times 3 \text{ m}^2$ subplots located inside the $20 \times 10 \text{ m}^2$ plots and along systemically established linear transects (Figure 1b). Leaf area index (LAI), which is a dimensionless measure of canopy foliage content defined as the amount of leaf area (m^2) in a canopy per unit ground area (m^2) and is considered a central descriptor of forest structure [27], was assessed inside the $20 \times 10 \text{ m}^2$ plots. It was measured as the average of five readings taken at each corner and center of the sampling plots (Figure 1b) using a LAI-2000 canopy analyzer (Li-Cor, Lincoln, NE, USA), positioning the sensor up to a maximum height of about 2 m.

2.3. Data Analysis

We assessed forests types in our study sites by analysis of (1) forest structure and regeneration, (2) forest diversity and composition, (3) importance value and the potential economical, ecological, and social use of native species. Forest structure, which is defined as the frequency distribution of individuals in a defined class [28], was evaluated in the overall native forests and plantations. The vertical structure of a forest includes its differentiation into layers expressed in height classes and horizontal structure expressed in diameter classes. The diameter of individual trees was divided into four diameter classes (2.5–10 cm, 11–30 cm, 31–50 cm, and $>50 \text{ cm}$) and three height classes (0–5 m, 6–10 m, and $>10 \text{ m}$). The density of each interval was used to construct the diameter distribution. We also calculated the horizontal and vertical structure diversity using the Shannon diversity index (H') [28,29]. We used the same index to evaluate species diversity. We used non-metric multidimensional scaling (NMDS) using the Bray–Curtis dissimilarity matrix [30] on species abundance with 999 permutations to visualize patterns of composition between forest types. The Bray–Curtis distance was chosen because it is based on quantitative data and has been shown to be one of the best for detecting gradients of species composition [31]. The significance of the compositional differences was tested with a permutational multivariate analysis of variance (PERMANOVA) with 999 permutations [32]. Ecological variables including tree density, regeneration, species diversity, horizontal and vertical structure diversity, LAI, and proportion of exotic and native richness, were fitted on the NMDS ordination plot based on 999 random permutations. The data were tested for normality using the Shapiro–Wilkes test. We used one-way analysis of variance to test for differences between forest types and the post-hoc Tukey test after finding significantly different results. Square root transformation was applied when the data was not normally distributed. The importance value index (IVI) of a given species indicates the relative ecological importance of that species at a particular site [33]. It was obtained by adding the percentage values of the relative frequency, relative density, and relative dominance. Statistical analyses were undertaken with the open-source software package R version 3.3.2 (R Foundation for Statistical Computing, Vienna, Austria) using the packages *vegan* [34] and *mass* [35] with an adopted alpha of ≤ 0.05 considered significant.

Finally, we reviewed the literature in the Web of Science for each native species identified in all of the forest types regarding any potential use. For specific information on the literature, see Appendix A.

We identified the following use categories: local fiber, source of nectar for bees and honey production, medicine, ornamental use, soil restoration, wood, and animal foods.

3. Results

3.1. Forest Structure and Regeneration

The diameter class distribution of *Eucalyptus* plantations showed a hump-shaped pattern with a higher density of middle-sized classes, whereas native forests depicted a reverse J-shaped pattern with a higher density of smaller size classes (Figure 2a). Native forests presented also a higher horizontal structure diversity (Figure 2f) in comparison with plantations. The height class distribution in *Eucalyptus* plantations showed a higher density of larger size classes in comparison with smaller classes, while native forests displayed a higher density of smaller size classes compared to higher size classes (Figure 2b). However, vertical structure diversity did not differ significantly between forest types (Figure 2g). Riverine forests showed the highest tree density between forest types (Figure 2c). *Allophylus edulis* (A. St.-Hil., A. Juss. & Cambess.) Hieron. ex Niederl. (AlEd), *Sebastiania brasiliensis* Spreng. (SeBr), and *Pouteria salicifolia* (Spreng.) Radlk. (PoSa) had the highest densities in riverine forests, while *Schinus longifolius* (Lindl.) Speg. (ScLo), *Celtis ehrenbergiana* (Klotzsch) Liebm. (CeTa), and *Blepharocalyx salicifolius* (Kunth) O. Berg (BlSa) had the highest densities in park forests. Regeneration was significantly different between forest types ($F = 15.7$, $p < 0.001$, Figure 2d). Post-hoc pairwise comparisons showed lower regeneration density in *Eucalyptus* plantations compared with native forests ($p < 0.05$), and riverine forests have higher regeneration compared to park forests ($p < 0.05$). The regeneration of eight native species was recorded in *Eucalyptus* plantations, including *Allophylus edulis*, *Blepharocalyx salicifolius*, and *Celtis ehrenbergiana*, among others. The regeneration of *Myrcianthes cisplatensis* (Cambess.) O. Berg (MyCi), *Myrcianthes pungens* (O. Berg) D. Legrand (MyPu), and *Allophylus edulis* was high in park forests, whereas *Maytenus ilicifolius*, *Allophylus edulis*, and *Blepharocalyx salicifolius* dominated in riverine forests (Table 1, Figure 3d).

