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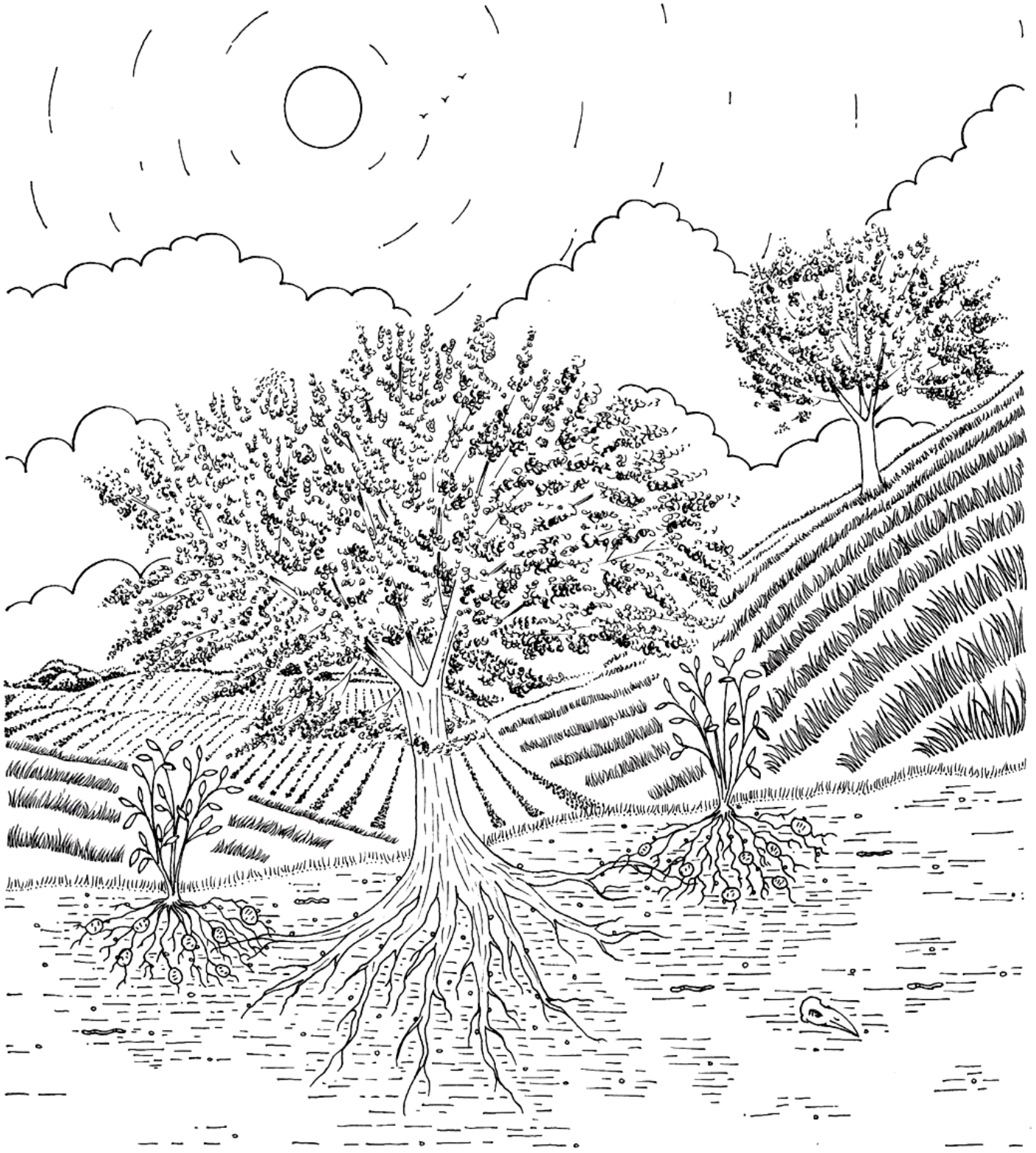Leonardo Henrique Teixeira Pinto

Restoration of plant diversity and ecosystem functioning:

Effects of species richness, phylogenetic distance, functional diversity and invasive plants

2017

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> Tese de doutorado apresentada à Coordenação do Curso de Pós-Graduação em Ecologia, da Universidade Federal do Rio Grande do Norte em cumprimento às exigências para obtenção do título de Doutor em Ecologia.

