Forest plantations and native forests: Strategies to achieve multifunctional, biodiverse and sustainable forest landscapes

Case Study: Uruguay, South America

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von der Fakultät VI-Planen Bauen Umwelt
der Technischen Universität Berlin
zur Erlangung des akademischen Grades

Doktorin in Naturwissenschaften rerum naturalium
-Dr. rer. nat.-

genehmigte Dissertation

Promotionsausschuss:

Vorsitzende: Prof. Dr. Gabriele Dolff-Bonekämper
Gutachterin: Prof. Dr. Eva Paton
Gutachter: Prof. Dr. Pierre L. Ibisch
Gutachterin: Dr. Ina Säumel

Tag der wissenschaftlichen Aussprache: 25. März 2019

BERLIN 2019

List of publications submitted within the thesis

How to Bloom the Green Desert: *Eucalyptus* Plantations and Native Forests in Uruguay beyond Black and White Perspectives. Paola Pozo and Ina Säumel. Published in Journal Forests 2018, 9(10), 614; https://doi.org/10.3390/f9100614.

Positive tree-tree interactions facilitate dry forests persistence in agricultural modified landscapes in Uruguay. Paola Pozo and Ina Säumel. Submitted to Plant Ecology

From master of one towards jack of all traits? Extending the range of ecosystem services provided by timber plantations using diversified tree trait selection in the Global South. Paola Pozo and Ina Säumel. To be submitted to New Forests

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Study case: Uruguay, South America

Multifunctional Native Forests (Rio Negro, Uruguay)

ACKNOWLEDGEMENTS

I would like to express my gratitude to all those people who have supported me and had bring their contributions to make this thesis possible.

Firstly, my special thanks to my supervisor Dr. Ina Säumel for giving me the opportunity to write my PhD in her research group. Thank you for encouraging my research, your suggestions and your valuable contributions.

I also would like to acknowledge my colleagues of the research group Multifunctional Landscapes for being willing to help and contributing in various ways and making this work an enriching learning environment.

I would like to thank John Wood from Oxford University, for his constant guidance, support and motivation during my career and for helping me with his corrections in the English language.

I am also thankful to the local communities and landowners of Uruguay, for letting me undertake the fieldwork and collect samples in their properties and their support during field work, making it an enjoyable experience. I extent my gratitude to Nicolas Silveira, Ignacio Balbis and Giannina Lemus for their assistance during the field work activities.

Finally, I would like to thank my parents and friends for providing me with unfailing support and continuous encouragement throughout my years of study and during the process of researching and writing this thesis.

The study was funded by the German Federal Ministry of Education and Research (BMBF) under the project "Rural Futures - Strategies towards multifunctional, biodiverse and sustainable productive landscapes in silvi- and agricultural modified grasslands in Uruguay" (01LN1315).

TABLE OF CONTENTS

Page

List of Tables

LIST OF FIGURES

FIGURE **Page**

Abstract

The area covered by monoculture timber plantations of fast-growing exotic species has increased exponentially over the last years and the impact on local ecosystems has been controversially debated, especially in the countries of the global South. With a current need to develop alternative approaches that achieve forest productivity while conserving biodiversity new strategies need to be tackled. In order to design strategies for multifunctional and sustainable forest landscapes, this research developed different studies with emphasis in Uruguay. In Chapter 2 a systematic review of literature was performed to study the potential use of native species for timber plantations, identify common traits and criteria of choosing species and propose alternative approaches for species selection. It was found that although research regarding the use of native species for timber plantations has increased about threefold in the last years, knowledge is still limited regarding silvicultural management. Most studies select native species purely for their potential for timber production, additional benefits and ecosystem services are regularly omitted. Species traits are chosen at the stand scale, the most frequent being (fast) *growth* and *wood quality*. Chapter 3 includes an evaluation of native forests and *Eucalyptus* plantations in Uruguay, their role in promoting diversity and the use of ecological properties of natural forests to better manage current plantations. Clear differences in the woody communities between native forests and *Eucalyptus* plantations were identified. Native forests harbor specialist species that are absent from plantations, and therefore perform a decisive role in maintaining local biodiversity. However, the regeneration of native woody species found in the understory of *Eucalyptus* plantations demonstrates the possibility of developing management strategies such as mixed-species and multiple-age plantations. Chapter 4 focused on the most threatened forest type of Uruguay and explored the role of scattered trees for the development of strategies to design multifunctional landscapes in grazed forests. The results highlight the role of scattered trees to the promotion of forest regeneration and recovery. Trees facilitate regeneration by providing shade, reducing grass competition, giving protection against herbivores and promoting species regeneration linked to the attraction of seed dispersers. In summary, there are potential strategies to develop biodiverse and multifunctional forest landscapes in Uruguay. It is important to promote the use of native species in plantations and incorporate traits with a wider range ecosystem functions and services. Those traits must be able to create connectivity across landscapes and build adaptability and resilience in timber plantations (i.e. *pollination mode*, *dispersal mode* and *N-fixing capacity*), while considering the wide spectrum of interests among landowners and local communities. The conservation of native forests and the development of mixed plantations should be encouraged in Uruguay, at least as buffer strips containing native species at the edge of plantations as potential measures to enhance biodiversity and foster the integration of plantations into the local landscape. Finally, scattered native trees in park

forests are of paramount importance not only for restoration measures but also for the creation of natural silvopastoral systems based on grazing and the maintenance of the native tree layer while preserving ecosystem functions. Future studies integrating other regions of Uruguay, multiple taxonomic groups and other land use types are necessary to develop definite landscape management schemes in Uruguay.

ZUSAMMENFASSUNG

Die Anbaufläche von Monokulturen mit schnell wachsenden exotischen Baumarten nahm in den letzten Jahren exponentiell zu und ihre Auswirkungen auf lokale Ökosysteme wurden besonders in Ländern des Globalen Südens kontrovers diskutiert. Mit dem aktuellen Bedarf, alternative Ansätze zu entwickeln, welche die Produktivität der Wälder bei gleichzeitiger Erhaltung der Biodiversität gewährleisten, müssen neue Strategien entwickelt werden. In der vorliegenden Arbeit wurden verschiedene Strategien für multifunktionale und nachhaltige Waldlandschaften entwickelt. Zunehmende Landnutzungsänderungen in Uruguay hin zu exotischen Monokulturen für den globalisierten Markt sind ein Schwerpunkt dieser Arbeit. In Kapitel 2 wurde eine systematische Literaturrecherche durchgeführt, um die Verwendung einheimischer Arten für Holzplantagen zu untersuchen, gemeinsame Merkmale und Kriterien für die Auswahl der Arten zu ermitteln und alternative Ansätze für die Artenauswahl vorzuschlagen. Obwohl sich die Forschung hinsichtlich der Nutzung einheimischer Arten in Holzplantagen in den letzten Jahren nahezu verdreifachte, ist das Wissen über die waldbauliche Bewirtschaftung jedoch immer noch begrenzt. Die meisten Studien untersuchen einheimische Arten nur aufgrund ihres Potenzials für die Holzproduktion, während zusätzliche Vorteile und Ökosystemleistungen häufig unbeachtet bleiben. Die Artmerkmale werden auf der Bestandesebene ausgewählt, wobei meist auf ein schnelles Wachstum und die Holzqualität fokussiert wird. Kapitel 3 beinhaltet die Bewertung der einheimischen Wälder und Eukalyptusplantagen in Uruguay und erfasst ihre Rolle bei der Förderung der Vielfalt und untersucht wie die ökologischen Eigenschaften natürlicher Wälder genutzt werden können um Plantagen besser bewirtschaften zu können. Es wurden deutliche Unterschiede in den Waldgemeinschaften zwischen einheimischen Wäldern und Eukalyptusplantagen festgestellt. Heimische Wälder beherbergen spezialisierte auf den Plantagen fehlende Arten, welche eine entscheidende Rolle für den Erhalt der lokalen Biodiversität spielen. Die Verjüngung einheimischer Holzarten, die im Unterwuchs von Eukalyptusplantagen zu finden ist, zeigt jedoch die Möglichkeit der Entwicklung von Bewirtschaftungsstrategien für Plantagen mit Mischarten oder mit diverser Altersstruktur. Kapitel 4 konzentriert sich auf den am stärksten bedrohten Waldtyp Uruguays und untersucht die Rolle von verstreut angeordneten Bäumen für die Entwicklung von Strategien zur Gestaltung multifunktionaler Landschaften in beweideten Wäldern. Die Ergebnisse unterstreichen den Einflusssolcher Bäume bei der Förderung von Verjüngung und Regeneration der Wälder. Bäume fördern die Verjüngung, indem sie Schatten spenden, den Grasbewuchs verringern, vor Pflanzenfressern schützen und die Artenregeneration fördern, die mit dem Anziehen von Saatgutverteilern zusammenhängt. Zusammenfassend lässt sich sagen, dass es mögliche Strategien zur Entwicklung von artenreichen und multifunktionalen Waldlandschaften in Uruguay gibt. Hierbei ist es jedoch wichtig, die Nutzung einheimischer Arten in Plantagen zu

fördern und Merkmale mit einer breiteren Palette von Ökosystemfunktionen und -dienstleistungen zu integrieren. Anhand diese Merkmale muss es möglich sein, Landschaften miteinander zu verbinden und Anpassungsfähigkeit und Widerstandsfähigkeit in Holzplantagen zu schaffen (zum Beispiel Bestäubungsmodus, Ausbreitungsmodus und N-Fixierungskapazität), wobei das breite Spektrum der Interessen zwischen Großgrundbesitzern und lokalen Gemeinschaften zu berücksichtigen ist. Die Erhaltung einheimischer Wälder und die Entwicklung von Mischplantagen sollte zumindest in einem Pufferstreifen am Rande von Plantagen angestrebt werden, der einheimische Arten enthält, um die Biodiversität zu erhöhen und die Integration von Plantagen in die lokale Landschaft zu stärken. Insgesamt sind verstreute einheimische Bäume in Parkwäldern nicht nur für Wiederherstellungsmaßnahmen von größter Bedeutung, sondern auch für die Schaffung natürlicher silvopastoraler Systeme, die auf Beweidung und Aufrechterhaltung der natürlichen Baumschicht beruhen, wobei die Ökosystemfunktionen erhalten bleiben. Weitere Studien in anderen Regionen des Uruguays, die mehrere taxonomische Gruppen und andere Landnutzungsarten integrieren, sind notwendig, um konkrete Landschaftsmanagementsysteme in Uruguay zu entwickeln.

CHAPTER 1

General Introduction

Global forest resources are essential for conservation of biological diversity, water and soil resources as well as for meeting human needs for wood and non-wood forest products (Siry et al. 2005). Alteration and fragmentation of forest landscapes compromise their ecosystem processes and functions (Laurance et al. 2002). It is estimated that more than one-third of global forest cover has been lost (Defries 2012)—whether converting natural landscapes for human use or changing management practices on human-dominated lands (Foley et al. 2005). Indeed, the global forest area declined by 3% from 1990 (4128 M ha) to 2015 (3999 M ha) (Keenan et al. 2015). Although causes of forest loss vary greatly across the world, their ultimate outcome is generally the same: the acquisition of natural resources for immediate human needs (Foley et al. 2005).

Forest loss varies considerably by region and is currently most severe in the tropics and highest in low income countries of Central America, South America, South and Southeast Asia and all three regions in Africa (Keenan et al. 2015). Forests have been cleared and converted for agricultural uses, resulting in habitat loss and carbon emissions (Nikolakis and Innes 2017). The development of oil palm plantations has been the major cause of recent forest loss in Malaysia and Indonesia (Wilcove and Koh 2010). While tropical dry forests of South America had the highest rate of tropical forest loss, due to deforestation dynamics in the Chaco woodlands of Argentina, Paraguay and Bolivia (Hansen et al. 2013). Of all countries globally, Brazil exhibited the largest decline in annual forest loss and Indonesia exhibited the largest increase in forest loss (Hansen et al. 2013).

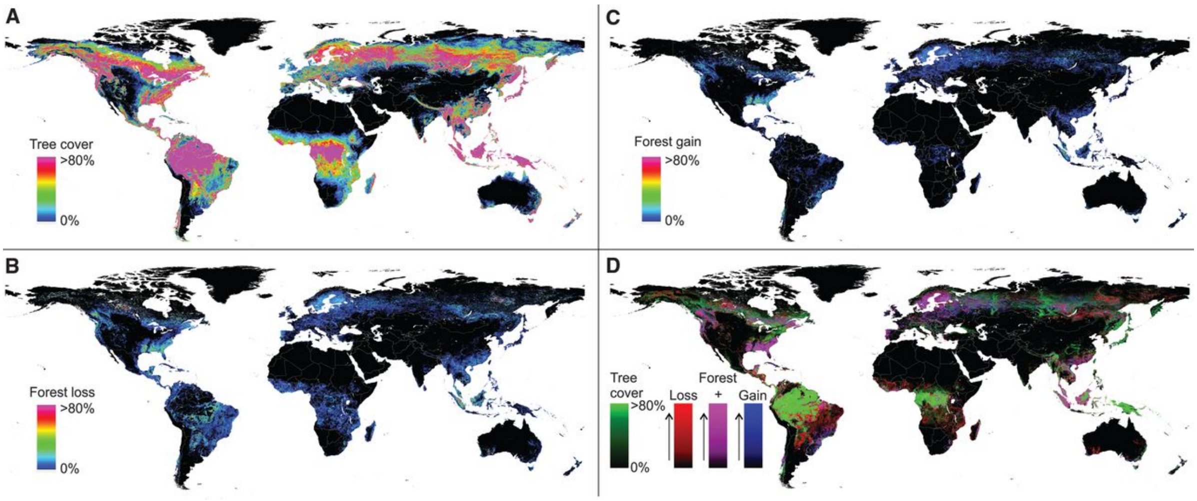

Figure 1.1 – (A) Tree cover, (B) forest loss, and (C) forest gain. A color composite of tree cover in green, forest loss in red, forest gain in blue, and forest loss and gain in magenta is shown in (D), with loss and gain enhanced for improved visualization. All map layers have been resampled for display purposes from the 30-m observation scale to a 0.05° geographic grid (Extracted from Hansen et al. 2013).

Contrary to the area of natural forests loss, plantations forests or planted forests — forest ecosystems established by processes of afforestation and reforestation — are expanding all over the world (Pawson et al. 2013). Their importance has increased exponentially not just in temperate countries but also in the tropics, primarily designed as climate change mitigation strategy (Gibbard et al. 2005) but also to meet demand for wood-based products and to protect remaining natural forests from over-exploitation (Bonan 2008). Planted forests (including plantation forests) nearly doubled since 1990 and comprise 278 million ha, equivalent to 7% of global forested area (Payn et al. 2015).

Afforestation—the conversion of non-forested lands to forest plantations—has rapidly increased in recent decades. It is estimated that 34 million more hectares will be afforested by 2020 (Berthrong et al. 2009a). Afforestation is often established as easily manageable monocultures (Nichols et al. 2006; Lang et al. 2014) of fast-growing exotic tree species, native species are only used in a smaller subset of afforested areas (Berthrong et al. 2009a). Well known species and interspecific hybrids of a few genera dominate afforestation worldwide (e.g., *Tectona*, *Eucalyptus*, *Pinus*, and *Acacia*) which are selected for their easy establishment and short-term higher productivity (Evans and Turnbull 2004).

In temperate grasslands of southern South America, habitat loss and degradation have been severe due to grassland afforestation and the conversion to agriculture, including row crops and cattle pasture (Six et al. 2014). Today, only 10% of the region's native grassland and savanna remains, with less than 1% currently protected within the global system of protected areas (Henwood 2010). Remnants of this habitat are located mainly in the norther part of the region, in the northeastern Argentina, Uruguay and southern Brazil (Vega et al. 2009). The extensive areas covered by native grasslands are still being afforested with non-native species at increasing rates (Six et al. 2014) often motivated by governmental policies and reinforced by the carbon sequestration market. As examples, Brazilian grasslands have undergone extensive transformation and large areas of native grasslands have been converted to monocultures of exotic trees such as *Eucalyptus*, *Pinus*, and *Acacia* (Overbeck et al. 2007; Bond and Parr 2010). *Eucalyptus* (mostly *Eucalyptus grandis*) is the dominant plantation tree expanding in the grasslands of Argentina and Uruguay, though *Pinus* is also present (FAO 2015; Phifer et al. 2017).

The implications for the conservation of biodiversity of afforestation and their continuing expansion are controversially debated in literature (Brockerhoff et al. 2008; Bremer and Farley 2010; Pawson et al. 2013). While some authors have described them as *green deserts* (Stephens and Wagner 2007) others highlighted the enhance landscape level biodiversity where natural forests are rare (Calviño-Cancela et al. 2012) and have been shown to provide suitable habitats for a wide range of forest species, including species of conservation concern (Brockerhoff et al. 2013). In natural grassland areas, however, afforestation is detrimental (Brockerhoff et al. 2008). The main biotic impacts in afforested grasslands with exotic species include changes in abundance, diversity and composition of species and disruption of ecological processes (Berthrong et al. 2009b; Six et al. 2014).

Alternative sustainable forest management approaches that include the use of mixed plantations or/and the use of native tree species in plantations are widely acknowledged (Davis et al. 2012; Puettmann et al. 2015). They aim to mimic natural processes and provide a large set of ecosystem services beyond timber production (Hall et al. 2011; Puettmann et al. 2015). Since the trend of increasing planted area is likely to continue, consequently, the planted forests of the future will increasingly need to provide important environmental benefits, including biodiversity conservation and associated ecosystem goods and services (Brockerhoff et al. 2013). Forest plantations that are diverse in genotypes, species, structure and function, should be better able to adapt to changing environmental conditions than monocultures (Verheyen et al. 2016).