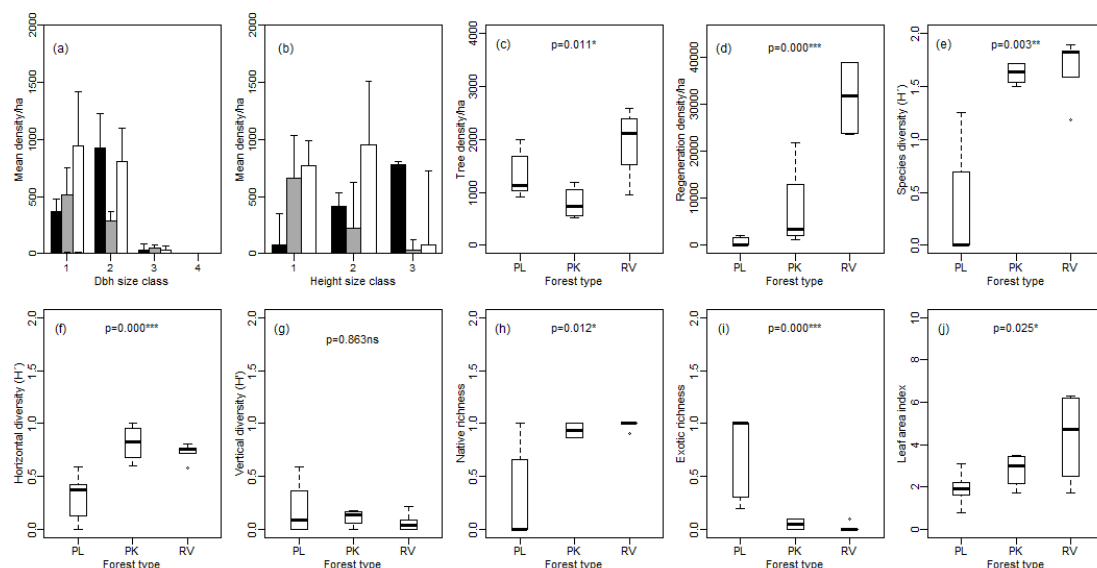


Figure 2. (a,b) The forest structure of the three forest types: *Eucalyptus* plantations (black bars), park forests (dark grey bars) and riverine forests (white bars): expressed as mean tree density per ha in diameter classes (1 = 2.5–10 cm, 2 = 10–30 cm, 3 = 30–50 cm, 4 = >50 cm) and height size classes (1 = 0–5 m, 2 = 5–10 m, 3 = >10 m); (c–j) For each forest type (PL: *Eucalyptus* plantations, PK: park forests, RV: riverine forest), variables of tree density, regeneration, Shannon diversity index, horizontal structure diversity, vertical structure diversity, proportion of native and exotic richness, and LAI are given. For parameter definition, see the Material and Methods section. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns: not significant. For results of statistical analysis, see Table 2.

Table 1. Species composition and potential use of woody species in different Uruguayan forest types: park forests (PK), riverine forests (RV), and *Eucalyptus* plantations (PL). Tree density (AD), regeneration density (RD), and potential use for each species are given. Use categories are local fiber (fb), source of nectar for bees and honey production (bee), medicine (med), ornamental use (or), soil restoration (re), wood (w), and animal foods (zoo). Exotic species (ex) have been introduced originally in the region for ornamental purposes [36]. References are indicated by superscript numbers. For use references, see Appendix material.