Orientadora: Prof. Dra. Gislene Ganade

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Restoration of plant diversity and ecosystem functioning:

Effects of species richness, phylogenetic distance, functional diversity and invasive plants

Leonardo Henrique Teixeira Pinto

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PREFÁCIO

A jornada desse doutorado...

Tem sido uma longa jornada. E pode-se dizer que foi curta também. O tempo voa. Comecei o doutorado em Maio de 2013 e quatro anos se passaram desde então. Cada ano com uma aventura diferente, uma descoberta diferente, um novo aprendizado. Em 2013, assim que comecei o doutorado, descobrimos que minha esposa (à época) estava grávida. A melhor notícia que já recebi. Eu estava em êxtase. Poucos meses depois, no mesmo ano, deixei a esposa grávida no Brasil e fui para a Alemanha. Primeira vez fora do meu país. Hora de provar a mim mesmo. Provar que eu poderia falar outra língua, mesmo que eu nunca tivesse frequentado uma escola de idiomas. Em 2014, voltei ao Brasil e, poucas semanas depois, minha filha nasceu. O dia mais feliz da minha vida. Linda Inaê! Meu eterno amor. E como nós nos amamos... Nós nos reconhecemos desde o primeiro momento. Até mesmo a enfermeira que a trouxe para eu ver entendeu que a Inaê reconheceu minha voz quando ela parou de chorar no momento em que eu falei com ela, enquanto a segurava em meus braços pela primeira vez. Inaê e eu tivemos longas conversas desde que ela estava no útero da mãe. Nós conversamos via Skype, nós cantamos e brincamos juntos desde o início. Nunca separados! Não importa quão distantes estejamos um do outro. E tem sido assim até hoje.

O ano de 2015 chegou muito rápido. Poucas semanas antes, Inaê dera seus primeiros passos e começara a esboçar suas primeiras palavras. Primeiro aniversário da Inaê, família reunida, mais um dia feliz. No mesmo ano, publiquei meu primeiro artigo. O primeiro trabalho científico em minha vida acadêmica. O trabalho da minha monografia como Bacharel em Ecologia. E como eu estava orgulhoso dessa realização. Excelente! A porta havia sido aberta. No entanto, a vida é cheia de inconstâncias. A vida é assim, como uma montanha-russa (totalmente clichê, mas é verdade). E, após onze anos juntos, meu casamento acabou. O dia

mais triste em toda a minha vida foi quando cheguei em casa, após ter levado minha ex-esposa e minha filha ao aeroporto, e o quarto da Inaê estava vazio. Nenhuma de suas roupas ou brinquedos estavam lá. Por sorte, minha mãe estava comigo para me apoiar e secar minhas lágrimas, assim como diz o poema que escrevi pra ela anos atrás. Em momentos como este, todos nós precisamos de palavras de apoio. Mas, às vezes, nossos melhores amigos não dizem as coisas que queremos ouvir. E é exatamente por isso que eles são nossos melhores amigos, porque eles são honestos conosco. Então, não fique zangado quando seu melhor amigo disser pra você que o tempo irá dizer, que o tempo é a resposta. Sim, é verdade. O tempo sempre diz... E o tempo me disse que a vida pode ser mais difícil do que imaginamos. Mas, depois de tudo, nós nos tornamos mais fortes.

O ano de 2016 veio com novas perspectivas. Publiquei meu segundo artigo. O trabalho do meu mestrado em Ecologia. 2016 também trouxe más notícias. Em 22 de março, perdi meu pai. Ele completou seu ciclo entre nós. Ele era amado e, às vezes, mal compreendido. Mas, no final, só o amor sobrevive ao tempo e à ausência. Ainda me lembro de sua voz, seu rosto e algumas de suas piadas. Isso é o que importa na vida. Como as pessoas que amamos irão lembrar de nós quando partirmos. Poucas semanas depois viajei para a Alemanha pela segunda vez. Desta vez, vim para solidificar as colaborações, terminar artigos, terminar minha tese e começar novos trabalhos. Estou morando na Alemanha desde então. E, pela segunda vez, este país me surpreendeu. Aqui tenho bons amigos. Pessoas com quem eu posso falar quando estou triste e que gostam de mim do jeito que eu sou, mesmo com as minhas piadas ruins.