In Uruguay, the rate of afforestation with exotic species increased over 400% from 201,000 to 1,062,000 hectares between 1990 and 2015 (FAO 2014), making it the country with the highest afforestation rate in South America (FAO 2018). Large-scale afforestation began in the 1980s, when large pulpwood companies were attracted to the region by governmental tax benefits and financial subsidies (Vihervaara et al. 2012). Plantations are located mainly in the north, northwest, and northeast of the country. Today, *Eucalyptus* (83%) and *Pinus* plantations (15%) (Paruelo et al. 2006) occupy more than 6% of the Uruguayan territory which represents a total of 58% of the forest cover in Uruguay while native forests occupy 42% of the forest cover (FAO 2015).

Native forests of Uruguay are scattered within a matrix dominated by grasslands and crops, forming biological corridors for avian and mammalian biodiversity (Nores et al. 2005; Haretche et al. 2012; Lucas et al. 2017). They range from savanna-like formations such as ‘park forests’ to riverine or gallery forests, creek forests, and hill forests (Brussa and Grela 2007). The predominant natural forest type in Uruguay is riparian (Lucas et al. 2017). In total, 150 different native tree species have been reported for Uruguay, which represents a high diversity for a temperate grassland region (Brussa and Grela 2007; Haretche et al. 2012). 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 (Bennadji et al. 2012; Castillo et al. 2014). However, the lack of knowledge and limited information on native species has promoted the use of exotic species in afforestation projects.

In order to develop strategies for multifunctional and sustainable forest landscapes in native forests and plantations, with special focus in Uruguay, this research developed different research studies.

i) **Chapter 2** ***“From master of one towards jack of all traits? Extending the range of ecosystem services provided by timber plantations using diversified tree trait selection in the Global South”*** performed a systematic review of literature regarding the selection of native species for timber plantations with the aim to identify common traits and criteria, summarize knowledge gaps on timber potential of native trees, and propose alternative approaches for native species selection.

ii) **Chapter 3** ***“How to Bloom the Green Desert: Eucalyptus Plantations and Native Forests in Uruguay beyond Black and White Perspectives”*** includes an evaluation of native forest and forests plantations of Uruguay (i.e., park forests, riverine forests, and *Eucalyptus* plantations) and the assessment of their value to promote biodiversity. In this chapter we also explored how the ecological properties of natural forests can be used to better manage current plantations.

iii) **Chapter 4** ***“Positive tree-tree interactions facilitate dry forests persistence in agricultural modified landscapes”*** includes and detailed evaluation of the most threatened forest type of Uruguay. Tree to tree interactions and the role of native scattered trees to promote forest regeneration and recovery in grazed forests are analyzed. The practical implications for the management of park forests and for the development of strategies to design multifunctional landscapes are discussed.

iv) **Chapter 5** ***“Synthesis”*** brings together individual results of the previous chapters, discuss them and bring some concluding remarks.

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CHAPTER 2

FROM MASTER OF ONE TOWARDS JACK OF ALL TRAITS? EXTENDING THE RANGE OF ECOSYSTEM SERVICES PROVIDED BY TIMBER PLANTATIONS USING DIVERSIFIED TREE TRAIT SELECTION IN THE GLOBAL SOUTH

Abstract. The area covered by industrial tree plantations of fast-growing exotic species has increased fourfold over the past two decades and continues to increase rapidly in South America and Africa. Experience using native species for timber production in countries of the Global North demonstrates that native trees fulfill multiple but often neglected ecosystem services, are attractive in terms of economic returns in the long term and are more stable and adaptable in our rapidly changing world. We performed a systematic review of literature in the Web of Science to identify the knowledge gap about forestry diversification in countries of the South. We evaluated the criteria and traits of the native species selection in 36 research papers. Although research has increased about threefold in recent years, knowledge of the use of native species in silvicultural management is still limited. Most studies select species purely for their potential for timber production, although some take into account the ecological benefits in soil restoration. Additional benefits and ecosystem services (e.g. for pollination, reduction in the risk of flooding or health promotion) and especially socio-cultural services are regularly omitted from the selection process. Up to now, traits for timber production were chosen at the stand scale, the most frequent being (fast) *growth* and *wood quality*. Future

trait selection has to expand at the landscape scale, supporting biogeochemical processes and trophic interactions (i.e. *pollination* and *dispersal mode* and *N-fixing capacity*) and include the preference of local residents. We advocate a multifunctional approach that incorporates a range of ecosystem functions and services creating connectivity across landscapes and building adaptability and fostering resilience in timber plantations, while taking into account the wide spectrum of interests among landowners and local communities.

Keywords: native species, forestry diversification, trait, multiple ecosystem service, adaptation

2.1 Introduction

Despite global efforts to integrate biodiversity goals in human modified landscapes, there is an active ongoing debate about the relative productivity of biodiverse forests versus monocultures (Barrett et al. 2016; Liang et al. 2016). From an ecological perspective one can marvel at the ecosystem services provided by forests and their structural, compositional, and dynamic variability, where each element has a function and adds complexity and resilience to ecosystems (Puettmann et al. 2010). In contrast, conventional forest management sees forests through a timber production-focused lens and considers forests in terms of the growth and survival of economically important tree species (Puettmann et al. 2010; Davis et al. 2012), often targeting at the transformation of degraded woodlands or natural forests into the more orderly arrangements of desired tree species with even age classes (Puettmann et al. 2015). Thus, forest management often attempts to deal with the potentially conflicting goals of timber production and biodiversity conservation (Gustafsson et al. 2012). Bridging the gap between these different aims on forests, and between ecological theory and the forester's practice remains challenging.

Different countries of the Global South (e.g. Brazil, Chile, Uruguay) have placed a greater emphasis on monocultures (Garen et al. 2011; Davis et al. 2012; Overbeek et al. 2012; Pozo and Säumel 2018), aiming to produce timber and pulp for paper by using a small set of well-known, fast-growing exotic species (i.e. *Acacia*, *Eucalyptus*, *Pinus*, *Tectona*) for established markets (Montagnini 2001). These species have been favored because of their apparent short-term higher productivity, management advantages (e.g. fast growth, germplasm availability) allowing harvesting in fixed rotation cycles (Evans and Turnbull 2004; Harrison et al. 2005; Calvo-Alvarado et al. 2007). However, they have been criticized for the limited ecosystem services and biodiversity co-benefits that they provide in the long-term (Lantschner et al. 2008; Liang et al. 2016; Lu et al. 2016). The benefits of more sustainable approaches to forest management are widely acknowledged (reviewed by Mori, Lertzman, & Gustafsson, 2017). These approaches aim to diversity the structure of plantations, develop mixed species systems, establish longer harvest rotation cycles, and use native tree species in plantations while avoiding intensive site-preparation methods (Puettmann et al. 2015). Thus, they are able to mimic natural processes and provide a large set of ecosystem services (Hall et al. 2011; Puettmann et al. 2015). The benefits go beyond timber production and include wildlife and ecological conservation, efficient soil restoration and meet several socio-cultural needs such as traditional uses (Montagnini et al. 2004; Garen et al. 2009; Hall et al. 2011; Irwin et al. 2014). The most promising approach, however, lies in changing the plantation paradigm and use native tree species (Davis et al. 2012).

Countries of the Global North (e.g. US, France, Germany and China) have long experienced the economically successful use of native forest plantations (Brockerhoff et al. 2008). Although there is a growing literature in the South regarding the use of native timber species in forestry projects, their potential for the forestry industry has received less attention. Thus, we performed a systematic review of literature to i) evaluate available studies of native timber potential in the Global South, ii) identify common traits and criteria for choosing native species for timber production, iii) summarize knowledge gaps on the timber potential of native trees, and iv) propose alternative approaches for the selection of native species in order to extend the range of ecosystem services provided by timber plantations.

2.2 Methods

We undertook a systematic review of scientific articles written in English in the Web of Science following PRISMA guidelines (Shamseer et al. 2015) by using keywords covering studies on native tree species and forestry projects (See Table 2.2 for details). The advanced keywords search in the web of science revealed 432 papers related to the topic or title fields. Numerous papers focus on species descriptions or non-wood forest products and were not relevant to the study; thus, we filtered the results using the following criteria: i) studies that include native species with timber potential-species with purely non-timber uses were excluded; ii) purely descriptions of species were not included; iii) studies of species native to the countries of the 'Global South' (i.e., countries in Africa, Asia, and Latin America). We filtered the results keeping 36 articles published between January 1998 and December 2018 that directly address the topic. As a first step, we screened the titles and abstracts of the remaining articles and eliminated articles that were not related to our topic. Secondly, we eliminated articles without access to the full text version but sent requests for the most relevant ones. Thirdly, we made a full text review of the remaining articles to gather relevant information. Additionally, relevant papers found by cross-references in our research were included. We identified the range of ecosystem services provided by timber plantations allocated in the triangle between economic, environmental and socio-cultural management approaches based on the Economics of Ecosystems and Biodiversity: Ecological and Economic Foundations (TEEB) (Kumar 2012) and identified those chosen in the in the analyzed studies (criteria of selection) for all papers and countries. We screened and identified the most frequent traits for selecting the native species. To standardize trait names, we used the classification used in plant trait databases (TRY, FLOWBASE; see Pérez-Harguindeguy et al. 2013).

2.3 Results

A total of 36 research papers were reviewed from 9 different countries for the years 1998-2018. The greatest number of papers originated from Central America (64%) followed by South America (17%) and Asia (14%). Overall, research on native species shows uneven use of ecological, economic and socio-cultural criteria. More than half of the studies (59%) focus purely on timber production, 36% incorporate an environmental criterion whereas the incorporation of socio-cultural criteria was considered in only 5% of the studies (Table 2.1, Figure 2.1b). Among the cited environmental criteria, soil restoration and connectivity are the most frequently cited (17%), these are mostly mentioned in Central American studies. In contrast, socio-cultural criteria including traditional uses are cited within studies originating from both Central America and Mexico (7%). The traits used to select native tree species differ largely among studies (Figure 2.1c, Table 2.1). The most frequent traits used in the selection process include *(fast) growth* (Eugenio González and Fisher 1994; Montagnini et al. 1994, 2003, Butterfield 1995, 1996; Haggar et al. 1998; Barchuk et al. 1998; Tilki and Fisher 1998; Foroughbakhch et al. 2001; Wightman et al. 2001; Engel and Parrotta 2001; Piotto et al. 2003a, b, 2004, 2010; Verzino et al. 2004; Carpenter et al. 2004; Petit and Montagnini 2006; Piotto 2007; Redondo-Brenes 2007; Wishnie et al. 2007; Calvo-Alvarado et al. 2007; Andrade et al. 2008; Santos Martin et al. 2010; Sovu et al. 2010; Arias et al. 2011; Hall et al. 2011; Plath et al. 2011; Breugel et al. 2011; Román-Dañobeytia et al. 2012; Schneider et al. 2014; Widiyatno et al. 2014; Chechina and Hamann 2015; Mayoral et al. 2017; Stuepp et al. 2017; Montes-Londoño et al. 2018), *wood quality* (Montagnini et al. 1994; Foroughbakhch et al. 2001; Piotto et al. 2003b, a; Carpenter et al. 2004; Redondo-Brenes 2007; Wishnie et al. 2007; Piotto 2007; Santos Martin et al. 2010; Breugel et al. 2011; Plath et al. 2011; Román-Dañobeytia et al. 2012; Widiyatno et al. 2014; Stuepp et al. 2017; Mayoral et al. 2017; Montes-Londoño et al. 2018) and *successional group* (Wightman et al. 2001; Engel and Parrotta 2001; Petit and Montagnini 2006; Redondo-Brenes 2007; Sovu et al. 2010; Breugel et al. 2011; Plath et al. 2011; Román-Dañobeytia et al. 2012; Widiyatno et al. 2014; Chechina and Hamann 2015; Stuepp et al. 2017; Mayoral et al. 2017; Montes-Londoño et al. 2018). *N-fixing capacity* (Tilki and Fisher 1998; Montagnini et al. 2003; Piotto et al. 2003b; Wishnie et al. 2007; Breugel et al. 2011) and *edibility* (Wightman et al. 2001; Piotto et al. 2004; Wishnie et al. 2007; Breugel et al. 2011; Stuepp et al. 2017) were the most frequent traits chosen with environmental criteria. Traits aiming at socio-cultural values were almost absent.

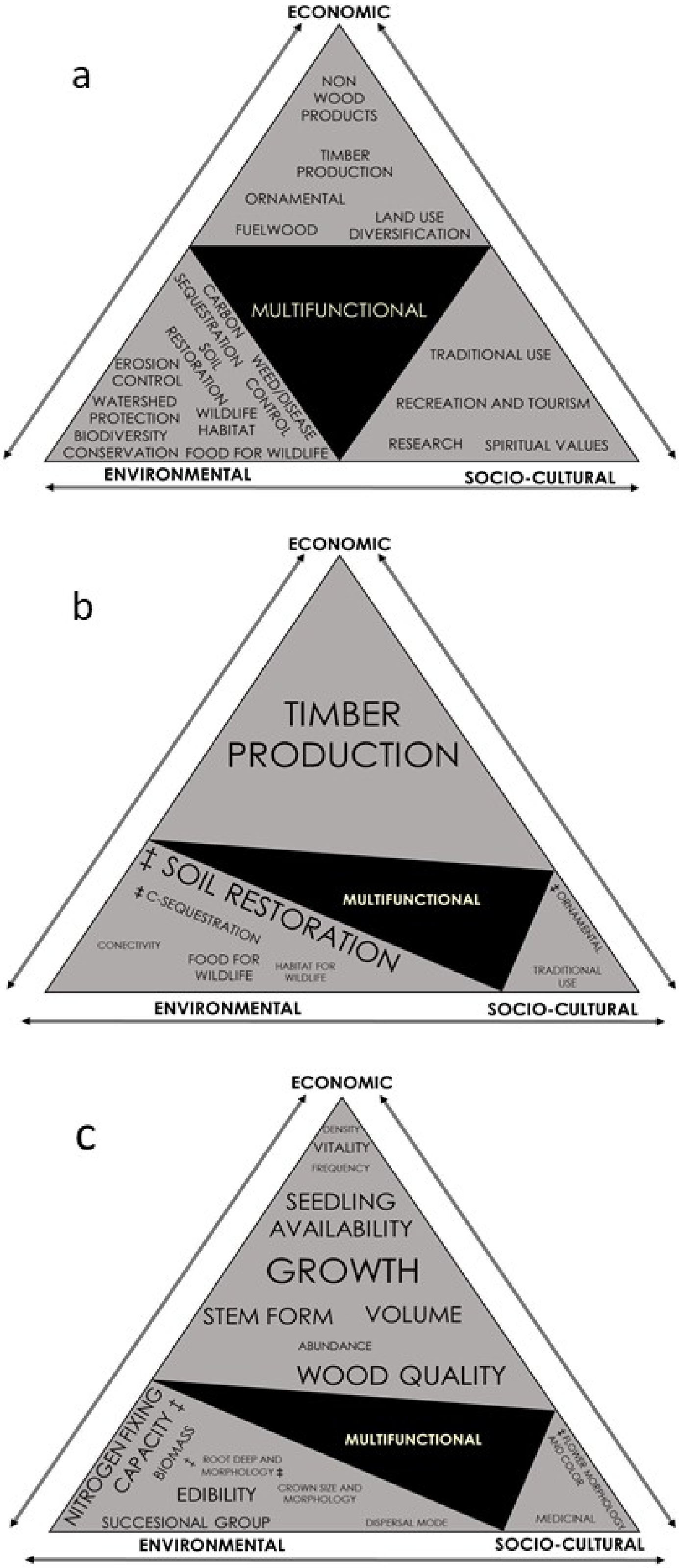

Figure 2.1 – a) Range of potential ecosystem services provided by timber plantations divided according to economic, environmental and socio-cultural management approaches. b) The frequency of criteria mentioned in the studies. The size of the triangle inside each of the three triangles represents the percentage of each approach in the overall studies. c) The frequency of traits used for native species selection mentioned in the analyzed papers. The font size of each word in Fig. b and c is equivalent to their frequency, (‡) traits that are shared in two approaches.

Table 2.1 – Summary of different management approaches in forestry projects of the Global South that use native tree species. Criteria and traits for species selection identified in the systematic literature review are described. The country, where studies were carried out is given. For shared traits used in different approaches, see Result section. The number in parenthesis indicates the reference*.