Species/Author/Code	Mean AD/ha	Mean RD/ha	Potential Use
<i>Schinus longifolius</i> (Lindl.) Speg. (ScLo)	250 ^{PK 3 RV}	185 ^{PK 20 RV}	med ⁹ or ⁹
<i>Patagonula americana</i> L. (PaAm)	90 ^{RV}	99 ^{RV}	re ⁷ w ^{8,20}
<i>Maytenus ilicifolia</i> Mart. ex Reissek (MaIl)	9 ^{PK}	370 ^{PK} 1175 ^{RV} 493 ^{PL}	med ⁸
<i>Escallonia bifida</i> Link & Otto (EsBi)	17 ^{RV}		or ⁸
<i>Sebastiania brasiliensis</i> Spreng. (SeBr)	447 ^{RV}	317 ^{RV}	re ^{1,2} med ^{1,18} or ¹⁸
<i>Citronella gongonha</i> (Mart.) R.A. Howard (CiCo)	3 ^{RV}	40 ^{RV}	zo ^{8,16}
<i>Ocotea acutifolia</i> (Nees) Mez (OcAc)	197 ^{RV}	119 ^{RV}	w ⁸ med ¹⁰
<i>Bauhinia forficata</i> Link (BaFo)	8 ^{PK}		med ¹⁶ or ⁸
<i>Gleditsia triacanthos</i> L. (GlTr)	8 ^{PK} 13 ^{RV}	185 ^{PK} 40 ^{RV}	ex
<i>Prosopis affinis</i> Spreng. (PrAf)	4 ^{PK}	154 ^{PK}	bee ^{8,6} re ¹⁴ zo ⁶ w ^{8,3}
<i>Vachellia caven</i> (Molina) Seigler & Ebinger (VaCa)	25 ^{PK}	247 ^{PK} 246 ^{PL}	bee ⁶ re ¹⁴ zo ⁶
<i>Melia azedarach</i> L. (MeAzr)	31 ^{PK}		ex
<i>Blepharocalyx salicifolius</i> (Kunth) O. Berg (BlSa)	129 ^{PK} 150 ^{RV}	247 ^{PK} 479 ^{RV} 1358 ^{PL}	zo ^{8,12,16} re ^{1,11} med ^{1,11}
<i>Eugenia uniflora</i> L. (EuUn)	38 ^{PK} 37 ^{RV}		zo ^{8–12,16,20} re ⁷ bee ^{9,11} or ⁸ med ^{4,5,20}
<i>Myrcianthes cisplatensis</i> (Cambess.) O. Berg (MyCi)	8 ^{PK} 350 ^{RV}	2746 ^{PK} 188 ^{RV} 740 ^{PL}	zo ¹¹ bee ¹¹ med ⁴
<i>Myrcianthes pungens</i> (O. Berg) D. Legrand (MyPu)	4 ^{PK} 70 ^{RV}	1296 ^{PK} 260 ^{RV} 246 ^{PL}	zo ^{8,11,12,16,20} re ^{1,7} bee ¹¹ med ⁵
<i>Myrrhinium atropurpureum</i> Schott (MyAt)	8 ^{PK} 17 ^{RV}		zo ^{12,16} re ¹¹ w ⁸ or ⁸ med ¹¹
<i>Ligustrum lucidum</i> W.T. Aiton (LiSi)	4 ^{PK} 87 ^{RV}	12395 ^{RV} 2222 ^{PL}	ex
<i>Colletia paradoxa</i> (Spreng.) Escal. (CoPa)	4 ^{PK}		bee ⁸ or ¹⁹
<i>Scutia buxifolia</i> Reissek (ScBu)	70 ^{PK} 157 ^{RV}	556 ^{PK} 96 ^{RV}	zo ¹⁶ re ¹ w ⁸ med ¹
<i>Discaria Americana</i> Gillies & Hook. (DiAmr)		185 ^{PK}	med ¹⁷
<i>Azara uruguayensis</i> (AzUr)	27 ^{RV}		or ⁸
<i>Salix humboldtiana</i> Willd. (SaHu)	17 ^{RV}		w ⁸
<i>Jodina rhombifolia</i> (Hook. & Arn.) Reissek (JoRh)	3 ^{RV}		med ¹³
<i>Allophylus edulis</i> (A. St.-Hil., A. Juss. & Cambess.) Hieron. ex Niederl. (AlEd)	38 ^{PK} 103 ^{RV}	987 ^{PK} 7679 ^{RV} 370 ^{PL}	zo ^{12,16,20} re ^{2,7} med ²⁰
<i>Pouteria salicifolia</i> (Spreng.) Radlk. (PoSa)	8 ^{PK} 353 ^{RV}	31 ^{PK} 247 ^{RV}	med ⁴
<i>Daphnopsis racemosa</i> Griseb. (DaRa)	27 ^{RV}	353 ^{RV}	fb ⁸ , or ¹⁹
<i>Celtis ehrenbergiana</i> (Klotzsch) Liebm. (CeTa)	133 ^{PK} 33 ^{RV}	278 ^{PK} 290 ^{RV} 740 ^{PL}	zo ⁸
<i>Citharexylum montevidense</i> (Spreng.) Moldenke (CiMo)	10 ^{RK}	10 ^{RV}	zo ¹⁶ w ¹⁵ or ⁸