Para 2017, novas oportunidades apareceram, novos desafios começarão. 2017 será um ano para fechar capítulos e para iniciar novas histórias. E o tempo ainda irá dizer...

Agradecimentos

Agradeço à natureza por ser tão bela, intrigante e desafiadora. Por inspirar continuamente em mim o desejo de entender um pouco mais sobre seus mistérios e, assim, aprofundar meu conhecimento sobre Ecologia. Agradeço aos grandes Ecólogos e Biólogos (todos os que trilharam esse caminho científico no qual eu tento seguir dia após dia) que com os trabalhos e esforços de toda uma vida contribuíram para o avanço da ciência e de nossa sociedade. Agradeço, também, à minha orientadora, Dra. Gislene Ganade (Gis) pelo acolhimento, pelos conselhos, pela paciência, carinho e amizade. Obrigado pelas conversas imprescindíveis que tivemos no decorrer desse doutorado e, também, antes dele. Conversas e conselhos que me auxiliaram a seguir firme nessa caminhada em busca de qualificação profissional e pessoal. Muito obrigado pela confiança.

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me envolver em problemas sem solução. Agradeço também à Raquel que sempre foi parte desse sonho. Obrigado pela ajuda, pelo incentivo e amor oferecidos a mim. Obrigado por ser uma mulher corajosa e uma mãe exemplar. Serei sempre grato por, mesmo após nossa separação, você não ter deixado que nossos desentendimentos interferissem em minha relação com a Inaê. A ti ainda ofereço os meus versos, pois juntos temos a responsabilidade de educar e preparar nossa filha para que ela também seja uma mulher inteligente, corajosa e sonhadora.

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de forma mais rápida e mais sincera do que discordávamos um do outro. Agradeço ao Rodrigo por ter embarcado comigo para Natal em 2002 quando iniciamos essa aventura de 'morar na praia' junto com o Rafael. Enfim, muito obrigado por tudo.

Dedico esta e toda conquista que ainda se fará possível em minha vida ao meu amor maior, minha filha Inaê.

Amor.

Leonardo H. Teixeira Pinto

PREFACE

The journey throughout my PhD…

It has been a long journey. And it was short as well. Time flies by. I started my PhD in May 2013 and four years has passed since then. Each year had a different adventure, a different discovery, a new learning. In 2013, as soon as I started the PhD, we discovered my wife (at the time) was pregnant. The greatest news I ever received. I was in ecstasy. Few months later in the same year, I left my wife pregnant in Brazil and went to Germany. First time outside my home country. Time to prove myself. Prove that I could speak another language, even though I've never studied how to. In 2014, I was back in Brazil. Few weeks later, my daughter was born. The happiest day in my whole life. Beautiful Inaê! My forever love. And how we love each other… We recognize each other since the very first moment. Even the nurse that brought her to me for the first time understood that Inaê recognized my voice when she stopped crying the first time I spoke to her in my arms. We have been talking since she was in her mother's uterus. We have been talking via skype, we have been singing and playing together since the very beginning. Never apart! No matter how distant we are from each other now.

The year 2015 came really fast. Few weeks before that, Inaê gave her first steps and she was trying her first words as well. Inaê's first anniversary, family gathered together, another happy day. In the same year, I published my first paper. The very first scientific work in my "academic career". The work from my Bachelor thesis. And how proud I was of my accomplishment. Well done! I've opened the door. However, life is full of inconstancies. Like a roller coaster (what a 'cliché'!). Life is just like that. And, after eleven years together, my marriage was over. The saddest day in my whole life was when I came back from the airport (after have accompanied my, now, ex-wife and my daughter) and my daughter's room was completely empty. None of her clothes or toys were there. Fortunately, my mother was there to

hold me and dry my tears, just like says the poem I wrote to her some years ago. In moments like this, we all need some words of support. But, sometimes, our best friends don't say the things we want to hear. And that is why they are our best friends, because they are honest with us. So, don't be angry when your best friend says to you 'time will tell', time is the answer. Yes, it is true. Time always tells… And the time told me, life can be harder than we thought about. But, after that, we grow stronger.