Approach	**Criteria**	**Approach Specific Traits**	**Country**
A) ECONOMIC			
Timber production	Species have potential or current use as wood products	Availability of seedling material (2, 4, 10, 16, 18, 24, 25, 27, 28, 30). Growth: Increase in height and diameter(1-36). Abundance: Number of individuals, abundant species have the ability to develop physiological adaptations depending on environmental conditions (1, 7). Density: Number of individuals over an area (22). Frequency: Occurrence of a species over an area (9). Stem form: Shape of the stem of a tree, characterized by the rate of decreasing diameter with height (1,5,6,11,12, 13,17, 18, 21,22,32,35). Vitality: Symptoms of damage that affect the vigor and productivity of a tree (5, 13, 32). Volume: Amount of wood, present in an individual tree (12, 13, 14, 19, 21, 22, 23, 24, 26, 32, 36). Wood quality: Species provide good quality wood (4, 8, 11, 15, 16, 17, 18, 20, 22, 23, 25, 26, 27, 28, 31, 34, 36). Successional group (4, 9, 10, 15, 18, 19, 25, 26, 27, 30, 31, 34, 35)	Argentina; Colombia; Costa Rica; Philippines; Panama; Brazil; Colombia; Indonesia; Mexico, Laos
B) ECONOMIC & ENVIRONMENTAL			
C-sequestration	Species have the capacity to fix and store greater amounts of atmospheric carbon in bark, stem, branches and leaves.	Biomass: amount of living matter in a given space (1, 2, 21).	Costa Rica
Soil restoration	Species have capacity to reduce erosion and increase soil fertility.	Root depth and morphology (12). Nitrogen fixing capacity (4, 16, 23, 32, 36).	Costa Rica; Panama; Brazil
C) ENVIRONMENTAL			
Habitat for wildlife	Species are fundamental in successional processes by creating local climate and habitat structures that favor the establishment of other species.	Crown size and morphology: Variation on size and shape of foliage or branches (35).	Costa Rica
Connectivity	Species are important fruit, seed and nectar resources for wildlife.	Edibility: Morphological characters and nutritional value of fruits, seeds, seedlings for wildlife (4, 24, 31, 35, 36).	Costa Rica; Panama; Brazil
	Species are key factors for landscape connectivity and ecological networks	Dispersal mode: Morphological characters of dispersion correlated to a particular agent (30)	Laos
D) SOCIO-CULTURAL			
Ornamental	Species have aesthetic characteristics and are commonly used for gardening or landscaping.	Flower morphology and color: Variation of the size and morphology of the flower (25)	Panama
Traditional uses	Species provide products for rural or local use	Medicinal properties (27)	Mexico

*1. Andrade et al., 2008; 2. Arias et al., 2011; 3. Barchuk et al., 1998; 4. Breugel et al., 2011; 5. Butterfield, 1995, 6. 1996; 7. Calvo-Alvarado et al., 2007; 8. Carpenter et al., 2004; 9. Chechina & Hamann, 2015; 10. Engel & Parrotta, 2001; 11. Foroughbakhch et al., 2001; 12. González & Fisher, 1994; 13. Haggar et al., 1998; 14. Hall et al., 2011; 15. Mayoral et al., 2017; 16. Montagnini et al., 2003; 17. Montagnini et al., 1994; 18. Montes-Londoño et al., 2018; 19. Petit & Montagnini, 2006; 20. Piotto, 2007; 21. Piotto et al., 2010; 22. Piotto et al., 2003b, 23. 2003a; 24. Piotto et al., 2004; 25. Plath et al., 2011; 26. Redondo-Brenes, 2007; 27. Román-Dañobeytia et al., 2012; 28. Santos Martin et al., 2010; 29. Schneider et al., 2014; 30. Sovu et al., 2010; 31. Stuepp et al., 2017; 32. Tilki & Fisher, 1998; 33. Verzino et al., 2004; 34. Widiyatno et al., 2014; 35. Wightman et al., 2001; 36. Wishnie et al., 2007.

2.4 Discussion

2.4.1 What limits the use of native species in the South?

Conventional forestry practices that maximize profits from timber production via intensive management systems have been strongly criticized for creating 'green deserts' (Brockerhoff et al. 2008; Bremer and Farley 2010). The use of native species contributes to changing the 'green desert' notion and amplify the range of ecosystem services provided by the plantations (Fonseca et al. 2009) as has been shown in temperate and boreal regions, where foresters have selected native trees for their improved yields (Price et al. 2005; Brockerhoff et al. 2008). Although, research into native species in the South has increased about threefold in the recent years, the identification of which native species have potential and which are best adapted to plantation management remains at initial stage. Knowledge gaps remain regarding the provenance and genetic improvement of native species, regarding their silvicultural management and the overall integration of timber plantations into the landscape. While extensive research into genetic improvement has been carried out for exotic plantations of *Pinus* and *Eucalyptus* (Montagnini et al. 2004), studies on native species cover only a small percentage of the available species. In only a few studies has a genetic selection program of the desired features (e.g. fast growth or soil recovery) been developed for native species, such as *Prosopis alba* in Argentina (Carreras et al. 2017) or *Myracrodruon urundeuva* in Brasil (Bertonha et al. 2016). Our results found that most research on native species was carried out in Central America (Table 2.1) and was supported by government incentives in reforestation projects. This has led to important advances in understanding of the silviculture of some native species in Central America (Montagnini et al. 2004; Piotto et al. 2010; Hall et al. 2011). In other countries expected to establish many plantations in the future, such as Brazil, Chile, Uruguay and Indonesia (Overbeek et al. 2012) the lack of information on native species and the undeveloped or unstable market for native species has resulted in the intensive use of a few well-known, fast growing exotics for timber production. More research into propagation methods, species-site matching and silvicultural management of poorly known species is needed in order to implement systems that include native species (Schneider et al. 2014). Selection, breeding programs and silvicultural improvement can contribute to the development of a profitable forestry industry based on native species (Nichols et al. 2006; Manson et al. 2013).

In general, native trees have been ignored due to the supposed lower productivity in comparison with fast growing exotic species (Bauhus et al. 2010; Davis et al. 2012). However, certain valuable timber species in Africa, Asia and Latin America have shown good growth performance when planted in open areas, sometimes equivalent to or better than that of exotic species (Santos Martin et al. 2010; Nath et al. 2011; Onefeli and

Adesoye 2014; Schneider et al. 2014; Fayolle et al. 2015). Studies from Latin America indicate that a number of species have achieved satisfactory biomass productivity, in some cases, greater than that of exotic species (*Stryphnodendron microstachyum, Vochysia ferruginea, V. guatemalensis, Hyeronima alchorneoides*) (Montagnini 2001). In certain cases, plantations composed of native species were equally profitable as those of exotic species, for instance, in Central America. It has been shown that plantations of *Swietenia macrophylla* and *Terminalia amazonica* can compete economically with exotic species like *Tectona grandis* (Griess and Knoke 2010) and similar patterns were seen when native *Dalbergia sissoo* and *Eucalyptus* (Jalota and Sangha 2000) were compared.

2.4.2 Integrating multifunctionality in species selection

Our analysis showed that environmental, economic and socio-cultural criteria were used unevenly in the selection of tree species in forestry projects (Figure 2.1b). The majority of the studies focus only on timber production and, when they consider environmental factors, the most frequently cited is soil restoration (Figure 2.1b, Table 2.1) since the majority of plantations are located on open and degraded lands that were formerly secondary forest or agricultural land (Andrade et al. 2008; Piotto et al. 2010). Environmental benefits such as species that provide food for wildlife and connectivity were included in less than twenty percent of the studies analyzed in this review. Species that provide food for wildlife are considered to be important for ecological succession (Sansevero et al. 2011) and to explain patterns of biodiversity in forest plantations (Calviño-Cancela et al. 2012). Forestry projects can provide a wide range of ecosystem services and functions (Figure 2.1a) including watershed protection, biodiversity conservation, carbon sequestration and those providing recreational, aesthetical and spiritual benefits to local communities (Montagnini et al. 2004; Hall et al. 2011). Market prices often fail to reflect the non-tradable benefits associated with ecosystem services (Barrett et al. 2016) and costs of disservices of monoculture plantations and related harvesting activities (e.g. road damages, forest fire events, impacts on water quality and quantity) are regularly not included in economic assessments and measures to balance negative environmental impacts have to be compensated often by public funds. Native species are expected to be well adapted to local biotic and abiotic conditions and support native biodiversity and related ecosystem functions to a greater degree than exotics (Tang et al. 2007). There is a growing literature showing that plantations with more complexity diminish herbivores and natural enemies of trees and hence reduces potential loss by pathogens and pests (Tscharntke et al. 2012) or as the consequences of climate change that forest industry is facing worldwide. Other regularly overlooked services with important economic implications are pollination, a decreased risk of flooding and health benefits. Learning how to simultaneously maximize complexity, resilience, nonmarket values and profitability is a central challenge (Messier et al. 2013). Regardless of the number of other potential benefits, native trees have to have the capacity to provide a substantial and recognizable contribution to the sustainability of yields and to the ecological stability of the system in the long-term (Aladi and Olagunju John 2014). Several recent publications have underlined the urgent need to adapt forest management to climate change and future uncertainty (Puettmann et al. 2010; Mori et al. 2017).

Only 5% of the reviewed studies included any socio-cultural approach to species selection, although these aspects are fundamental for the legitimization for local stakeholder management and project legitimacy (Quintana-Ascencio et al. 2004; Plath et al. 2011). Inclusion of local people in decision-making as part of good neighbor politics is fundamental to legitimize forest company's activities and maintain social license to operate them (Driscoll and Crombie 2001; Mikkilä and Toppinen 2008; Bauhus et al. 2010). Cross-sectoral approaches, improved communication and the participation of ecological, economic and social sciences are needed to develop multifunctional, productive and environmentally friendly forest systems. Socio-cultural preferences, and the ecological attributes of tree species must be balanced against economic goals in order to achieve multifunctionality. There is evidence of the integration of local knowledge in the diverse uses of species from ethnoecological studies that demonstrate, that traditional practices can satisfy the needs of local people for food, medicine, fodder, fiber, construction material or fuel (Montagnini et al. 2004; Diemont et al. 2011; Moreno-Calles et al. 2012). When multiple functions are considered the advantages of native species over exotics are highlighted (Garen et al. 2009; Irwin et al. 2014). The wide range of benefits provided by multifunctional forest landscapes such as those that include the use of native species or incorporate mixed species systems are widely recognized and can be supported by land-sharing policies (Mertz and Mertens 2017). 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 and are potential measures to enhance biodiversity and foster the integration of plantations into the local landscape (Pozo and Säumel 2018). Appropriately planned, designed and managed forests deliver a wide range of ecosystem goods and services, at both landscape and stand scales (Bauhus et al. 2010). The next generation of multifunctional forestry practices have to take into account the wide range of ecosystem services provided (Mori et al. 2017) as a crucial step towards sustainable forestry.

2.4.3 Do we include the right species traits to enhance multi-functionality at landscape scale?

Up to now, the traits of most tree species were chosen at stand scale and focused on timber production. The most frequently cited was (fast) *growth* (Table 2.1). Specific traits for timber production include: *wood quality*, *volume* and *stem form* (straight boles), displacement (leaning or crooked), multiple stems or shrubby habits are treated as undesirable traits. Species of certain families known for high quality wood are preferred e.g. Dipterocarpaceae (Santos Martin et al. 2010). The most frequent trait that targets soil restoration is *N-fixing capacity*, Leguminosae being the most desired family (Montagnini et al. 1994; Wishnie et al. 2007). Trees are also pivotal to other important services and processes at the landscape scale. For instance, edibility and dispersal mode are relevant traits for landscape connectivity. In this evaluation five of the studies consider edibility in the selection process and only one study includes *dispersal mode* (Sovu et al. 2010). Edible tree species are important fruit, seed and nectar resources, at the same time allowing for the continued interaction between native animal and plant species and contribute to pollination, dispersion, regeneration and other natural processes (Wishnie et al. 2007; Breugel et al. 2011; Plath et al. 2011; Schneider et al. 2014). Traits like *dispersal mode* are indicated as being important in selecting native tree species for plantations, where zoochorous species are positively correlated with natural regeneration and are considered as an important strategy to accelerate ecological succession (Sansevero et al. 2011), reduce the negative impacts of landscape fragmentations (Rocha-Ortega et al. 2017) and promote connectivity. *Crown size and morphology* was a selected trait in one of the studies. Native species are also fundamental in successional processes as they create the climate and structures that favor the growth and protection of other native species at local and landscape scales (Wishnie et al. 2007). The optimal tree crown morphology varies according to the prevailing light environment. Yet most species used for timber production have been selected because they allocate a high proportion of biomass to the stem rather than to the crown morphology (Evans and Turnbull 2004; Wishnie et al. 2007). There is great potential in rather conserve species by their functional roles as a driver and source of ecosystem functions at the landscape scale (Mace et al. 2012; Karp et al. 2013), which could contribute to the sustainability and functionality of the system and avoid the conventional perspective in biodiversity conservation. Traits have to support biogeochemical processes and trophic interactions (i.e. *pollination* and *dispersal mode* and *N-fixing capacity*). These traits contribute to services and processes and are likely to maintain greater diversity in forests. However, selecting native species on the basis of functional groups, requires more knowledge than is currently available (i.e. traits associated with their reproductive biology, phenology and propagation). This knowledge gap often compromises the optimal selection and use of native species so resulting on better documented but less appropriate exotic species (Thomas et al. 2014).

2.5 Conclusion

Our review highlights, the multifunctional benefits of native species at local and landscape level. In order to maximize the benefits from native species use in forest plantations and outcompete with the widespread exotics, we encourage a multifunctional approach that incorporates a wider range of ecosystem functions and services beyond timber production and enhance the adaptability and resilience of the system in the interests of landowners and users. Ecological and forestry views have to be included in the design process. Based on the evidenced reviewed, we propose the following steps in the selection of native species: (1) screening of native species based on desired and adaptive traits (e.g. fast growth, nitrogen fixing capacity, food for wildlife, dispersal mode); species have to match with plantation sites based on current and future site conditions. The process can be guided by a combination of ecological indicators with the results of sociological surveys of local cultural preferences to provide legitimacy for the activities of forestry companies. Species with high value of ecological importance in the landscape can be easily screened from their abundance, dominance and frequency in the landscape (see Pozo and Säumel 2018) (2) Governments can support to gain knowledge of native tree species by plantation trials to evaluate species performance and identify species with high rates of growth and survival. Nurseries can be set up in specific project areas covering a wide range of sites where the species occurs and have to focus also on genetic improvement by the selection of desired traits as the high diversity of genetic material will be important for the selection of superior phenotypes. This can support the green economy through measures to strengthen local nurseries or initiate local entrepreneurship on production of native tree saplings for forestry projects. (3) Implement landscape planning so plantations are integrated into the landscape context and the broader surrounding landscape matrix.

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2.A Supplementary material

Table 2.2 – Keywords relating to native species potential in forestry projects. The terms shown in column "Keywords" were inserted in the Web of Science search engine combined by 'AND' with keywords

Search for	Keywords	No of publications 9/11/2018	Relevant publications
Native species * forestry projects	native species, indigenous species, local species, multipurpose, trees, plantation, reforestation, enrichment planting, afforestation, plantation forestry	432	33

TS= ("native species" or "indigenous species" or "local species" or "multipurpose" and "tree*" not exotic not non-native* not introduced) and TS= (plantation, reforestation or enrichment planting or afforestation or plantation forestry).

CHAPTER 3

HOW TO BLOOM THE GREEN DESERT: *Eucalyptus* PLANTATIONS AND NATIVE FORESTS IN URUGUAY BEYOND BLACK AND WHITE PERSPECTIVES

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 m^2 plots and regeneration was assessed along transects in 9 m^2 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; multi-functional landscapes; park forest; species composition; species diversity

3.1 Introduction

Tree plantations are expanding around the world (Payn et al. 2015) for multiple purposes such as restoring degraded landscapes (Rappaport and Montagnini 2014), conserving native tree species (Yang et al. 2013), satisfying timber and pulp demand (Payn et al. 2015), or carbon sequestration (Miah et al. 2009; Arias et al. 2011), 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 (Payn et al. 2015). 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 (Evans and Turnbull 2004).

In Uruguay, small *Eucalyptus* plantations (<0.5 ha) were established to provide shelter and shade for livestock in the 1970s (FAO 2007). Subsequently, large-scale *Eucalyptus* plantations were promoted by governmental policies, financial incentives, and investors' expectations (Payret et al. 2009; Redo et al. 2012), 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 (Piñeiro 2012). 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 (FAO 2014). Most plantations occur in the form of monocultures of fast-growing non-native *Eucalyptus* and *Pinus* species at the expense of grasslands (MGAP 2016). In some cases, forestry companies lease their plantations for grazing to local farmers forming silvopastoral systems (Cubbage et al. 2012).

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 (Brussa and Grela 2007; Haretche et al. 2012). 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 (Bennadji et al. 2012; Castillo et al. 2014). 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 (Bremer and Farley 2010; Gautreau 2014), or whether *Eucalyptus* can be a useful tool for restoring degraded land (Boulmane et al. 2017). Nowadays, *Eucalyptus* plantations are progressively replacing *Pinus*. Current afforestation practices may reduce species richness and alter the composition of grassland vegetation in Uruguay (Six et al. 2014). 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 (Bremer and Farley 2010). Native species meet better local cultural needs (Hall et al. 2011) and provide a greater range of goods and services (i.e., ‘multi-use species’) than exotic species (Hall et al. 2011; Fayolle et al. 2015). Additionally, native species are considered to provide longer-term benefits and be more stable in the face of disturbances in our changing world (O’Hara 2016).

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.

3.2 Materials and Methods

3.2.1 Study Area

With an area of about 176,215 km^2, 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 (Haretche et al. 2012). The FAO estimates that 6% of the land area is afforested with *Eucalyptus* and pine plantations (FAO 2014). 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 (Brussa and Grela 2007). 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 3.1a) 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 3.1c) 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 (Brussa and Grela 2007; Gautreau et al. 2008). Riverine forest (Figure 3.1d) 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 (Brussa and Grela 2007; Guido and Mársico 2011). Forest plantations are monospecific *Eucalyptus grandis* and *E. dunnii* stands (Figure 3.1e) 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.