Table 2. Forest variables determining tree species composition in *Eucalyptus* plantations and in native forests. Ecological variables fitted on the non-metric multidimensional scaling (NMDS) ordination plot. Results of the analysis of variance among forest types, r^2 , F, and p values are given. For variable definitions, see the Material and Methods section.

Parameters	NMDS		ANOVA	
	r^2	p	F	p
Tree density (AD)	0.04	0.701ns	6.2	0.0106 *
Regeneration density (RD)	0.50	0.002 **	22.9	0.000 ***
Species diversity (SD)	0.94	0.001 ***	8.2	0.003 **
Horizontal structure (HS)	0.54	0.004 **	16.1	0.000 ***
Vertical structure (VS)	0.17	0.237ns	0.1	0.863ns
Native proportion (NP)	0.86	0.001 ***	6.0	0.0119 *
Exotic proportion (EP)	0.90	0.001 ***	23.4	0.000 ***
Leaf Area Index (LAI)	0.39	0.020*	4.7	0.025 *

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns not significant.

3.2. Diversity and Composition

The Shannon diversity index was different between forest types ($F = 8.2$, $p < 0.01$, Figure 2e). Post-hoc pairwise comparisons indicated lower values in plantations compared to park ($p < 0.05$) and riverine forests ($p < 0.01$), and no significant difference between native forests ($p > 0.05$). Riverine forests had the highest Shannon diversity index (2.5) followed by park forests (2.1) and *Eucalyptus* plantations (1.3). NMDS ordination showed clearly distinctive community groups between forest types (PERMANOVA $F = 12.5$, $p < 0.001$, Figure 3b). Riverine and park forests shared 34% of the species, whereas *Eucalyptus* plantations shared 30% (from the regeneration strata) with park forests and 21% with riverine forests.

The response variables, including species diversity, regeneration density, proportion of native and exotic richness, horizontal structure diversity, and LAI showed the highest degree of correlation to species composition. Tree density and vertical structure diversity did not display any strong correlation to species composition (Figure 3a, Table 2). Native forests did not show significant differences in the proportion of native and exotic tree richness (Figure 2h,i). Exotic species such as *Melia azedarach*, *Ligustrum lucidum*, and *Gleditsia triacanthos* were recorded in native forests. *L. sinense* and *G. triacanthos* had higher density in the tree strata of riverine forests. *G. triacanthos* had higher densities in the regeneration strata of park forests. *M. azedarach* was only recorded in park forests (Table 1).

Leaf area index values differed between forest types (Figure 2j, Table 2). There was a significantly higher LAI in riverine forests. Park forests had lower LAI in comparison with riverine forests, demonstrating that parks forests were more open and homogeneous.

3.3. Importance Value and Potential Use of Native Species

The most important species in terms of abundance, dominance, frequency, and therefore importance value index (IVI) in park forests were *Schinus longifolius*, *Celtis ehrenbergiana*, *Blepharocalyx salicifolius*, *Prosopis affinis*, and *Scutia buxifolia*. In riverine forests, the most important species recorded were *Allophylus edulis*, *Pouteria salicifolia*, *Sebastiania brasiliensis*, *Patagonula americana*, *Scutia buxifolia*, *Ocotea acutifolia*, and *Salix humboldtiana* (Figure 3c). The most important species in terms of IVI comprise various potential ecological and economic uses. More than half of the species fall into at least two different use categories. Some species are used for more than five different purposes (e.g., *Eugenia uniflora* or *Myrrhinium atropurpureum*). Traditional knowledge of medicinal use is frequently reported in the literature. One-third of the species have ornamental and soil restoration uses. Over one-third are a food source for animals (Table 1).