The year 2016 came with new perspectives. I've published my second paper. The work from my Master thesis. But it also brought bad news. In March 22th, I lost my father. He completed his life cycle among us. He was loved and, sometimes, misunderstood. But, at the end, only love survives the time and the absence. I still remember his voice, his face and some of his jokes. This is what matters in life. How people we love will think about us from the moment we are gone. Few weeks later I traveled to Germany for the second time. This time I came here to strengthen the collaborations, to finish papers, to finish my thesis and I start new works. I'm living in Germany since then. And, for the second time, this country has surprised me. Here I have good friends. People to whom I can talk when I'm sad and people that like me the way I am, even with my bad jokes.

For 2017, new opportunities have appeared, new challenges will start. 2017 will be the year for closing chapters, for writing new ones. And time will still tell…

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I thank nature for being so beautiful, intriguing and challenging. For continuously inspiring in me the desire to understand a bit more about its mysteries, thus increasing my knowledge about Ecology. I thank the great Ecologists and Biologists (all those who have followed the same scientific path I try to follow day after day in my life) which the work and efforts from a lifetime have contributed to the advancement of science and to making our society better. Thanks also to my supervisor, Dr. Gislene Ganade (Gis) for receiving me, for the advices, for the patience, for the affection and friendship. Thank you for the essential conversations we had during this PhD and, also, before it has started. Your advices helped me to keep strong in this journey seeking for professional and personal qualifications. Thank you very much for your confidence.

I thank my great friend and Professor Coca (Dr. José Luiz Attayde) for his trust and affection. For the inspiring lessons that have helped me to develop the desire for becoming a scientist. I thank Coca, most of all, for believing in my potential even when I doubted myself. I am grateful to Professor Johannes Kollmann for welcoming me so well among his students in the Chair of Restoration Ecology at the Technical University of Munich. Thank you for allowing me to develop an experiment of my PhD at the dependencies of this great university and, also, for the supervision and all the valuable contributions to the development of this thesis.

I want to deeply thank my family (my mother Sueli, my sisters Elaine, Bárbara and Regina, and my niece Fran) for the fundamental support during all the time I have been studying at UFRN. Thank you very much for your advices, for all the examples of courage and, also, for being my strength during times when life seemed to involve me with endless problems. I also thank Raquel who was always part of this dream. Thanks for the help, for the encouragement and love you offered me. Thank you for being such a brave woman and an exemplary mother.

I will be always grateful that, even after our divorce, you did not let our misunderstandings interfere in my relationship with Inaê. I still offer you my poems, because together we have the responsibility to educate and prepare our daughter so she can also grow a dreamy, intelligent and brave woman.

I thank my friends from the Restoration Ecology Lab (LER - UFRN) Adler, Felipe, Jane, Marina (Mai), Rafael (Rafa), Cíntia (Tida), Bruna and Hudson for the affection, for the companionship, for the help, for the ideas and for making every field work, experiment implementation and data collection a pleasure activity, even if it was during the hottest day in the Caatinga. Thanks to my good friend Gustavo for all the help, advices and friendship, for the Saturday evenings eating at Dedé's restaurant and, also, for the Sundays playing guitar, eating pasta and drinking beer. Thanks for the songs and poems we wrote together to calm down our hearts and drive away our sorrows. Thank you very much, my friend.

I thank my friends from the Aquatic Ecology Lab (LEA - UFRN) Pablo, Fabiana, Mariana, Marcolina, Danyhelton and Gabi for all the moments we shared. For all the fieldwork that has always been more fun and rewarding together with you guys. Thanks for your support, inspiration and complicity. Our fields are slightly different, but you are also part of this thesis. I am very grateful to Dr. Vanessa Becker for allowing me to use LARHISA's facilities to perform the nutrient analysis for one of the experiments in this thesis. Your support was fundamental.