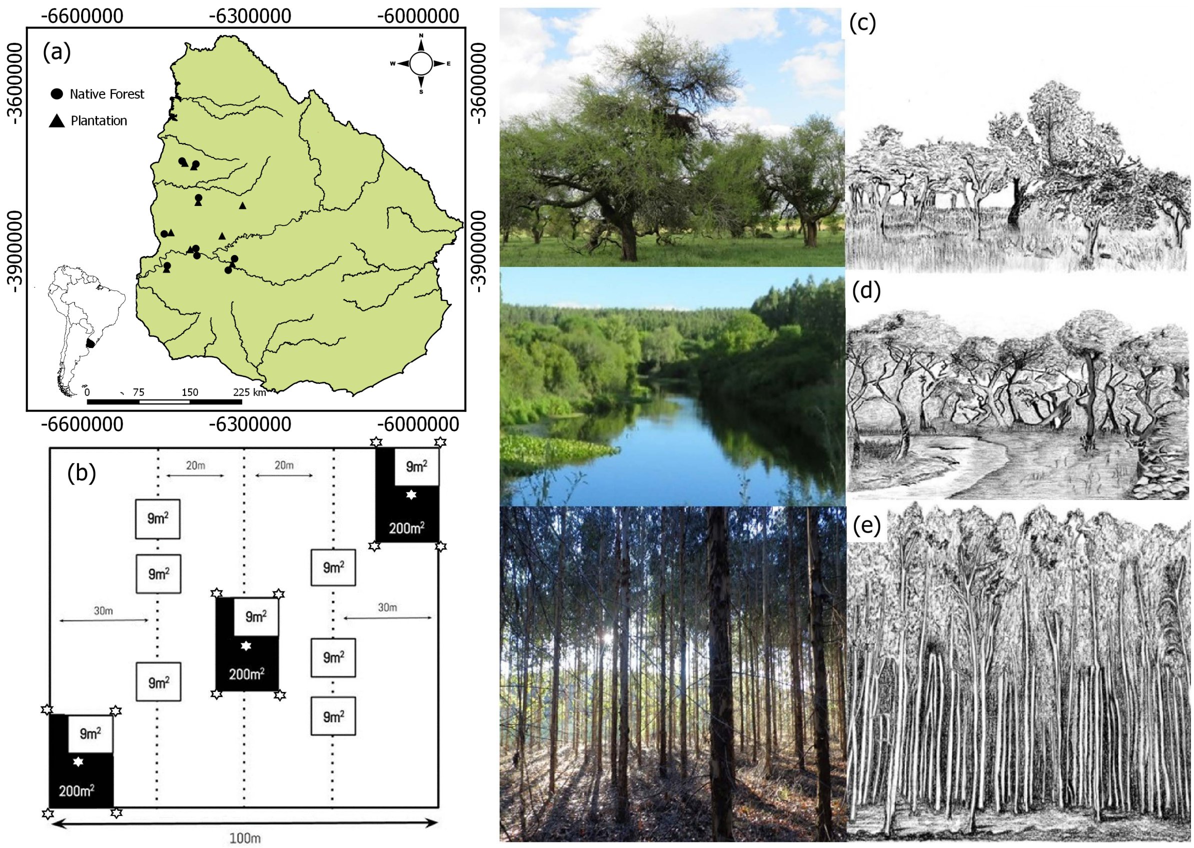

Figure 3.1 – Map of the study area with: (a) the study sites in the northwestern part of Uruguay (black dots: native forests and black triangles: *Eucalyptus* plantations); (b) sampling design composed of permanent plots (100 × 100 m2), inventory plots for trees (20 × 10 m2), regeneration subplots (3 × 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.

3.2.2 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 3.1a). 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 (Haretche et al. 2012). Tree assessment was undertaken in three 20 × 10 m^2 plots that were systematically distributed in the corners and center of the permanent plot (Figure 3.1b). 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 DBH ≥2.5 cm at 1.3 m. Regeneration assessment (individuals with <2.5 cm diameter and height <1 m) was evaluated in nine 3 × 3 m^2 subplots located inside the 20 × 10 m^2 plots and along systemically established linear transects (Figure 3.1b). 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 (Asner et al. 2003), was assessed inside the 20 × 10 m^2 plots. It was measured as the average of five readings taken at each corner and center of the sampling plots (Figure 3.1b) using a LAI-2000 canopy analyzer (Li-Cor, Lincoln, Nebraska, USA), positioning the sensor up to a maximum height of about 2 m.

3.2.3 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 (Krebs 1999), 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 cm) and three height classes (0–5 m, 6–10 m, and >10 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´) (Shannon and Weaver 1949; Krebs 1999). We used the same index to evaluate species diversity. We used non-metric multidimensional scaling (NMDS) using the Bray–Curtis dissimilarity matrix (Clarke 1993) 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 (Minchin 1987). The significance of the compositional differences was tested with a permutational multivariate analysis of variance (PERMANOVA) with 999 permutations (Anderson 2001). 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 (Kent and Coker 1994). 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 (Oksanen et al. 2017) and mass (Ripley et al. 2017) 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.

3.3 Results

3.3.1 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 3.2a). Native forests presented also a higher horizontal structure diversity (Figure 3.2f) 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 3.2b). However, vertical structure diversity did not differ significantly between forest types (Figure 3.2g). Riverine forests showed the highest tree density between forest types (Figure 3.2c). *Allophylus edulis*, *Sebastiania brasiliensis*, and *Pouteria salicifolia* had the highest densities in riverine forests, while *Schinus longifolius*, *Celtis ehrenbergiana*, and *Blepharocalyx salicifolius* had the highest densities in park forests. Regeneration was significantly different between forest types ($F = 15.7$, $p < 0.001$, Figure 3.2d). 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*, *Myrcianthes pungens*, and *Allophylus edulis* was high in park forests, whereas *Maytenus ilicifolius*, *Allophylus edulis*, and *Blepharocalyx salicifolius* dominated in riverine forests (Table 3.1, Figure 3.3d).

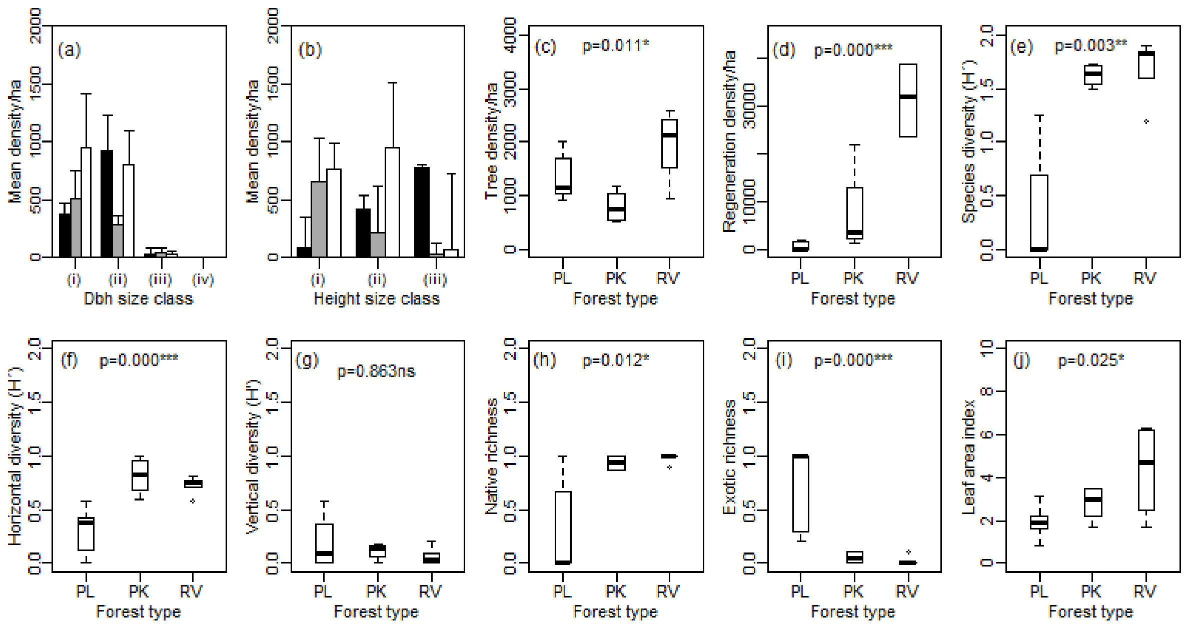

Figure 3.2 – (a,b) The forest structure of the three forest types: *Eucalyptus* plantations (black bars), park forests (dark grey bars) and riverine forests (white bars): expresed as mean tree density per ha in diameter classes (1 = 2.5–10 cm, 2 = 10–30 cm, 3= 30–50 cm, 4 = >50 cm) and height size classes (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 3.2

Table 3.1 – 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 (Nebel and Porcile 2006). References are indicated by superscript numbers. For use references, see Appendix A.

Species/Author/Code	**Mean AD/ha**	**Mean RD/ha**	**Potential Use**
Schinus longifolius (Lindl.) Speg. (ScLo)	250[PK] 3[RV]	185[PK] 20[RV]	med[9] or[9]
Patagonula americana L. (PaAm)	90[RV]	99[RV]	re[7] w[8,20]
Maytenus ilicifolia Mart. ex Reissek (MaIl)	9[PK]	370[PK] 1175[RV] 493[PL]	med[8]
Escallonia bifida Link & Otto (EsBi)	17[RV]		or[8]
Sebastiania brasiliensis Spreng. (SeBr)	447[RV]	317[RV]	re[1,2] med[1,18] or[18]
Citronella gongonha (Mart.) R.A. Howard (CiCo)	3[RV]	40[RV]	zo[8,16]
Ocotea acutifolia (Nees) Mez (OcAc)	197[RV]	119[RV]	w[8] med[10]
Bauhinia forficata Link (BaFo)	8[PK]		med[16] or[8]
Gleditsia triacanthos L. (GlTr)	8[PK] 13[RV]	185[PK] 40[RV]	ex
Prosopis affinis Spreng. (PrAf)	4[PK]	154[PK]	bee[8,6] re[14] zo[6] w[8,3]
Vachellia caven (Molina) Seigler & Ebinger (VaCa)	25[PK]	247[PK] 246[PL]	bee[6] re[14] zo[6]
Melia azedarach L. (MeAzr)	31[PK]		ex
Blepharocalyx salicifolius (Kunth) O. Berg (BlSa)	129[PK] 150[RV]	247[PK] 479[RV] 1358[PL]	zo[8,12,16] re[1,11] med[1,11]
Eugenia uniflora L. (EuUn)	38[PK] 37[RV]		zo[812,16,20] re[7] bee[9,11] or[8] med[4,5,20]
Myrcianthes cisplatensis (Cambess.) O. Berg (MyCi)	8[PK] 350[RV]	2746[PK] 188[RV] 740[PL]	zo[11] bee[11] med[4]
Myrcianthes pungens (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]
Myrrhinium atropurpureum Schott (MyAt)	8[PK] 17[RV]		zo[12,16] re[11] w[8] or[8] med[11]
Ligustrum lucidum W.T. Aiton (LiSi)	4[PK] 87[RV]	12395[RV] 2222[PL]	ex
Colletia paradoxa (Spreng.) Escal. (CoPa)	4[PK]		bee[8] or[19]
Scutia buxifolia Reissek (ScBu)	70[PK] 157[RV]	556[PK] 96[RV]	zo[16] re[1] w[8] med[1]
Discaria Americana Gillies & Hook. (DiAmr)		185[PK]	med[17]
Azara uruguayensis (AzUr)	27[RV]		or[8]
Salix humboldtiana Willd. (SaHu)	17[RV]		w[8]
Jodina rhombifolia (Hook. & Arn.) Reissek (JoRh)	3[RV]		med[13]
Allophylus edulis (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]
Pouteria salicifolia (Spreng.) Radlk. (PoSa)	8[PK] 353[RV]	31[PK] 247[RV]	med[4]
Daphnopsis racemosa Griseb. (DaRa)	27[RV]	353[RV]	fb[8], or[19]
Celtis ehrenbergiana (Klotzsch) Liebm. (CeTa)	133[PK] 33[RV]	278[PK] 290[RV] 740[PL]	zo[8]
Citharexylum montevidense (Spreng.) Moldenke (CiMo)	10[RK]	10[RV]	zo[16] w[15] or[8]

Table 3.2 – 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.

	NMDS		ANOVA	
Parameters	**r2**	**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	0.0119 *
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.

3.3.2 Diversity and Composition

The Shannon diversity index was different between forest types ($F = 8.2$, $p < 0.01$, Figure 3.2e). 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 3.3b). 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 3.3a, Table 2.2). Native forests did not show significant differences in the proportion of native and exotic tree richness (Figure 3.2h-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 3.1). Leaf area index values differed between forest types (Figure 3.2j, Table 3.2). 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.

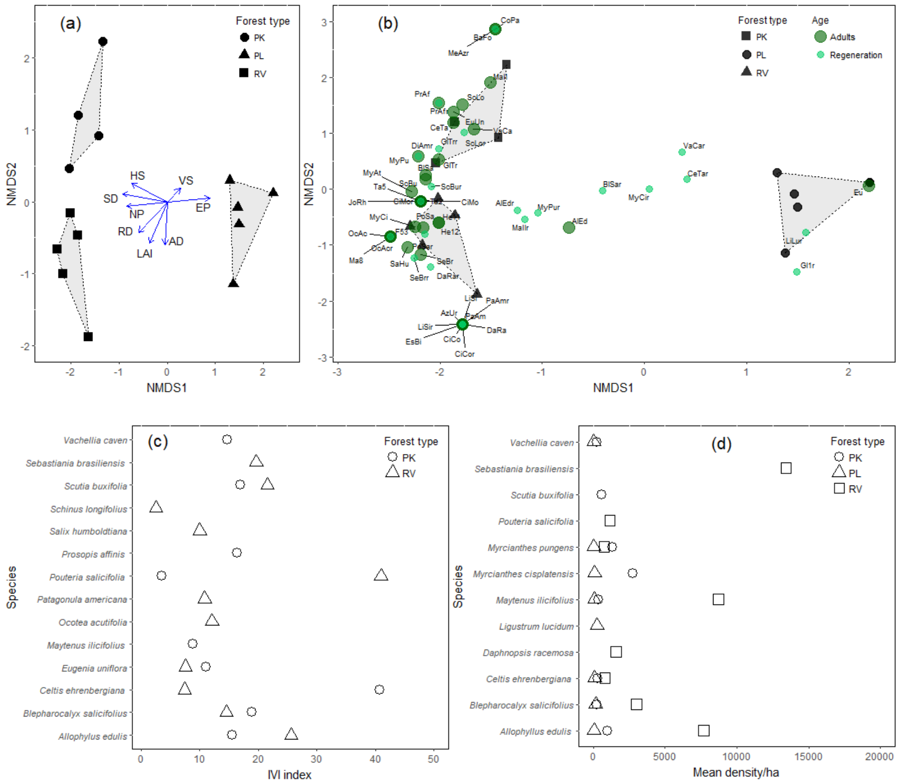

Figure 3.3 – (a) Non-metric multidimensional scaling (NMDS) ordination of species from different forest types (PL: *Eucalyptus* plantations, RV: riverine forests, PK: park forests) and plots using the Bray–Curtis distance based on species abundance, showing distance between plots and eight explanatory 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., AlEd: *Allophyllus edulis* AlEdr, respectively). Dashed lines show the convex hull within forest types; for species list and abbreviations, see Table 3.1, 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.

3.3.3 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 3.3c). 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 3.1).

3.4 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 (Brockerhoff et al. 2008; Bremer and Farley 2010), others point out the negative effects of plantations on biodiversity compared to natural forests (Calviño-Cancela et al. 2012). 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 (Zhang et al. 2016) or manage plantations as nurse systems for restoration purposes (Shiferaw and Pavlis 2012; Sun et al. 2017). 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 (Hartley 2002; Calviño-Cancela et al. 2012).

3.4.1 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 3.2a). A similar pattern has been reported in other riverine forests of the Campos biome in Uruguay and Brazil (Budke et al. 2004; Guido and Mársico 2011; Abruzzi et al. 2016). 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 3.1), 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 3.2a-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 (Chu et al. 2014; Zhang et al. 2016). 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 3.1). 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 (Rodrigues and Brooks 2007). 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 (Zhang et al. 2016).

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 (Hartley 2002; Calviño-Cancela et al. 2012). 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 (Bremer and Farley 2010). Particularly at the landscape level, plantations can provide habitats for native species (Calviño-Cancela et al. 2012) and catalyze secondary successional process (de Pinho Júnior et al. 2015). Taking into account the current planted area in Uruguay and the expected increase for the future (FAO 2014), 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 (Donaldson et al. 2017). 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 (Hartley 2002; Brockerhoff et al. 2008).

3.4.2 Forest Diversity and Composition

Between native forests, species diversity was highest in riverine forests (Figure 3.2e). Similar values of diversity indices have been reported for the forests of the Queguay River in Uruguay (Guido and Mársico 2011) and for a forest of the Ibirapuitã River in Brazil (Abruzzi et al. 2016). Another study (Gautreau et al. 2008) 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 3.3a). These variables are often reported to positively correlate with native communities and negatively correlate with plantations (Gossner et al. 2014). The majority of the native forest species that were found in our study have a wide distribution in Uruguay and South America (Brussa and Grela 2007; González 2013), and have been reported in other riverine and park forests of Uruguay (Costa and Delgado 2001; Grela and Brussa 2003).

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 3.1). 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 (Piaggio and Delfino 2009; Traversa-Tejero and Alejano-Monge 2013). In our study, the total proportion of exotic species did not differ between native forest types (Figure 3.2i). 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 (Traversa-Tejero and Alejano-Monge 2013). 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 (Ghersa et al. 2002; Chaneton et al. 2013). *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 *Allophyllus edulis* due to its high adaptability and regeneration capacity (Costa and Delgado 2001). In Argentina, *L. lucidum* causes high mortality rates of *Celtis ehrenbergiana*, limiting its regeneration (Plaza Behr et al. 2016). 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 (Sosa et al. 2015).