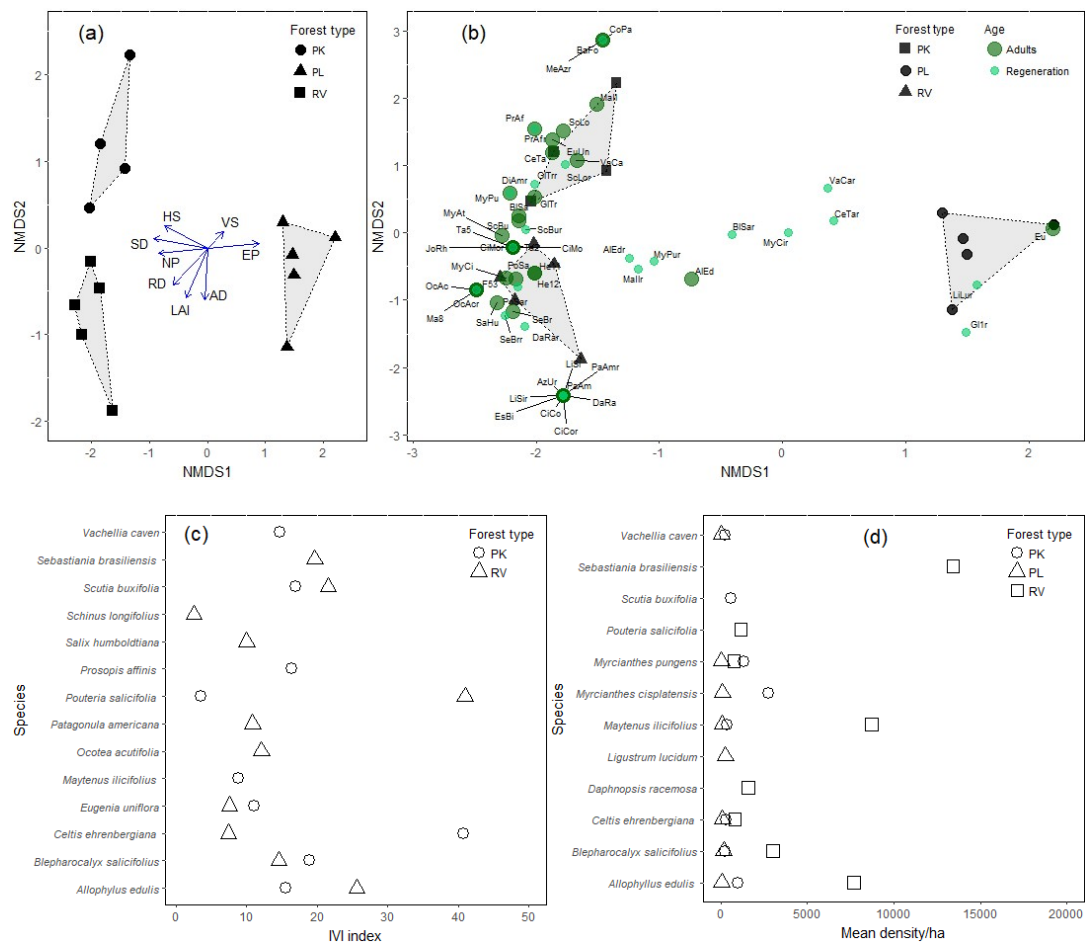


Figure 3. (a) Non-metric multidimensional scaling (NMDS) ordination of species from different forest types (PL: *Eucalyptus* plantations, RV: riverine forests, PK: park forests) and plots using the Bray–Curtis distance based on species abundance, showing distance between plots and eight explanatory variables: AD (Tree density), RD (Regeneration density), SD (Species diversity), HS (Horizontal structure diversity), VS (Vertical structure diversity), NP (Proportion of native richness as a proxy for naturalness), EP (Proportion of exotic species richness of all species as a proxy for non-nativeness), LAI (Leaf area index); (b) NMDS ordination of woody species showing distance between sites and tree species composition and regeneration species composition. Species were abbreviated, with the first four letters of the names and finishing in r for regeneration (e.g., AIEr: *Allophylus edulis* AIEr, respectively). Dashed lines show the convex hull within forest types; for species list and abbreviations, see Table 1, circle sizes correspond to the age category; (c) tree species with the highest mean IVI in native forests; (d) regeneration species with the highest mean density in the three forest types.