I thank my friend (and now Professor) Rosemberg for all the advices, cooperation, encouragement and honesty. I thank my friend Lucyanno for making the maps from the areas where I performed my experiments. I thank the great artist and my friend from childhood, Eduardo (Du), for accepting my invitation to draw this thesis' cover and for gift me with such a beautiful piece of art.

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Thanks to my friends Brunno and Mona for their support. For the sincere friendship built along these 13 years. For listening to my questions and for all the help and advices during the moments of difficulty. I'm very grateful to Brunno for the valuable suggestions during the development of one of the chapters of this thesis. Hope this is the first of many other collaborations between us. I thank Florencia Yannelli for her contributions, ideas and corrections for the paper we produced in collaboration. I thank my friends from Germany (Romy, Katharina, Ferdinand, Nicolas, Lucian, Willi, Gerson, Lena, Raquel, Cristina, Iris and Cristiane) for receiving me in their homes and in their lives. For making me feel like home (even with the Atlantic Ocean between me and Brazil) and also for participating in this important moment in my life. Thanks to all my colleagues from the Department of Restoration Ecology at the *Technische Universität München*.

I especially thank my great friend Rodrigo for the partnership, for the honesty in our friendship, for the discussions (and there were many). But, we always solved our problems faster than we disagreed with each other. Thanks for joining me in 2002 when we started this adventure of moving to Natal together with Rafael. I thank Rodrigo for all the moments we shared during these 19 years of friendship. Thank you very much, my friend.

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I dedicate this and every achievement that will still be possible in my life to my greatest love, my daughter Inaê.

Love.

Leonardo H. Teixeira Pinto

THESIS CONTENT

THESIS SUMMARY

Biodiversity positively affects several ecosystem functions. Nevertheless, the mechanisms by which biodiversity affects ecosystems are still poorly understood and call for new experimental studies designed to identify its underlying components. Previous studies have suggested that more diverse plant communities can provide more ecosystem stability due to complementarity and redundancy effects. Plant species diversity can act on different levels of the ecosystem properties. A clear example is the effect of plant diversity on nutrient dynamics of terrestrial ecosystems. Plant diversity can alter rates of soil nutrient accumulation and nutrient loading in aquatic systems. However, human impacts on natural ecosystems are leading to habitat and biodiversity loss. Such losses will ultimately jeopardize ecosystem functions and its associated services that are vital for human well-being. Therefore, the development of adequate restoration projects is paramount to mitigate anthropogenic impacts, while contributing to the conservation of biodiversity. Restoration projects offer the possibility to develop a solid knowledge on the functioning of ecosystems facing disturbance. For achieving this knowledge, we need to conduct theory-based restoration experiments in order to assess the variability, predictability and reliability of functioning from restored ecosystems. In this context, this PhD thesis is based on three experiments testing how plant diversity and functional traits would influence the functioning of restored ecosystems. The objectives are to investigate (i) the plant species and traits that are most efficient for retaining nutrients in the soil, thus reducing nutrient leaching losses and its consequent impact on aquatic systems; (ii) the effects of plant species richness and phylogenetic diversity on restoration success (measured as biomass production and plant survival) in a recently restored riparian forest; and (iii) the influence of an invasive alien plant species on soil and soil water nutrients in communities with different levels of functional diversity. The experiments conducted

during this thesis are in accordance with recent studies that investigate how different measures of biodiversity and sources of stress could affect ecosystem functioning. The main results of this thesis reveal that (i) only one species (*Mimosa tenuiflora*) could influence water cleaning and soil nutrient content. Additionally, plant traits related to shoot dry matter content (SDMC) and root water content (RWC) are more important for controlling individual functions related to water and nutrient retention in the soil, while only traits related to biomass production affected ecosystem multifunctionality; (ii) the use of phylogenetically distant species can increase restoration success by positively affecting plant biomass production; and (iii) plant functional diversity partially promotes water cleaning and soil fertility in restored systems, nevertheless did not prevent invasion. In turn, invasive species disrupts the influence of plant diversity on soil nutrient dynamics by jeopardizing native plant biomass production thus, potentially, creating a positive feedback for further invasions. These results support future restoration projects focusing on invasive species control and ecosystem functions, indicating which species are most suitable for restoration to maximizing soil fertility and soil water quality. Finally, this thesis offers a contribution to the knowledge of plant-soil feedbacks.