3.4.3 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 *Allophyllus edulis*, *Pouteria salicifolia*, and *Sebastiania brasiliensis*. This is consistent with other studies in riverine forests in Uruguay (Piaggio and Delfino 2009; Traversa-Tejero and Alejano-Monge 2013) or in Brazil (Budke et al. 2004; Prata et al. 2011). The IVI values are comparable with those reported for Brazil (Abruzzi et al. 2016), 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* (Watzlawick et al. 2014). Even though Uruguay has the highest afforestation rate in South America (FAO 2018), the use of native species in afforestation is absent. This was related to the growth habits of multi-branched, short, and thin tortuous trunks (Traversa-Tejero and Alejano-Monge 2013). The traditional use of native trees is mostly restricted to fuelwood (Costa and Delgado 2001). Nevertheless, our study demonstrated that species with high IVI and regeneration density have a great variety of potential uses (Figure 3.3c-d, Table 3.1).

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 (García-Fernández et al. 2008), but also provides challenges to establishing local markets and enhancing the livelihood of local communities (Pokorny and Pacheco 2014). As an example, *Allophyllus edulis*, *Sebastiania brasiliensis*, and *Pouteria salicifolia* have potential for restoration projects due to their high IVI values and considerable representation in riverine forests. *Allophyllus edulis* and *Sebastiania brasiliensis* were already used for the environmental restoration of degraded areas in the Atlantic forest of Brazil (Araujo et al. 2014). 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 (Root-Bernstein and Jaksic 2013; Castillo et al. 2014). 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 (Root-Bernstein and Jaksic 2013). Moreover, these species provide refuge for native wildlife and food for livestock and wild animals, such as nectar for honey-producing bees (Castillo et al. 2014). *Prosopis affinis* is also important by its high wood quality (Bennadji et al. 2012). 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* (Chu et al. 2014). 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 ecosystems services in China (Zhang et al. 2016). 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 (Gomes et al. 2017). Others such as *Eugenia uniflora*, *Myrcianthes cisplatensis*, and *Myrcianthes pungens* provide fruits and pollen for wildlife, and are used as ornamental trees (Gomes et al. 2017). 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 (Diniz and Buschini 2015). Although the trunk of *Schinus longifoulis*, 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 (Piaggio and Delfino 2009).

3.5 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*, *Allophyllus 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 (McFadden and Dirzo 2018). 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 (Felton et al. 2016). 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 (Mertz and Mertens 2017). 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.

3.6 References

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3.A Appendix A: Supplementary References

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CHAPTER 4

POSITIVE TREE-TREE INTERACTIONS FACILITATE DRY FORESTS PERSISTENCE IN AGRICULTURAL MODIFIED LANDSCAPES

Abstract. Uruguayan 'park forests' are understudied dry forests shaped by extensive cattle ranching in the transition between natural riverine forests and open grasslands. Although the underlying mechanisms driving tree regeneration have not been studied, they determine forest biodiversity, sustainability and multifunctionality. We explored forest community composition in different types of park forests across Uruguay in the departments of Artigas, Rio Negro, Paysandú and Tacuarembo. Additionally, we evaluated the role of scattered trees for regeneration by analyzing nurse–beneficiary interactions. We carried out forest inventories within one-hectare plots of ten park forests to assess community composition and diversity. To assess the regeneration performance of tree species we established 205 (1x1 m2) paired plots in open habitat and under the tree canopy. We used multivariate analyses to assess forest community composition and nurse–beneficiary interactions. Tree communities vary between forest types and spatially closer forests were more similar. Scattered trees in park forests have a positive effect on tree regeneration density, whereas, dense grass coverage has a negative effect. Regeneration density increased (+1600%) under the canopy of nurse trees. Trees increase shade (+61%) and reduce grass cover (-24%) and grazing by the presence of thorns, spines and multibranched stems. Regeneration beneficiaries were mainly bird dispersed species with different life strategies. Our study demonstrates that park forest trees are essential to the promotion of forest regeneration and recov-

ery in grazed forests. They facilitate regeneration by providing shade, reducing grass competition, giving protection against herbivores and promoting species regeneration by attracting seed dispersers.

Key words: park forest, composition, regeneration, nurse tree, silvopastoral systems, grazing

4.1 Introduction

Shifting the scientific gaze from merely natural ecosystems to human modified landscapes regarding biodiversity conservation is an important goal to meet the challenges of the anthropocene (Seddon et al. 2016; Johnson et al. 2017). Within the South American grassland biome, the heavily used, socio-ecological Campos region of Uruguay is subject to expanding land use changes to establish monocultures for the globalized market (Céspedes-Payret et al. 2012). Thus, timber plantation in Uruguay has increased over 400% from 201,000 to 1,062,000 hectares between 1990 and 2015 (FAO 2014), making it the country with the highest afforestation rate in South America (FAO 2018) but with less than one percent of Uruguayan territory enjoying protected status (MVOTMA 2018).

Timber plantations cover around six percent of Uruguay and dominate the forest cover, whereas native forests cover approximately four percent (FAO 2015, Haretche et al. 2012). Native forests are scattered within a landscape matrix dominated by grasslands, timber and crop plantations, forming biological corridors for avian and mammalian biodiversity (Nores et al. 2005; Haretche et al. 2012). They range from open dry forests such as park forests to riverine forests, creek forests and hill forests (Brussa and Grela 2007). Among them, the so-called 'park forests' are composed of native xerophilous trees growing in a dense herbaceous stratum shaped by cattle ranching. Quantitative studies in 'park forests' are scarce (Pozo and Säumel 2018). Some qualitative studies have reported on the geographical variation in species composition denoting a high affinity with the Flora Paranaense and the seasonal dry forests of the Chaco and Espinal of central South America (Brussa & Grela, 2007; Grela, 2004).

As with the worldwide loss of dry forests (Miles et al. 2006; Hansen et al. 2013), park forests have been greatly threatened by agricultural expansion. The western part of Uruguay, in particular, has experienced the highest loss of natural habitat due to soybean farming and afforestation (Brazeiro et al. 2008). The survival of park forests depends on forest regeneration, which is determined by a balance of complex biotic and abiotic interactions.

In general, several biotic factors negatively affect forest regeneration (Catterall 2016; Martinez-Ramos et al. 2016). Wild and domestic herbivores can deter regeneration

(Macdougall et al. 2010), annual herbs out-compete tree seedlings when colonizing fields or large forest gaps (Cuesta et al. 2010) or exotic species suppress the growth of native species (Catterall 2016). There is evidence that exotic trees in Uruguay (e.g. *Ligustrum lucidum* and *Gleditsia triacanthos*) inhibit the regeneration of native species (Costa and Delgado 2001; Plaza Behr et al. 2016).

In contrast, positive interactions have been recognized as a major driving force for species coexistence in plant communities, particularly in harsh environments (Bertness and Callaway 1994). Nurse plants facilitate regeneration and maintain plant species richness under grazing across a range of ecosystems and productivity levels (Smit et al. 2007; Manning et al. 2009; Catterall 2016). The nurse plant mitigates the abiotic and/or biotic stresses that plants experience outside the nurse canopy (Gómez-Aparicio 2009), such as high temperatures, lack of water and nutrients, and/or a high rate of herbivory (Andivia et al. 2017).

Facilitation has been examined across many species and a wide range of environmental conditions under high abiotic stress especially in semi-arid and arid ecosystems and at high elevations (e.g. Andivia et al. 2017; Anthelme et al. 2017; Soliveres et al. 2012). However, few studies have addressed facilitation in temperate forests, productive grasslands or its function in protecting against herbivory (Oesterheld and Oyarzábal 2004; Fidelis et al. 2009). Specifically, no studies exist on patterns and mechanisms of tree regeneration in Uruguayan park forests, but such knowledge is critical to their conservation and the sustainable management.

We studied plant communities in Uruguayan park forests qualitatively and quantitatively and we explored the role of scattered trees in regeneration by analyzing the natural occurrence of nurse–beneficiary interactions. We assumed that scattered trees facilitate tree regeneration under their canopies in four different ways: i) by providing shade for light sensitive or shade tolerant species; ii) by reducing grass competition within the dense grass matrix; iii) by serving as a refuge against herbivores because of their physical structures that deter access by livestock; iv) by promoting forest regeneration linked to the attraction of seed dispersers. Assessing these questions contribute to the development of strategies to design multifunctional landscapes in agri-and silviculturally landscapes in Uruguay and provide valuable information for the management and restoration of one of the most threatened and poorly studied forests of Uruguay.

4.2 Methods

4.2.1 Study Area

Uruguay is located in the temperate zone of South America and covers an area of about 176,215 km^2. Mean annual temperature ranges from 16°C in the south to 20°C in the north and the annual rainfall average is approximately 1,500 mm in the north to 1,000 mm in the south (Redo et al. 2012). Livestock ranching on grasslands is one of the main economic activities. Livestock roams through nearby forests looking for shade, water, and forage, especially when grassland productivity is low (Etchebarne and Brazeiro 2016), forming natural silvopastoral systems.

Native forests are classified according to their physiognomy and topographic location into gallery forests along rivers, park forests -a transition zone between riverine forest and grasslands, creek forest in the rocky parts of the mountains that surround water streams, and hill forests on hillsides (Brussa and Grela 2007). Park forests are composed of scattered thorny tree species and an understory of grasses. They vary from the typical, relict park forest known as 'algarrobal' composed mainly of *Prosopis affinis* and *P. nigra* to a successional and sometimes invasive form named 'espinillar' composed mainly of *Vachellia caven* (Haretche et al. 2012; Delgado and Nebel 2014). When these are associated with alkaline soils, they are known as 'blanqueales' (Brussa and Grela 2007).

Our study sites are located where park forests are principally distributed including the north, west and the central part of Uruguay within the departments of Rio Negro, Paysandú, Artigas and Tacuarembo (Figure 4.1a).

4.2.2 Field Inventory Design

Forest inventories were undertaken between October and December 2017 in four departments of Uruguay (3 in Rio Negro, 2 in Artigas, 3 in Paysandú and 2 in Tacuarembo). We used the FAO forest definition that forests have at least 10% of the canopy coverage with trees higher than 5 m and stand area of more than 0.5 ha (FAO 2015). A total of ten plots each of one hectare were established in park forests where livestock ranching is the most extensive, traditional productive activity. The initial location of the plots was selected on arbitrary bases to avoid the selection of habitat formations outside the scope of the study. Tree inventories were undertaken in three 20 ×10 m2 plots located in the corners and center of the permanent plot (Figure 4.1b). Attributes such as species name, diameter at breast height (DBH) and height were recorded for all individual or multi-stem adult living trees (DBH ≥ 2.5 cm at 1.3 m) and regenerating trees (DBH < 2.5 cm diameter and height < 1 m).

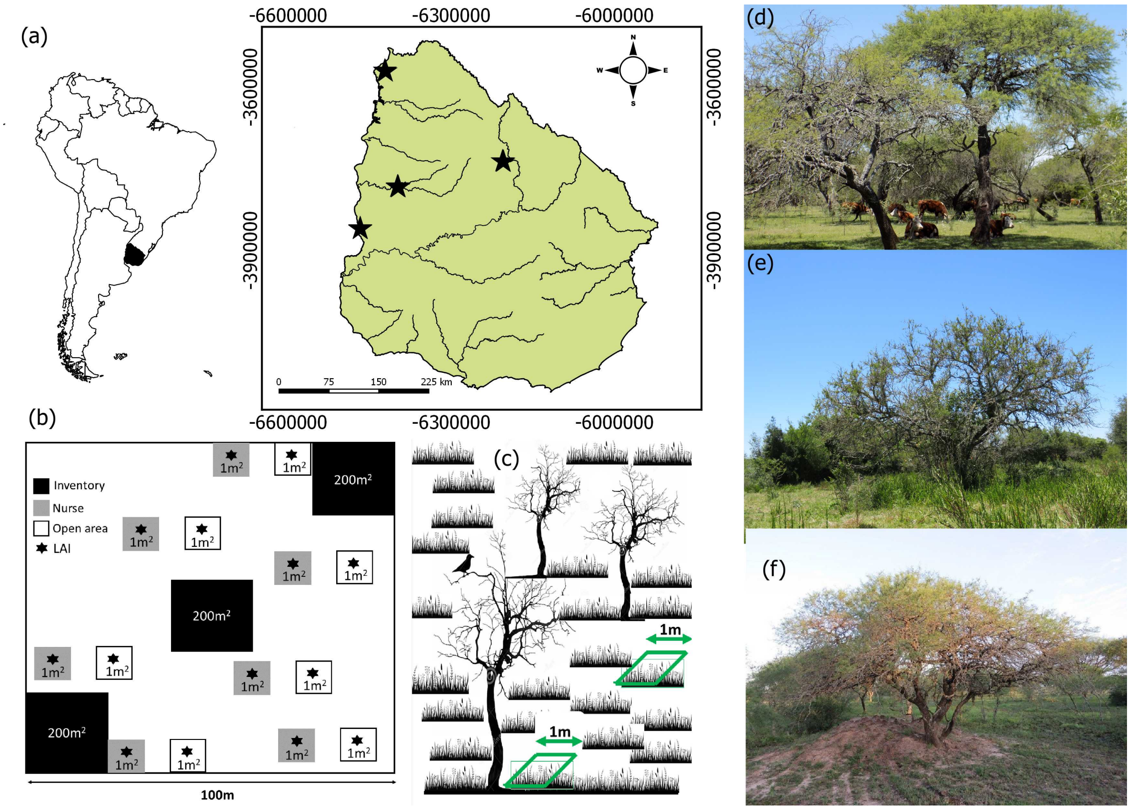

Figure 4.1 – Map of the study area: (a) the study sites in Uruguay; (b) sampling design composed of permanent plots (100x100 m^2), inventory plots (200 m^2), treatment plots (1 m^2), and measurement points of LAI; (c) nurse interaction design showing the 'open habitat' and 'nurse' treatments and measurement points of LAI; (d) (e) and (f) park forests characterized by dispersed trees of *Prosopis spp.* 'algarrobal' (Department of Artigas), *Vachellia caven* 'espinillar' (Department of Tacuarembo) and with alkaline soils 'blanqueal' (Department of Rio Negro) respectively (Figure 4.1d-f). Coordinate system UTM zone 21 S.

4.2.3 Nurse Interactions

To assess the performance of regeneration of tree species we designed a series of paired 1x1 m^2 plots located under the canopy of the trees and the other in the open area, approximately two times the crown distance from the nurse tree (Figure 4.1c). Each paired treatment was repeated 210 times: 60 in 'blanqueales' of Rio Negro, 45 in 'algarrobales' of Artigas, 60 in 'algarrobales' of Paysandú and 45 in 'espinillares' of Tacuarembo. We recorded grass and vegetation cover as a percent of the total plot from 0 to 100. For each tree, we recorded species, total height, crown area, leaf area index (LAI) and the diameter at breast height. Crown area was measured as the average lengths of the longest spread from edge to edge across the crown and the longest spread perpendicular to the first cross section through the central mass of the crown (Pretzsch et al. 2015). LAI is a dimensionless measure defined as the amount of leaf area (m^2) in a canopy per unit ground area (m^2) (Asner et al. 2003) which was used as a proxy to estimate the effect of shading by nurse trees. LAI was measured with the LAI-2000 canopy analyzer (Li-Cor, Lincoln, NE, USA) as the average of three readings taken under the canopy and in the open area (Figure 4.1c).

4.2.4 Data Analysis

We analyzed the park forest communities in our study sites by forest composition and species diversity. We used non-metric multidimensional scaling (NMDS) on the Bray-Curtis dissimilarity matrix of tree species abundance, a robust unconstrained ordination method to visualize patterns of composition between forest sites (Clarke 1993). 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 (Minchin 1987). The significance of the compositional differences was tested with a permutational multivariate analysis of variance (PERMANOVA) using the Adonis function in the vegan package (Anderson 2001). To assess species diversity, we calculated the Shannon index (H´) (Shannon and Weaver 1949).

The nurse effects of trees on plant regeneration were analyzed with generalized linear mixed-effects models (GLMMs) using Poison distribution. We tested for multicollinearity among the variables by calculating variance inflation factors (VIF). A VIF value greater than 10 is regarded as severe multicollinearity (Zuur et al. 2010). VIF analysis suggested that no input variables were problematically correlated.

We assessed how the density of regeneration of tree species was affected by the presence or absence of scattered trees in the plot, LAI and relative grass cover. We used paired treatments and forest site as a random effect to account for unmeasured influences within paired plots and forest sites. We carried out the same analysis with relative grass cover as response variable and habitat and LAI as predictor variables. We separately analyzed plots with scattered trees using the same mixed-effects model and using canopy cover, height, DBH as explanatory variables to identify differences in interactions across tree nurse variables. We calculated the 'relative interaction index' (RII) to estimate the intensity of the interactions (Armas et al. 2004). RII indices were used to directly compare the performances of understory regenerating trees among treatments:

$$RII = \frac{(P_{+N} - P_{-N})}{(P_{+N} + P_{-N})} \tag{4.1}$$

where P_{+N} and P_{-N} denote the performance of regeneration in the presence and absence of the nurse tree, respectively. RII was calculated based on the density of the regeneration. RII results significantly above zero indicated facilitation, which intensity increases up to 1. RII significantly below zero revealed competitive interactions, which intensity increases up to –1 (Armas et al. 2004).

We reviewed existing literature by carrying out a systematic search in the web of science on each species for three different traits: dispersal mode, life strategy and facilitation type. The dispersal mode was classified in anemochoric (seeds or fruits wind dispersed), zoochoric (seed or fruits dispersed by animals) and autochoric species (seed or fruits dispersed by explosive mechanism); see van der Pijl, (1982). Categories of "shade-tolerant" and "shade-intolerant" species refer to their ability to germinate and grow under various light regimes (Swaine and Whitmore 1988; Whitmore 1989). We classified tree species according to their life strategy as light demanding shade intolerant, intermediate shade tolerant and shade tolerant species (Anderson et al. 1969).