4. Discussion

The impact of plantations on local ecosystems within cultural landscapes is controversially debated. While some authors highlight the capacity of plantations to harbor native species and thus contribute to local biodiversity, for example, if they are established on degraded lands [18,37], others point out the negative effects of plantations on biodiversity compared to natural forests [38]. Biodiversity studies on *Eucalyptus* plantations in Uruguay are almost absent. Therefore, our study provides novel evidence for a characteristic landscape element of the northwestern part of Uruguay and for the interplay between plantations and native forests. We evaluated plantations and native forests beyond black and white perspectives in order to provide insights for developing multifunctional landscape forests. For instance, these forests can be developed to guide toward a species selection for mixed-species systems of native species within *Eucalyptus* plantations [39] or manage plantations as

nurse systems for restoration purposes [40,41]. This is crucial, especially for countries with landscapes where *Eucalyptus* plantations are already widely established and acknowledged as an important economic sector by national stakeholders [38,42].

4.1. Forest Structure and Regeneration

The native forests of Uruguay are typically unevenly aged, which is a feature of little or no disturbed multi-species forests with a high regeneration capacity and numerous suitable microsites for germination and seedling establishment (Figure 2a). A similar pattern has been reported in other riverine forests of the Campos biome in Uruguay and Brazil [26,43,44]. High regeneration was recorded for *Maytenus ilicifolius*, *Allophylus edulis*, and *Blepharocalyx salicifolius* in riverine forests, and for *Myrcianthes cisplatensis*, *Myrcianthes pungens*, and *Allophylus edulis* in park forests (Table 1), indicating a good reproduction and recruitment potential that allows them to maintain their dominance in the forest. *Eucalyptus* plantations exhibit a homogeneous horizontal and vertical structure (Figure 2a,b) with poor reproduction and recruitment of species, which is associated with intense asymmetric competition from the surrounding trees. The allelopathic effect of *Eucalyptus* plantations on the establishment of native species is due to chemicals released from the leaves, bark, and roots, and has been reported on Chinese plantations [39,45]. Research of these effects in South American plantation systems is lacking.

Even though regeneration is significantly higher in native forests than in plantations, we found the regeneration of woody species in *Eucalyptus* plantations under almost no management after planting. Our study found eight native tree species in the understory of plantations, including multi-use species such as *Allophylus edulis*, *Blepharocalyx salicifolius*, and *Celtis ehrenbergiana*, among others (Table 1). The management cycle of *Eucalyptus* plantations to produce large-diameter trees in Uruguay reduces species richness and composition, especially in plantations that are seven to eight years old (21). Native understory plants are recognized as an important cross-taxon biodiversity surrogate [46]. The potential regeneration of native tree species within *Eucalyptus* plantations is dependent on species traits such as their nitrogen (N)-fixing capacity, which promotes growth in the plantations [39].

Thus, our results clearly demonstrate the possibility of developing mixed species approaches incorporating native species within *Eucalyptus* plantations. These strategies will amplify the habitat services that are provided by plantations. Depending on management and rotation times, plantations can harbor a range of species and enhance the conservation value and landscape connectivity for these species, partially at the expense of lower timber production [38,42]. Even if plantations often support fewer specialist species than natural ecosystems, under some conditions they can play an important role in biodiversity conservation and recuperation [18]. Particularly at the landscape level, plantations can provide habitats for native species [38] and catalyze secondary successional process [47]. Taking into account the current planted area in Uruguay and the expected increase for the future [11], improving the ability of plantations to harbor a higher diversity of native species becomes an important goal to meet the challenges of the 21st century. Nature conservation approaches have to pass traditional reserve-based approaches toward the landscape scale. It is crucial to marry productive land uses with biodiversity targets by offering an evidence-based practical blueprint for effective decision making for local stakeholders [48]. This includes the implementation of mixed species stands, mixed plantation buffer strips, and approaches to balance the coverage of young and older stands in order to reduce the biodiversity loss within aging *Eucalyptus* plantations [37,42].