Thesis keywords: *Biodiversity and ecosystem functioning, functional diversity, invasive species, nutrient retention, phylogenetic diversity, plant traits, soil fertility, tropical dry forests.*

Chapter 1

GENERAL INTRODUCTION

> *"It may well be that natural systems are not so very fragile; they are, after all, complex adaptive systems that will probably change and become new systems in the face of environmental stresses. What is fragile, however, is the maintenance of the services on which humans depend. There is no reason to expect systems to be robust in protecting those services—recall that they permit our survival but do not exist by virtue of permitting it, and so we need to ask how fragile nature's services are, not just how fragile nature is. These questions are perhaps the fundamental ones in the ecological sciences today..."*

Levin (1999, p. 15)

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Theoretical background

While describing the experiments conducted by George Sinclair, the Duque of Bedford's head gardener, Charles Darwin realized that a number of grass species resulted in a higher amount of biomass compared to a monoculture (*The Origin of Species*, p. 185). Some scientists argue that this was the first description of a diversity–productivity relationship, and the discovery of the fact that plant diversity is important for ecosystem functioning and human wellbeing (McNaughton 1993; Hector & Hooper 2002; Hector &

Bagchi 2007; Hector et al. 2009). Since then, numerous studies have been conducted on biodiversity and ecosystem functioning (BEF) and its results have confirmed Darwin's expectations. Over the years, several hypotheses have been proposed to explain the effects of diversity on ecosystems. Such hypotheses account (i) for complementarity and dominance effects (Cardinale *et al.* 2007; Winfree *et al.* 2015), (ii) for species diversity effects on ecosystems productivity and stability (Tilman, Reich & Knops 2006; Fornara & Tilman 2009; Prado-Junior *et al.* 2016), and (iii) for the effects of diversity on ecosystem resilience and resistance, thus reducing uncertainties about functioning reliability (Bellwood, Hoey & Howard Choat 2003; Folke *et al.* 2004; Milcu *et al.* 2010; Craven *et al.* 2016).

Indeed, many studies have proven that plant species richness positively affect different aspects of ecosystems (Tilman, Isbell & Cowles 2014). However, since the early 2000s, studies have shown that functional diversity (Díaz & Cabido 2001) and, more recently, that phylogenetic and genetic diversities are also very important for ecosystem functioning (Srivastava *et al.* 2012; Salo & Gustafsson 2016). The term *ecosystem functioning* can be defined as the joint effect of all functions, services and processes that play some role in a given ecosystem (Gamfeldt, Hillebrand & Jonsson 2008). Hence, for understanding, evaluating and making predictions about the functioning and stability of ecosystems in face of stressors we need to assess different functions combined. Nevertheless, only during the past decade scientists have started to evaluate the so-called ecosystem multifunctionality; i.e. the simultaneous provision of several ecosystem functions (Hector & Bagchi 2007; Isbell *et al.* 2011; Maestre *et al.* 2012; Gamfeldt *et al.* 2013; Soliveres *et al.* 2016).