Finally, positive interactions were classified into either facilitation obligates and facilitation beneficiaries (Butterfield 2009). We considered as facilitation obligates those species found only under the canopy of a given nurse tree but not in the open habitat, while facilitation beneficiaries were species with more individuals growing under the canopy of a nurse than in the open habitat. For specific information on literature see Table 4.2. We then calculated the regeneration density of each trait (0 to 100) by dividing the density of a given trait by the total density of all the traits and multiplying by 100.

We compared the variation of i) species diversity between forest types; ii) strength and direction of the relative interaction index between forest types; iii) regeneration density, LAI and relative grass cover between open and close habitats; iv) regeneration density within dispersal modes, life strategies and facilitation types. The data were tested for normality using the Shapiro-Wilk test. We used one-way analysis of variance to test for differences in species diversity between forest types and *post-hoc* Tukey test after finding significantly different results. Kruskal-Wallis H test followed by Dunn *post-hoc* tests were used with non-parametric data. 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 (Oksanen et al. 2017), mass (Ripley et al. 2017) and lme4 (Bates et al. 2015) with an adopted alpha of ≤ 0.05 considered as significant.

4.3 Results

4.3.1 Composition and Diversity

In total, we identified 21 tree species (see Appendix A) from 14 different families, 20 native species and the exotic, *Populus alba*. The tree layer was composed of 14 species and the regeneration layer of 20 species. 75% of the sampled individuals belong to *Vachellia caven*, *Prosopis nigra* and *P. affinis*. Differences in the composition of plant communities were denoted between park forest types ($F=1.59$; $R2=0.44$; $p<0.01$), the 'espinillares' having the greatest distance to the 'blanqueales' and 'algarrobales' (Figure 4.2a). Tree species diversity ($F= 4.39$; $p=0.058$, Figure 4.2b) and regeneration species diversity ($F= 3.34$; $p=0.097$, Figure 4.2c) did not vary between different park forest types.

Espinillares were dominated by *Vachellia caven* and species like *Blepharocalyx salicifolius*, *Celtis ehrenbergiana* with regeneration of *Allophyllus edulis*, *Maytenus ilicifolia* and *Vachellia caven*. Blanqueales were dominated by *Prosopis nigra* followed by *Vachellia caven* and *Aspidosperma quebracho-blanco*, regeneration was significant in species like *Schinus longifolius*, *Celtis ehrenbergiana* and *Xylosma tweediana*. Algarrobales were dominaded by *Prosopis affinis* followed by *Vachellia caven* and *Celtis ehrenbergiana*, the most abundant regeneration species were *Celtis ehrenbergiana*, *Vachellia caven*, *Schinus longifolius* and *Prosopis affinis*.

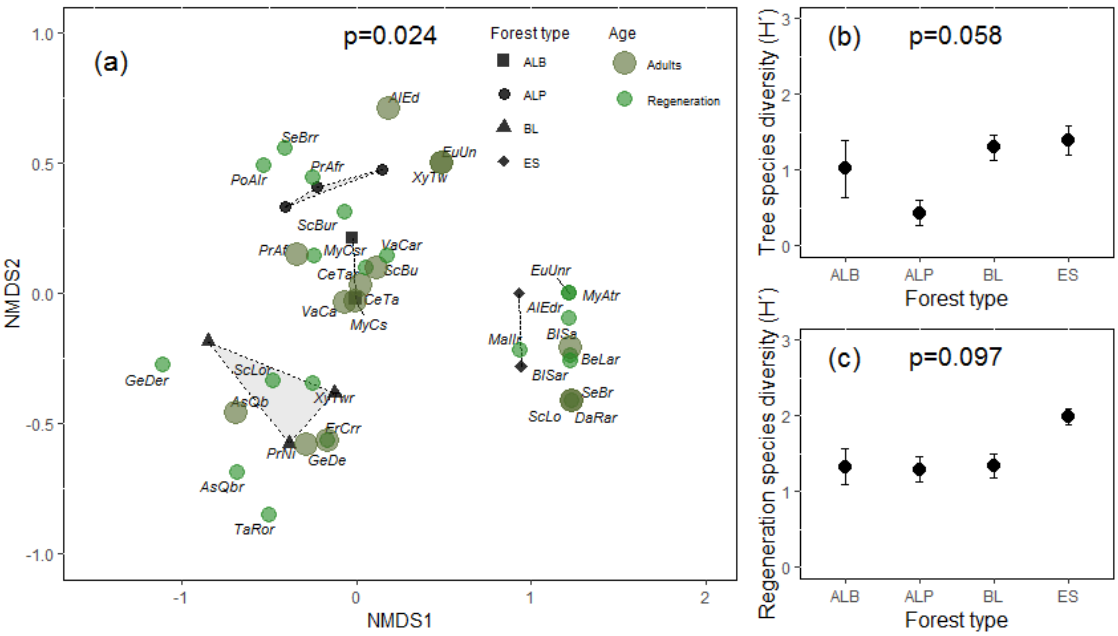

Figure 4.2 – (a) NMDS ordination of tree species from different park forests using the Bray-Curtis distance based on species abundance, showing distance between sites and tree species composition and regeneration species composition. Species were abbreviated with the first four letters of the names and finishing in r for regeneration (e.g. *AlEd: Allophyllus edulis AlEdr*; for species list and abbreviation see Table 4.1), circles size correspond to the age category; Shannon diversity index (H´) of tree species (b) and regeneration species (c), circles show aritmetic means, error bars represent standard errors. Abreviations: BL ('blanqueales', Rio Negro), ALB ('algarrobales', Artigas), ALP ('algarrobales', Paysandú), ES ('espinillares', Tacuarembo).

4.3.2 Nurse Interactions

Park forest trees have a positive effect on tree regeneration density (Table 4.1, Figure 4.3a) indicated by the higher regeneration density under trees than in the open area (H= 92.8; p<0.001) with an increase of around 1600%. In total, 16 tree species were recorded regenerating under the canopy of park forest trees (Table 4.2). *Schinus longifolius*, *Celtis ehrenbergiana* and *Blepharocalyx salicifolius* were the densest species, whereas *Erythrina crista-galli*, *Geoffroea decorticans* and *Populus alba* were not recorded under the nurse trees. High grass coverage had a significant negative effect on tree regeneration density (Table 4.1, Figure 4.3b). Nurse specific variables including variations on the DBH; height and crown area do not influence tree regeneration density (Table 4.1,

Figure 4.3d-f). There is a shift from significantly facilitative net interactions in 'espinillares' to facilitative and neutral net interactions in 'algarrobales' (H= 36.3; $p<0.001$, Figure 4.4a). The nurse trees evaluated, *Prosopis affinis*, *P. nigra* and *Vachellia caven*, were characterized by the presence of thorns and spines (Table 4.2), *V. caven* additionally presented multiple branches creating a entwined structure. Leaf Area Index (LAI) was higher under the trees than in the open area (H=249.1; $p<0.001$, Figure 4.4b) displaying 61% more shade under the tree than in the open area, while, grass cover was significantly lower (H=53.8; $p<0.001$, Figure 4.4c) with a decrease of around 24% under the tree. Within all regenerating species, dispersal mode varied significantly (H=23.5; $p<0.001$, Figure 4.4d, Table 4.2), pairwise comparisons showed that the density of zoochorous species was significantly higher (mainly mediated by birds) compared to anemochorous ($p<0.001$) and autochorous species ($p<0.001$). Life strategy did not vary significantly among light demanding, intermediate shade tolerant or shade tolerant species (F=0.6; $p>0.05$, Figure 4.4e, Table 4.2). Facilitation type differed between regeneration species (H=12.9; $p<0.01$, Figure 4.4f, Table 4.2). Post-hoc pairwise comparisons indicated higher density of facilitative obligates ($p<0.01$) and facilitative beneficiary trees ($p<0.01$) in comparison with non-facilitated trees.

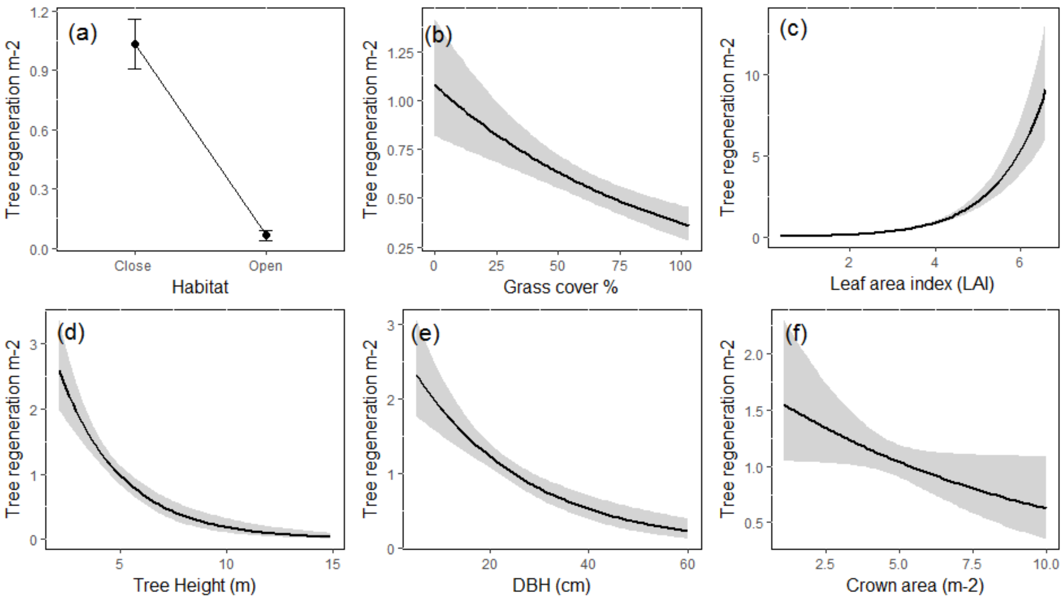

Figure 4.3 – Effect graphs based on the Generalized Lineal Mixed Model (GLMM), testing the effects of habitat and tree parameters on tree regeneration. Mean partial effects on tree regeneration are shown (solid line). Circles show arithmetic means, error bars represent standard errors. Shaded regions correspond to 95% confidence intervals for each section. For parameter definition see Methods, for results see Table 4.1.

Table 4.1 – Effects of trees on tree regeneration. Results of the generalized lineal mixed models (GLMM), Z values for the fixed effects and SD that fitted the random effects (sites and treatments) from the mixed model are shown. Symbols show **** p <0.001, ** p<0.01, * p<0.05, ns* not significant.

Model	Fixed terms	Z value	P value	Random effects	SD
Regeneration (m^2)	Habitat	-7.3	<0.001***	Sites	0.84
Open and Nurse	Grass cover	-4.5	<0.001***	Treatment	0.00
	LAI	1.6	<0.09ns		
Grass cover (%)	Habitat	13.4	<0.001***	Sites	0.27
Open and Nurse	LAI	0.4	0.64ns	Treatment	0.00
Regeneration (m^2)	Grass cover	-3.4	<0.001***	Sites	0.92
Nurse	LAI	1.3	0.18 ns		
	Tree Height	-0.5	0.60 ns		
	DBH	0.8	0.38 ns		
	Crown area	0.1	0.87 ns		

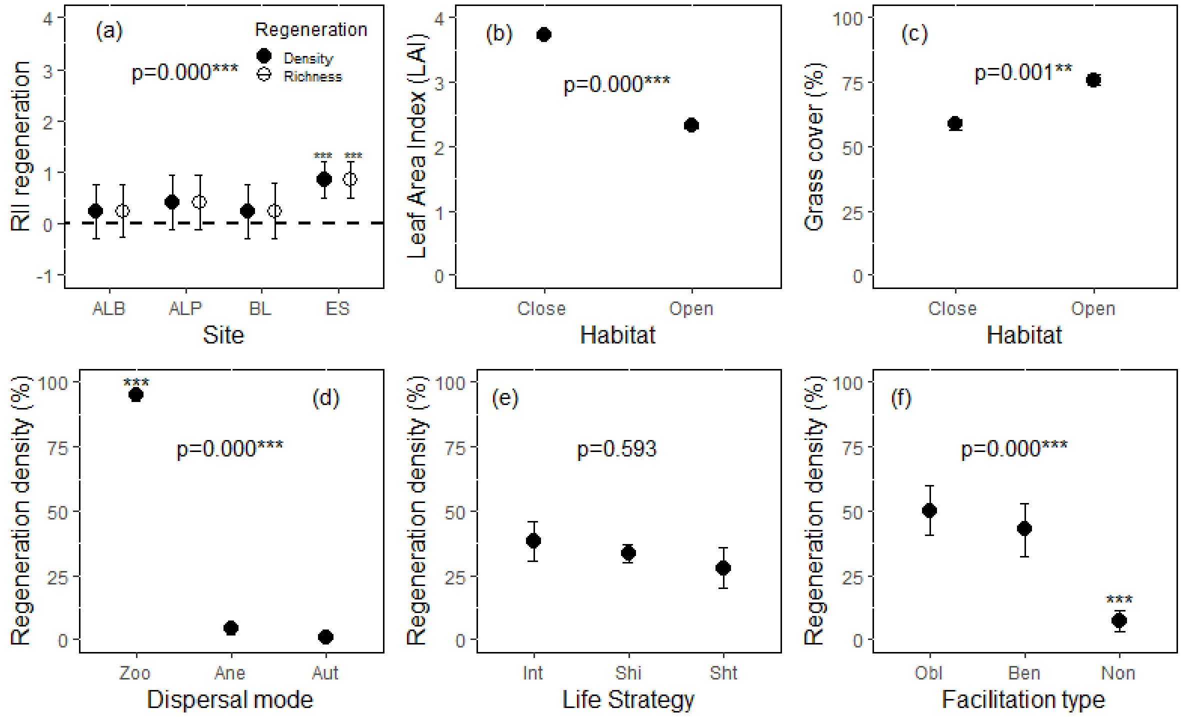

Figure 4.4 – Variations of (a) Leaf Area Index between open and closed habitats; (b) Relative interaction index (RII) of trees on tree regeneration density and richness; (c) Grass cover between open and closed habitats; (d) regeneration density distributed in dispersal modes; (e) life strategy and (f) facilitation type. Abreviations: BL ('blanqueales', Rio Negro), ALB ('algarrobales', Artigas), ALP ('algarrobales', Paysandú), ES ('espinillares', Tacuarembo); Zoo (Zoochorous), Ane (Anemochorus), Aut (Autochorus); Shi (light demanding shade intolerant), Int (intermediate shade tolerant), Sht (shade tolerant species); Obl (facilitation obligates), Ben (facilitation beneficiaries), Nof (species non-facilitated). Circles show aritmetic means, error bars represent standard errors. P values are given. Symbols at the top show **** p <0.001, ** p<0.01, * p<0.05*. For parameter definition see Methods.

Table 4.2 – Tree and regeneration species composition in park forests in Uruguay, codes used in the NMDS analysis. Physical structures (PS): Spi (Spines), Th (Thorns), Ab (Absence of structures). Dispersal mode (DM): Zoo (Zoochorous), Ane (Anemochorus), Aut (Autochorus). Life strategy (LS): Shi (light demanding shade intolerant), Int (intermediate shade tolerant), Sht (shade tolerant species). Facilitation type (FT): Obl (facilitation obligates), Ben (facilitation beneficiaries), Nof (species non-facilitated). R: Species recorded in the facilitation experiments. For references see Appendix B.