4.2. Forest Diversity and Composition

Between native forests, species diversity was highest in riverine forests (Figure 2e). Similar values of diversity indices have been reported for the forests of the Queguay River in Uruguay [26] and for a forest of the Ibirapuitã River in Brazil [43]. Another study [25] registered a higher number of species within the large national nature reserve of Montes del Queguay (Uruguay). In the latter study, the differences could be explained by the methodology used, which consisted of smaller plots that included various types of riverine and park forests. Forest composition showed significant distinctive

community groups, which were highly correlated with species diversity, horizontal structure diversity, and regeneration (Figure 3a). These variables are often reported to positively correlate with native communities and negatively correlate with plantations [49]. The majority of the native forest species that were found in our study have a wide distribution in Uruguay and South America [14,50], and have been reported in other riverine and park forests of Uruguay [51,52].

Native forests of the northwestern part of Uruguay have species that are absent in *Eucalyptus* plantations such as *Citharexylum montevidense*, *Cordia americana*, *Prosopis affinis*, *Pouteria salicifolia*, and *Sebastiania brasiliensis*, among others (Table 1). This highlights the importance of native forests as refuges for native tree species in highly modified landscapes. We recorded the exotic species *Ligustrum lucidum*, *Gleditsia triacanthos*, and *Melia azedarach* regenerating in native forests. All were registered in other native forests of Uruguay [53,54]. In our study, the total proportion of exotic species did not differ between native forest types (Figure 2i). This contrasts a study that found higher densities of exotic species in riverine forests compared to park forests along roads near the Uruguayan city of Rivera [54]. However, our study demonstrates that both park and riverine forests are similarly invaded by exotics. Riparian zones have also been invaded by *G. triacanthos* and *L. lucidum* in Argentina [55,56]. *G. triacanthos* comprises a set of characteristics that are typical for successful invaders such as fast growth, clonal reproduction, and high seed production and germination ability, and is currently expanding in Uruguay in areas that are frequently grazed by livestock and in transition zones between invaded native forests and adjacent extensively used grasslands, suggesting a grazing mediated dispersal (unpublished data). *L. lucidum* is able to easily dominate the native forests by competing and suppressing the growth of native species such as *Myrcianthes cisplantensis* and *Allophylus edulis* due to its high adaptability and regeneration capacity [51]. In Argentina, *L. lucidum* causes high mortality rates of *Celtis ehrenbergiana*, limiting its regeneration [57]. Management programs of these invasive species, especially of *G. triacanthos*, must be developed urgently in the riverine and park forests of Uruguay. Up to date, the first experiments on invasion control along the National Park of the Uruguay River focused only on the application of systemic herbicides in riverine forests [58].

4.3. Native Species Importance Value Index and Potential Use

To our knowledge, our study analyzed for the first time the IVI for native forest species including park forests in Uruguay, besides local case studies. The species with the highest IVI were *Allophylus edulis*, *Pouteria salicifolia*, and *Sebastiania brasiliensis*. This is consistent with other studies in riverine forests in Uruguay [53,54] or in Brazil [44,59]. The IVI values are comparable with those reported for Brazil [43], which also showed high values for *Pouteria salicifolia*. Similar forest types in Argentina and Brazil also recorded high IVI values for *Prosopis affinis* and *Vachellia caven* [60]. Even though Uruguay has the highest afforestation rate in South America [61], the use of native species in afforestation is absent. This was related to the growth habits of multi-branched, short, and thin tortuous trunks [54]. The traditional use of native trees is mostly restricted to fuelwood [51]. Nevertheless, our study demonstrated that species with high IVI and regeneration density have a great variety of potential uses (Figure 3c,d, Table 1).

The wide range of non-timber forest products and services offers pathways toward a multifunctional silviculture in moving from timber or pulp-dominated models into more pluralistic production models [62], but also provides challenges to establishing local markets and enhancing the livelihood of local communities [63]. As an example, *Allophylus edulis*, *Sebastiania brasiliensis*, and *Pouteria salicifolia* have potential for restoration projects due to their high IVI values and considerable representation in riverine forests. *Allophylus edulis* and *Sebastiania brasiliensis* were already used for the environmental restoration of degraded areas in the Atlantic forest of Brazil [64]. These species can be used as buffers between plantations and riverine forests. Legumes with the highest IVI value such as *Vachellia caven* and *Prosopis affinis* in park forests are also relevant due to their capacity to biologically fix atmospheric nitrogen, ecological plasticity, and colonization capacity [17,65]. Our data demonstrate that both species have a potential for buffer strips between plantations and neighboring native

grasslands to foster the local biodiversity pool. They have been identified as keystones promoting forest regeneration and recovery in highly modified landscapes (Pozo and Säumel, in preparation). *Vachellia caven* and *Prosopis affinis* have already been used for the reforestation of degraded habitats and for silvopastoral systems in Argentina and Chile [65]. Moreover, these species provide refuge for native wildlife and food for livestock and wild animals, such as nectar for honey-producing bees [17]. *Prosopis affinis* is also important by its high wood quality [16]. It is necessary to explore the potential of these and other Leguminosae species that can establish under plantations. N-fixing species could be a potential choice for the establishment of mixed stands with *Eucalyptus* [45]. Compared with monocultures, mixed-species plantations of *Eucalyptus* with N-fixing species are reported to result in increased productivity, while maintaining soil fertility and improving ecosystem services in China [39]. Species of Myrtaceae with high IVI value, such as *Blepharocalyx salicifolius*, are used for urban afforestation and restoration, and have also been used for medicinal purposes [66]. Others such as *Eugenia uniflora*, *Myrcianthes cisplatensis*, and *Myrcianthes pungens* provide fruits and pollen for wildlife, and are used as ornamental trees [66]. Studies in the Atlantic forest highlight the role of *Eugenia uniflora*, which contributes to bee biodiversity, and at the same time provides food for the avifauna [67]. Although the trunk of *Schinus longifolius*, which is a common species in park forests with high IVI values, has small dimensions, it has been used to produce furniture. Its fruits have been used to produce beverages and vinegar, and the plant itself has medicinal and ornamental potential, and is well known because of its tanning properties [53].

5. Conclusions

Native forests in Uruguay have high structural diversity, regeneration capacity, and species diversity. They harbor a distinctive species composition that is absent or rare in *Eucalyptus* plantations, including the presence of *Citharexylum montevidense*, *Cordia americana*, and *Jodina rhombifolia*, among others. Therefore, they play a decisive role in maintaining biodiversity in agricultural and silvicultural modified landscapes. The abundance of exotic species such as *Ligustrum lucidum*, *Gleditsia triacanthos*, and *Melia azedarach* is also noted in native forests. The invasion of exotic tree species into native forests is ongoing, and strategies to face this are urgently needed. The regeneration of native woody species such as *Allophylus edulis*, *Blepharocalyx salicifolius*, and *Celtis ehrenbergiana* in the understory of *Eucalyptus* plantations demonstrates the possibility of developing management strategies such as mixed-species and multiple-age plantations. Native species with the highest importance value indexes such as *Eugenia uniflora*, *Allophylus edulis*, *Vachellia caven*, and *Prosopis affinis* promise various ecological, economic, and social benefits for future forestry projects. More research is needed to develop approaches using native tree species in order to foster the multifunctionality of productive landscapes. The lack of studies is evident in South America, although it is crucial for the development of biodiversity-friendly plantations [68]. The critical stages for biodiversity outcomes in plantation management have to be identified in order to promote understory diversity and foster habitat services for native species. Experience and guidelines that consider wood production, management simplicity, logging costs, and financial security, among others, can be adapted from forest projects worldwide [69]. As grassland afforestation will continue rising in the near future in Uruguay, the sustainability of *Eucalyptus* plantations, including other ecosystem services beyond wood provision, is an important need. The wide range of benefits provided by 'shared' mosaic landscapes composed of different native forests, plantations, crops, and grassland are widely recognized, and can be effectively supported by land-sharing policies [70]. Mixed plantations, at least in buffer strips between exotic plantations and native forests, can provide case studies for long-term and larger-scale evaluations on the potential of the native tree species assessed in this study, and are a promising step toward multifunctional, sustainable, productive, and biodiversity-friendly landscapes.

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Appendix A

Supplementary References for Table 1 Species Composition and Potential Use of Tree Species in Different Uruguayan Forest Types

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