Family	**Species/Author/Code**	**PS**	**DM**	**LS**	**FT**	**DE, References**
Anacardiaceae	*Schinus longifolius* (Lindl.) Speg. (ScLo)	Th	Zoo	Sht	Ben	1. Abraham de Noir, Fidelina; Juárez, María Luisa; Boletta, Pedro; Saavedra de Avila, 2002
Apocynaceae	*Aspidosperma quebracho-blanco* Schltdl. (AsQb)	Ab	Ane	Int	Ben	2. Assunção et al., 2014
Berberidaceae	*Berberis laurina* Billb. (BeLa)[R]	Th	Zoo	Shi	Obl	3. Barberis et al., 2002
Bignoniaceae	*Tabebuia impetiginosa* (Mart. ex DC) Standley (TaRor)[R]	Ab	Ane	Int	Obl	4. Barchuk & Díaz, 2005
Celastraceae	*Maytenus ilicifolia* Mart. ex Reissek (MaIlr)[R]	Spi	Zoo	Int, Sht	Obl	5. Chaneton et al., 2013
Euphorbiaceae	*Sebastiania brasiliensis* Spreng. (SeBr)	Ab	Aut	Shi, Int	Obl	6. Etchebarne & Brazeiro, 2016
Flacourtaceae	*Xylosma tweediana* (Clos) Eichler (XyTw)[R]	Th	Zoo	Shi	Obl	7. Fontoura et al., 2006
Leguminosae	*Erythrina crista-galli* L. (ErCrr)[R]	Spi	Ane	Shi	Nof	8. González & Cadenazzi, 2015
Leguminosae	*Geoffroea decorticans* (Gillies ex Hook. & Arn.) Burkart (GeDe)	Th	Zoo	Shi, Int	Nof	9. Madeira et al., 2009
Leguminosae	*Prosopis affinis* Spreng. (PrAf)[R]	Spi	Zoo	Shi	Ben	10. Mielke & Schaffer, 2010
Leguminosae	*Prosopis nigra* (Griseb.) Hieron. (PrNi)	Spi	Zoo	Shi	Nof	11. Plaza Behr et al., 2016
Leguminosae	*Vachellia caven* (Molina) Seigler & Ebinger (VaCa)[R]	Spi	Zoo	Shi	Ben	12. Possette et al., 2015
Myrtaceae	*Blepharocalyx salicifolius* (Kunth) O. Berg (BlSa)[R]	Ab	Zoo	Int, Sht	Obl	13. Redin et al., 2017
Myrtaceae	*Eugenia uniflora* L. (EuUn)[R]	Ab	Zoo	Shi, Int	Obl	14. Risio et al., 2014
Myrtaceae	*Myrcianthes cisplatensis* (Cambess.) O. Berg (MyCi)	Ab	Zoo	Shi	Obl	15. Streit et al., 2014
Myrtaceae	*Myrrhinium atropurpureum* Schott (MyAt)[R]	Ab	Zoo	Int, Shi, Sht	Obl	16. Zalba & Villamil, 2002.
Rhamnaceae	*Scutia buxifolia* Reissek (ScBu)[R]	Th	Zoo	Shi, Int	Obl	
Salicaceae	*Populus alba* (PoAl)[R]	Ab	Ane	Shi	Nof	
Sapindaceae	*Allophylus edulis* (A. St.-Hil., A. Juss. & Cambess.) Hieron. ex Niederl. (AlEd)[R]	Ab	Zoo	Shi	Obl	
Thymelaeaceae	*Daphnopsis racemosa* Griseb. (DaRar)[R]	Spi	Zoo	Shi, Int, Sht	Obl	
Ulmaceae	*Celtis ehrenbergiana* (Klotzsch) Liebm. (CeTa)[R]	Spi	Zoo	Int	Obl	

4.4 Discussion

4.4.1 Community composition but not diversity varies across park forests

Quantitative studies on park forests are scarce and for the first time, a large number of park forests were characterized across Uruguay. The park forests analyzed are similar in species diversity (Figure 4.2b-c) and the values are comparable with another study that evaluated other park forests in the northwestern Uruguay (Pozo and Säumel 2018) but higher than those recorded in the 'espinillares' in Brazil (Watzlawick et al. 2010; Redin et al. 2011). Tree communities have a distinct species composition, the 'espinillares' were distant to the 'blanqueales' and 'algarrobales', while, 'blanqueales' were distant to 'algarrobales' (Figure 4.2a). In general, *Vachellia caven*, *Prosopis affinis* and *P. nigra* were the most characteristic and abundant species, comprising 75% of the total abundance, as has been recorded for other park forests of Uruguay and Brazil (Redin et al. 2011; Pozo and Säumel 2018). Species like *Aspidosperma quebracho-blanco*, *Geoffroea decorticans* and *Prosopis nigra* were more common in 'blanqueales'. This observation agree with previous studies in Uruguay which highlight the presence of P. nigra exclusively on halomorphic soils in 'blanqueales' (Fagúndez 2015). *Prosopis affinis* was the most common species in 'algarrobales' followed by *Vachellia caven* and *Celtis ehrenbergiana*. The dominance of *V. caven* and the absence of *Prosopis* species were notable in 'espinillares'. The majority of native forest species found in our study have wide distribution in Uruguay and in South America (Brussa and Grela 2007; González 2013) and have been reported in other park forests of Uruguay (Costa & Delgado 2001; Grela & Brussa 2003). Affinity with Chaco and Espinal flora was evident in the park forests from the presence of species like *Vachellia caven*, *Celtis ehrenbergiana*, *Prosopis affinis*, *P. nigra*, *Schinus longifolius*, *Aspidosperma quebracho-blanco* and *Scutia buxifolia* (Haretche et al. 2012; Noy-Meir et al. 2012; Watzlawick et al. 2014; Cabido et al. 2018). We recorded the exotic species *Populus alba* regenerating in the 'algarrobales'. This species was originally introduced in Uruguay by silvicultural practices (Masciadri et al. 2010). Likewise, other studies in Uruguay, recorded exotic species such as *Ligustrum lucidum*, *Gleditsia triacanthos*, and *Melia azedarach* invading park forests in Uruguay (Piaggio and Delfino 2009; Traversa-Tejero and Alejano-Monge 2013; Pozo and Säumel 2018) and invading Espinal forests in Argentina (Lewis et al. 2009; Noy-Meir et al. 2012).

4.4.2 Trees facilitate regeneration in grazed park forests

Studies in Uruguay have been limited to the assessment of the grazing effect on tree regeneration of hill forests (Etchebarne and Brazeiro 2016), palm forests (Báez and

Jaurena 2000; Rivas et al. 2005) and a coastal forest (Rodríguez-Gallego 2006). To our knowledge, no study has assessed the occurrence and importance of facilitation mechanisms in Uruguayan park forests. Our study clearly confirmed the facilitation effect of nurse trees on tree regeneration in park forests with 1600% more seedling density under the trees than in open areas (Figure 4.3a, Table 4.1). This indicates that adult trees are exerting a nurse effect on the establishment of new individuals, a form of 'parental care' in plants as was found in a sclerophyllus forest and a forest–grassland ecotone in Chile (Fajardo and McIntire 2011; Cavieres and Peñaloza 2012; Root-Bernstein and Jaksic 2013) and seasonally dry forests in Argentina (Tálamo et al. 2015a; Torres and Renison 2015). Our results showing facilitation in grazed park forests agree with the hypothesis that plant-plant interactions in the presence of herbivores tend to be primarily facilitative (Gómez-Aparicio et al. 2008).

Specific nurse effects including fine variations of shape and size are suggested as major drivers of interactions (Anthelme et al. 2017). However, in our study we did not find an effect of variations from the diameter, height and crown area of nurse trees on tree regeneration (Figure 4.3d-f, Table 4.1).

In our study, trees significantly increase shade in the understory (+61%) (Figure 4.4b). Studies on facilitation emphasize the improvement of microclimatic conditions of nurse plants on their nursing, for example, providing shade and reducing light intensity (De Castanho and Prado 2014), resulting in lower seedling mortality compared to open habitats (Manning et al. 2006). The nurse trees analyzed in this study, *Prosopis sp*, and *Vachellia caven*, presented different traits such as spines and multibranched stems (Table 4.2). Nurse plants enhance the recruitment of other species through indirect mechanisms such as possessing conspicuous herbivore-deterrent traits or extreme chemical defenses (Barchuk et al. 2008; Barbosa et al. 2009; Graff and Aguiar 2011). This was evidenced in dry forests in Argentina by the presence of nurse plants with physical structures that limit the access of cattle so favoring tree regeneration (Barchuk et al. 2008; Tálamo et al. 2015a ; Tálamo et al. 2015b ; Torres & Renison 2015). The nurse effect of *V. caven* was also recorded in a sclerophyllous forest of central Chile (Root-Bernstein et al. 2017). *V. caven* presented a lower height, multibranched steams and the presence of spines that creates a structure that restricts cattle browsing, grazing and trampling. In fact, our data provide evidence for the greater effectiveness of *Vachellia caven* ('espinillares') in facilitating regeneration in comparison with *Prosopis spp.* ('algarrobales' and 'blanqueales') (Figure 4.4a). In contrast, despite the presence of spines *Prosopis* species have characteristics that limit their protective role, such as a growth architecture that leaves open spaces beneath them, allowing relatively easy access to herbivores. Studies in the Chaco forest suggest that less thorn or thornless nurse plants may have a negligible effect on tree regeneration (Tálamo et al. 2015b)

Park forest trees reduce grass cover under the canopy. We recorded 24% less grass cover under trees compared to the open habitat (Figure 4.4c). The limitation of herb development because of the shade provided by the nurse plant reduces the competition with woody plants (Prévosto et al. 2012). Such indirect facilitative interactions play an important role in systems where grass competition is an important limiting factor. Grasses have large negative effects on woody species (Gómez-Aparicio 2009) due to their fibrous roots and a large root: shoot ratio, which allows them to compete efficiently for soil and water resources.

Attenuation of competition and facilitation can be explained by the reduction of herb competition due to the shade provided by the neighbours. Hence, indirect facilitation could play a greater role in systems where competition by herbs is a main limiting factor due to a fast development of strongly competing species such as grasses.

Recruited tree species in our study were predominantly zoochorous and dispersed mainly by birds (Table 4.2, Figure 4.4d). Dispersal mode can dominate environmental factors because of the more pronounced impact of zoochory (Brooker et al. 2008; Soliveres et al. 2012). Scattered trees in landscapes used by livestock are known to act as habitat islands providing connectivity across open habitats and attracting frugivorous birds that use trees for perching, which results in a seed rain beneath nurse trees (Manning et al. 2006). Regeneration species were predominately facilitative obligates and facilitative beneficiaries, whereas non-facilitated species were significantly lower (Figure 4.4f, Table 4.2). Some species like *Schinus longifolius, Celtis ehrenbergiana, Blepharocalyx salicifolius* showed a notably higher regeneration density. This is consistent with the fact that these species are intermediate shade-tolerant species, whereas, light demanding species like *Erythrina crista-galli* and *Geoffroea decorticans* were only recorded in open areas (Table 4.2). In general, studies have shown that the nurse effect is more beneficial for stress-intolerant than for stress tolerant species (Gómez-Aparicio et al. 2008). Shade tolerant species were also benefitted when livestock was excluded from a hillside forest in Uruguay (Etchebarne and Brazeiro 2016). Life strategies did not vary significantly between light demanding, intermediate shade tolerant or light sensitive species. In fact, park forest trees were able to promote the regeneration of species with three different life strategies highlighting their multifunctional role (Figure 4.4e, Table 4.2).

4.5 Conclusion

Scattered trees exert a parental care in highly modified agricultural and silvicultural park forests of Uruguay and therefore they act as important refugia promoting tree recovery with paramount importance in these ecosystems. Trees facilitate tree regeneration by providing shade, limiting grass development and therefore reducing grass competition, protecting against herbivores explained by the presence of physical structures, and promoting species regeneration linked to attraction of zoochorous seed dispersers. Our results have practical implications for the management of park forests: the use of pre-existing pioneer trees as nurse plants will enhance the success of active restoration measures, such as direct seeding or planting of seedlings of light sensitive and shade tolerant species. Woody species appeared as excellent candidates for use as nurses in the restoration of all system types and can be combined with temporal exclosures of grazing to foster the regeneration and growth. Restoration approaches that promote revegetation and minimize cost and effort can be achieved using facilitation as a restoration tool, especially in developing countries that have few resources at their disposal and lack incentives to restore degraded forests (Gómez-Aparicio 2009). In addition, our results suggest that preserving forest remnants or creating islets of tree species will accelerate secondary succession in these areas (passive restoration) by acting as seed sources and providing a habitat for dispersers (Rey Benayas et al. 2008). As in the majority of dry forests worldwide (Miles et al. 2006; Hansen et al. 2013), park forests have been destroyed because of agricultural expansion, over-grazing and selective wood extraction for fuel or other products (especially *Prosopis spp.*). The same forest type in Argentina, the Espinal, has been almost completely destroyed due to agricultural intensification (Noy-Meir et al. 2012). In areas where most dry forest have been converted into pasture a conservative approach has led to the creation of silvopastoral systems based on grazing and the maintenance of the native tree layer while preserving ecosystem functions (Rejžek et al. 2017). This can be a strategy to maintain or restore natural park forests especially using species like *Aspidosperma quebracho-blanco*, *Prosopis affinis*, *P. nigra* and *Vachellia caven* that are already used in other natural silvopastoral systems (Root-Bernstein and Jaksic 2013; Rejzek et al. 2017). We propose that floristically diverse park forests have to be protected for conservation and restored whenever possible, without necessarily preventing their use for traditional silvopastoralism. An integrated view of the forest-grassland mosaic has to be included in management practices, e.g., by assisting tree establishment and survival in grasslands (Erdös et al. 2018) to create silvopastoral systems. Further studies are therefore needed on the outcome of tree–tree regeneration interactions in a scenario of increased magnitude and frequency of grazing.

4.6 References

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4.A Appendix A: Composition of Woody Species

Table 4.3 – Composition of woody species mean tree density (AD) and mean regeneration density (RD) are given. Abreviations include: BL ('blanqueales', Rio Negro), ALB ('algarrobales', Artigas), ALP ('algarrobales', Paysandú), ES ('espinillares', Tacuarembo).

Family	**Species/Author/Code**	**Mean AD/ha**	**Mean RD/ha**	**Forest types**
Anacardiaceae	*Schinus longifolius* (Lindl.) Speg.	3	1396	ES, ALP, ALB, BL
Apocynaceae	*Aspidosperma quebracho-blanco* Schltdl.	46		BL, ALB
Berberidaceae	*Berberis laurina* Billb.		2625	ES
Bignoniaceae	*Tabebuia impetiginosa* (Mart. ex DC) Standley		42	BL
Celastraceae	*Maytenus ilicifolia* Mart. ex Reissek		354	BL, ES
Euphorbiaceae	*Sebastiania brasiliensis* Spreng.	3	42	ALP, ES
Flacourtaceae	*Xylosma tweediana* (Clos) Eichler	3	1687	ES, ALP, BL
Leguminosae	*Erythrina crista-galli* L.		41	BL
Leguminosae	*Geoffroea decorticans* (Gillies ex Hook. & Arn.) Burkart		83	BL
Leguminosae	*Prosopis affinis* Spreng.	432	433	BL, ALB, ALP
Leguminosae	*Prosopis nigra* (Griseb.) Hieron.	10		BL, ALB
Leguminosae	*Vachellia caven* (Molina) Seigler & Ebinger	201	875	BL, ALB, ALP, ES
Myrtaceae	*Blepharocalyx salicifolius* (Kunth) O. Berg	21	1875	ES
Myrtaceae	*Eugenia uniflora* L.	14	437	ALP, ES
Myrtaceae	*Myrcianthes cisplatensis* (Cambess.) O. Berg	2	83	ALP, BL
Myrtaceae	*Myrrhinium atropurpureum* Schott		687	ES
Rhamnaceae	*Scutia buxifolia* Reissek	48	437	BL, ALB, ALP, ES
Salicaceae	*Populus alba* L.		125	ALP
Sapindaceae	*Allophylus edulis* (A. St.-Hil., A. Juss. & Cambess.) Hieron. ex Niederl.	7	812	ALP, ES
Thymelaeaceae	*Daphnopsis racemosa* Griseb.		125	ES
Ulmaceae	*Celtis ehrenbergiana* (Klotzsch) Liebm. (CeTa) R	40	983	BL, ALB, ALP, ES

4.B Appendix B: Supplementary References

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CHAPTER 5

SYNTHESIS

The ongoing expansion of intensive management operations that target at monoculture plantations of few fast-growing exotic species has sparked off controversy whether these systems are 'green deserts' or useful tools for restoring degraded land (Bremer and Farley 2010; Boulmane et al. 2017). With a current demand for higher production levels and ecosystems services there has been a shift to develop alternatives to conventional management practices. Studies have shown that the use of native species in forestry projects facilitates processes that are associated with natural ecosystems (Bremer and Farley 2010), meet better local cultural needs (Hall et al. 2011) and are able to provide benefits in the long-term (O'Hara 2016). At the same time, studies in temperate and tropical regions have shown that mixed plantations are able to provide a wider range of ecosystem services than monocultures (Piotto et al. 2010; Puettmann et al. 2015). Since monoculture plantations with exotic species are expected to continue increasing in the future, forestry approaches must develop alternatives that are able to mimic natural processes and reduce the negative impact of exotic species on the environment. This thesis discussed and presented different strategies to design multifunctional and biodiverse forests in silvicultural and agricultural modified landscapes. A special focus is placed in Uruguay, a country where the rate of afforestation with exotic species increased exponentially in the last years, making it the country with the highest afforestation rate of South America (FAO 2018). Plantations in Uruguay occupy more than the native forest cover and are composed mainly of *Eucalyptus* species (Paruelo et al. 2006; FAO 2015), detailed inventory data are lacking for most native forests resulting in the selection of better documented but less appropriate exotic species.

Chapter *"From master of one towards jack of all traits? Extending the range of ecosystem services provided by timber plantations using diversified tree trait selection in the Global South"* focused on the potential of native species for timber plantations, knowledge gaps and strategies to select native species. A systematic review of literature was performed in order to identify common traits and criteria of choosing native species for timber plantation and propose alternative approaches for the selection of species that incorporates a wider range of ecosystem functions and services. The results shown that although research regarding the use of native species for timber plantations has increased about threefold, knowledge regarding silvicultural management is still limited. Most studies select native species purely for their potential for timber production, additional benefits and ecosystem services are regularly omitted. Up to now, the traits of most tree species were chosen at stand scale and focused on timber production. The selection of native species must incorporate the landscape scale and support wider range of ecosystem functions and services, provide adaptability and resilience to the system in the long-term and consider the interests of landowners and users. The use of native species is highlighted over exotic species when multiple benefits beyond timber production are included. Some traits such as pollination mode, dispersal mode and N-fixing capacity contribute to services and processes and are likely to maintain greater diversity in forests. However, selecting native species based on functional groups, requires more knowledge than is currently available. Therefore, more research of native tree species by plantation trials to evaluate species performance and identify species with high rates of growth and survival is needed. Nurseries can be set up in specific project areas covering a wide range of sites where the species occurs and have to focus also on genetic improvement by the selection of desired traits.

Chapter *"How to Bloom the Green Desert: Eucalyptus Plantations and Native Forests in Uruguay beyond Black and White Perspectives"* placed a special emphasis on native forests and timber plantations in Uruguay. The diversity of woody species in native forests and in *Eucalyptus* plantations were evaluated, and the potential use of native species to enhance plantation management was discussed. For this purpose, one-hectare permanent plots were established in nine native forests and nine *Eucalyptus* plantations in the northwestern part of Uruguay. It was found that native forests have a high diversity of woody species and high regeneration capacity, they harbor specialist species that are absent from plantations, which play a decisive role in maintaining biodiversity in agricultural and silvicultural modified landscapes of Uruguay. Moreover, native tree species have potential use to enhance current plantation management. Species such as *Eugenia uniflora*, *Allophyllus edulis*, *Vachellia caven*, and *Prosopis affinis* promise various ecological, economic, and social benefits for future forestry projects. 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. Management programs of the exotic species *Ligustrum lucidum*, *Gleditsia triacanthos* and *Melia azedarach* regenerating in native forests have to be developed urgently. Special effort need to be placed in the riverine forests of the Uruguayan lowlands (currently under high invasion of *Gleditsia triacanthos*) by enriching planting or restoration to provide a buffering function to water resources. Up to now Uruguay does not include policy directives to forest regeneration or reforestation. First experiments on invasion control along the National Parque of Rio Uruguay focused only on the application of systemic herbicides. On the other hand, the regeneration of native woody species such as *Allophylus edulis*, *Blepharocalyx salicifolius*, and *Celtis ehrenbergiana* in the understory of exotic *Eucalyptus* plantations demonstrates the possibility of developing management strategies such as mixed-species and multiple-age plantations to reduce the negative impact of monocultures. It is important to encourage the conservation or sustainable use of native forests and the development of alternative strategies such as mixed systems, at least as buffer strips containing native species at the edge of plantations as potential measures to enhance biodiversity and foster the integration of plantations into the local landscape.

Chapter *"Positive tree-tree interactions facilitate dry forests persistence in agricultural modified landscapes"* provided detailed information about one of the most threatened forest types in Uruguay, the so called park forests. Forest community composition in different types of park forests across the country were explored in one-hectare plots. Additionally, the role of scattered trees for regeneration was assessed by evaluating nurse–beneficiary interactions in a series of paired plots located under the canopy of the trees and in the open area. Native trees play a crucial role in highly modified agricultural and silvicultural landscapes of Uruguay. The results highlight their role to the promotion of forest regeneration and recovery in grazed forests. Tree to tree facilitation effects were denoted by the greater regeneration density under the tree than in the open area. Trees provide shadow, limit grass competition, protect against herbivores and promote species regeneration linked to the attraction of dispersers. The species *Prosopis affinis*, *P. nigra* and *Vachellia caven* have potential in restoration projects either by using them as pioneer trees for direct seeding under their canopy of light sensitive and shade tolerant species, or by preserving them in order to accelerate secondary succession. Moreover, their use for natural silvopastoral systems constitutes a highly potential multifunctional strategy to maintain and restore natural park forests. This strategy can constitute places where meet production shares spaces with native biodiversity. The use of other potential species such as *Aspidosperma quebracho-blanco*, *Celtis tala* should be addressed in futures studies.

Uruguay as a heavily used region subject to expanding land use changes to establish monocultures of exotics species requires to develop alternative approaches that achieve productivity while conserving biodiversity and that take into account the interest of landowners and local communities. Those strategies vary from improving the selection and research of native species for timber plantations, diversifying plantations with mixed systems and enhancing the conservation and sustainable use of native forests as natural silvopastoral systems. Future studies integrating other regions of Uruguay, other taxonomic groups of fauna, herbs, insects and other land use types are necessary to develop definite landscape management schemes in Uruguay.

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General Appendix

List of Publications and Self-Contribution

forests

MDPI

Article

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

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Received: 6 August 2018; Accepted: 27 September 2018; Published: 6 October 2018

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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 m^2 plots and regeneration was assessed along transects in 9 m^2 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 km^2, 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.

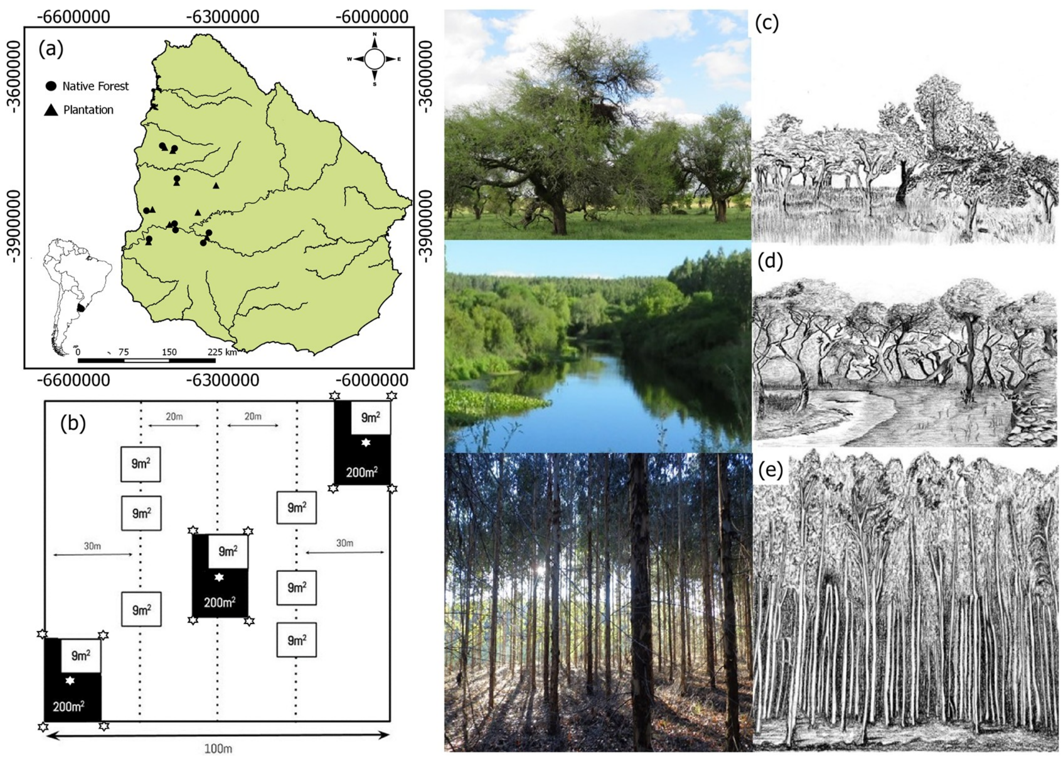

Figure 1. Map of the study area with: (**a**) the study sites in the northwestern part of Uruguay (black dots: native forests and black triangles: *Eucalyptus* plantations); (**b**) sampling design composed of permanent plots (100 × 100 m^2), inventory plots for trees (20 × 10 m^2), regeneration subplots (3 × 3 m^2) 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 20×10 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 DBH $\geq$ 2.5 cm at 1.3 m. Regeneration assessment (individuals with <2.5 cm diameter and height <1 m) was evaluated in nine 3×3 m^2 subplots located inside the 20×10 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 assesssed inside the 20×10 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 cm) and three height classes (0–5 m, 6–10 m, and >10 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 $\leq$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.

Forests 2018, 9, 614 5 of 16

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).

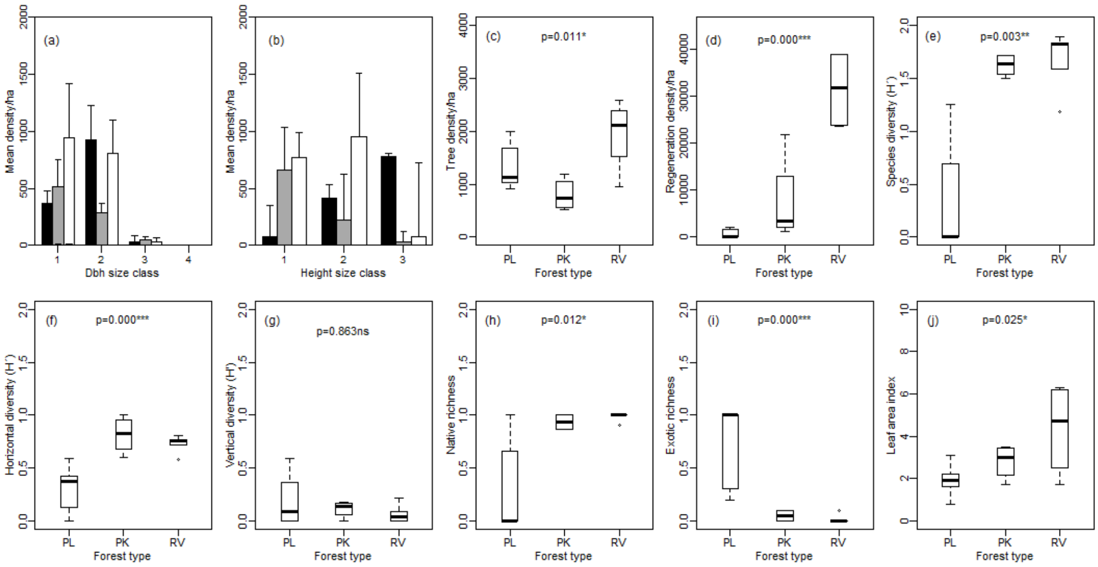

Figure 2. (**a**,**b**) The forest structure of the three forest types: *Eucalyptus* plantations (black bars), park forests (dark grey bars) and riverine forests (white bars): expresed as mean tree density per ha in diameter classes (1 = 2.5–10 cm, 2 = 10–30 cm, 3 = 30–50 cm, 4 = >50 cm) and height size 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
Schinus longifolius (Lindl.) Speg. (ScLo)	250 [PK] 3 [RV]	185 [PK] 20 [RV]	med [9] or [9]
Patagonula americana L. (PaAm)	90 [RV]	99 [RV]	re [7] w [8,20]
Maytenus ilicifolia Mart. ex Reissek (MaIl)	9 [PK]	370 [PK] 1175 [RV] 493 [PL]	med [8]
Escallonia bifida Link & Otto (EsBi)	17 [RV]		or [8]
Sebastiania brasiliensis Spreng. (SeBr)	447 [RV]	317 [RV]	re [1,2] med [1,18 or 18]
Citronella gongonha (Mart.) R.A. Howard (CiCo)	3 [RV]	40 [RV]	zo [8,16]
Ocotea acutifolia (Nees) Mez (OcAc)	197 [RV]	119 [RV]	w [8] med [10]
Bauhinia forficate Link (BaFo)	8 [PK]		med [16] or [8]
Gleditsia triacanthos L. (GlTr)	8 [PK] 13 [RV]	185 [PK] 40 [RV]	ex
Prosopis affinis Spreng. (PrAf)	4 [PK]	154 [PK]	bee [8,6] re [14] zo [6] w [8,3]
Vachellia caven (Molina) Seigler & Ebinger (VaCa)	25 [PK]	247 [PK] 246 [PL]	bee [6] re [14] zo [6]
Melia azedarach L. (MeAzr)	31 [PK]		ex
Blepharocalyx salicifolius (Kunth) O. Berg (BlSa)	129 [PK] 150 [RV]	247 [PK] 479 [RV] 1358 [PL]	zo [8,12,16] re [1,11] med [1,11]
Eugenia uniflora L. (EuUn)	38 [PK] 37 [RV]		zo [8–12,16,20] re [7] bee [9,11] or [8] med [4,5,20]
Myrcianthes cisplatensis (Cambess.) O. Berg (MyCi)	8 [PK] 350 [RV]	2746 [PK] 188 [RV] 740 [PL]	zo [11] bee [11] med [4]
Myrcianthes pungens (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]
Myrrhinium atropurpureum Schott (MyAt)	8 [PK] 17 [RV]		zo [12,16] re [11] w [8] or [8] med [11]
Ligustrum lucidum W.T. Aiton (LiSi)	4 [PK] 87 [RV]	12395 [RV] 2222 [PL]	ex
Colletia paradoxa (Spreng.) Escal. (CoPa)	4 [PK]		bee [8] or [19]
Scutia buxifolia Reissek (ScBu)	70 [PK] 157 [RV]	556 [PK] 96 [RV]	zo [16] re [1] w [8] med [1]
Discaria Americana Gillies & Hook. (DiAmr)		185 [PK]	med [17]
Azara uruguayensis (AzUr)	27 [RV]		or [8]
Salix humboldtiana Willd. (SaHu)	17 [RV]		w [8]
Jodina rhombifolia (Hook. & Arn.) Reissek (JoRh)	3 [RV]		med [13]
Allophylus edulis (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]
Pouteria salicifolia (Spreng.) Radlk. (PoSa)	8 [PK] 353 [RV]	31 [PK] 247 [RV]	med [4]
Daphnopsis racemosa Griseb. (DaRa)	27 [RV]	353 [RV]	fb [8], or [19]
Celtis ehrenbergiana (Klotzsch) Liebm. (CeTa)	133 [PK] 33 [RV]	278 [PK] 290 [RV] 740 [PL]	zo [8]
Citharexylum montevidense (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.

NMDS			ANOVA	
Parameters	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).

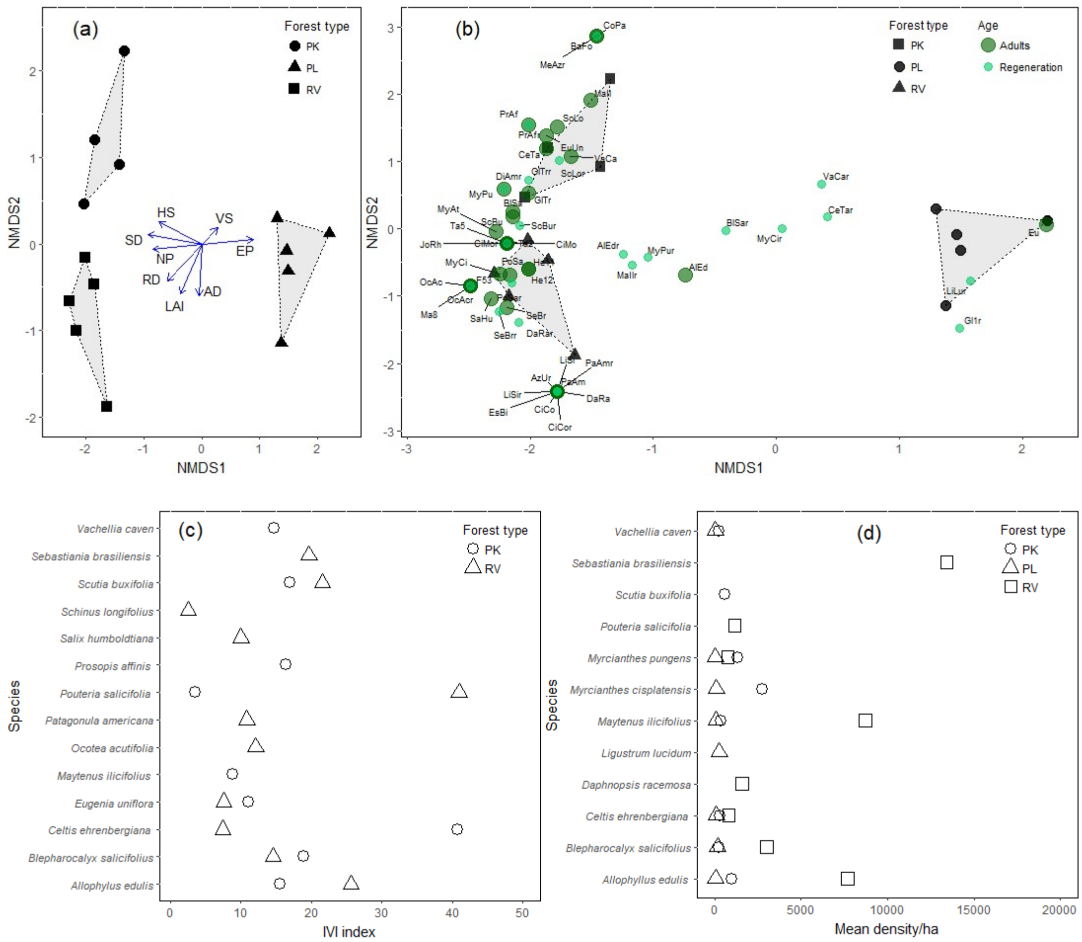

Figure 3. (**a**) Non-metric multidimensional scaling (NMDS) ordination of species from different forest types (PL: *Eucalyptus* plantations, RV: riverine forests, PK: park forests) and plots using the Bray–Curtis distance based on species abundance, showing distance between plots and eight explanatory 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., AlEd: *Allophyllus edulis* AlEdr, 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 *Allophyllus 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 *Allophyllus 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, *Allophyllus edulis*, *Sebastiania brasiliensis*, and *Pouteria salicifolia* have potential for restoration projects due to their high IVI values and considerable representation in riverine forests. *Allophyllus 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 ecosystems 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 longifoulis*, 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*, *Allophyllus 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.

Author Contributions: Conceptualization of the study, I.S.; Implementation and adaptation of the study, P.P.; Methodology design and validation, P.P. and I.S.; Data acquisition and analysis, P.P.; Draft writing, P.P.; Review & Editing, I.S.; Visualization, P.P..; Supervision, I.S.; Funding acquisition, I.S.

Funding: The study was funded by the German Federal Ministry of Education and Research (BMBF) under the project "Rural Futures—Strategies towards multifunctional, biodiverse and sustainable productive landscapes in silvi- and agricultural modified grasslands in Uruguay" (01LN1315).

Acknowledgments: We are very grateful to Nicolas Silveira and Giannina Lemus for their assistance in field work and to Celso Erazo for drawing the forest types in Figure 1. We thank John Wood who helped with corrections of the English language and three anonymous reviewers for helpful comments on an earlier version of the manuscript.

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, and in the decision to publish the results.

Appendix A

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

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