Plant diversity affects several ecosystem functions by complementarity and redundancy effects (Fonseca & Ganade 2001; Naeem & Wright 2003). Such mechanisms can lead to more stable ecosystems, ensuring ecosystem functioning and human welfare during environmental fluctuations (Yachi & Loreau 1999; Loreau 2010; Cardinale *et al.* 2012). One important example is the control of nutrient fluxes, intrinsically, related to soil and water quality and ecosystems productivity (Cardinale *et al.* 2012; Balvanera *et al.* 2014). Several studies have demonstrated that the composition or the functional identity of the plant species in a community is a better predictor of ecosystem functioning than species number *per se* (Mokany, Ash & Roxburgh 2008; Mouillot *et al.* 2011; Sasaki & Lauenroth 2011). However, plant species can trade-off different functions or processes (Lavorel & Grigulis 2012), so the number of redundant species would be lower than previously thought, thus increasing the number of unique functions being performed (Bowker *et al.* 2011). In fact, communities are more likely to provide higher levels of functioning for a few set of functions rather than performing similarly for several functions (Heemsbergen *et al.* 2004). Therefore, when many functions are considered together for evaluating the functioning of ecosystems, species effects become unique, because the same species cannot perform similarly for contrasting functions (Petchey & Gaston 2002). Such trade-offs can be especially important for controlling soil nutrient dynamics. Since plant species have nutrient limitations and differential functional traits, they will affect nutrient pools and cycling differently during their life cycle (Cardinale *et al.* 2011; Conti & Díaz 2013; Machovsky-Capuska *et al.* 2016).

Another biodiversity aspect that has been considered in BEF studies (and that could also be important for the restoration of degraded areas) is the phylogenetic diversity of plant communities (Hipp *et al.* 2015). Higher phylogenetic diversity can increase ecosystems stability (Cadotte, Dinnage & Tilman 2012), productivity (Cadotte 2013),

reduce herbivore effects for native plants (Schuldt *et al.* 2014) or increase herbivory for non-native ones (Pearse & Hipp 2014). In fact, phylogenetically diverse communities increase biological resistance in forests (Iannone *et al.* 2016), while in grasslands phylogenetic diversity was found to constrain invasion impacts but not to increase resistance against invasions (Bennett, Stotz & Cahill 2014). Plant communities composed of phylogenetically distant species can have a wide variety of functional traits and, therefore, more complementarity effects for multiple functions (Srivastava *et al.* 2012; Cadotte 2015). We can use phylogenetic diversity to explain how plant species interact, for example, phylogenetic diversity could explain interactions among native and invasive species, and therefore, predict resistance to invasions and its impacts (Cahill *et al.* 2008; Godoy, Kraft & Levine 2014; Yannelli *et al.* 2017). However, more evidence is needed regarding how phylogeny influences functioning of invaded systems, mainly when considering nutrient dynamics.

Plant diversity is also suggested to prevent establishment of invasive plants. The diversity–invasibility hypothesis argues that, by occupying larger dimensions of the ecological niche, high diversity communities tend to be more resistant to invasion (Brym *et al.* 2011; Zeiter & Stampfli 2012). Additionally, ecological interactions in more diverse communities can regulate invader establishment and spread (Levine, Adler & Yelenik 2004). Indeed, invasion success seems to depend more on the conditions of invaded sites than on the dispersal or growth abilities of the invader (Vicente *et al.* 2013). If ecosystems lack native species diversity, alien species will have more opportunities for becoming invasive (Funk *et al.* 2008a; Staab *et al.* 2015).

Biodiversity and functioning in altered ecosystems

Biodiversity and ecosystem functioning studies are crucial for understanding anthropogenic impacts on natural ecosystems and for predicting future scenarios, allowing scientists and stake holders to adopt new strategies for reducing the risks of losing ecosystem functions and services that are important for human wellbeing (Scheffers *et al.* 2012). Indeed, there are two main threats to ecosystem health and stability, i.e. habitat loss and invasive alien species (Millennium Ecosystem Assessment 2005; CBD 2010). Both threats can positively interact, thus amplifying anthropogenic impacts on ecosystems. Land transformation and the consequential destruction of habitats by human activities will negatively affect native species diversity, while making ecosystems less stable and less resistant to invasion. Invaded ecosystems will be, then, modified by the impacts of alien species on native community dynamics. The effects of the invader on native species occurrence and abundance, community composition and ecosystems properties will, ultimately, favor further invasions (Gurevitch & Padilla 2004; MacDougall & Turkington 2005).

Recent studies performed around the world have shown that climate changes might have a more drastic effect on species diversity and distribution, ecosystem stability and human wellbeing than invasive species (Van Der Putten, Macel & Visser 2010; Bellard *et al.* 2012; Scheffers *et al.* 2016). Furthermore, climate changes can increase the range of alien species distribution across regions or even continents (Morriën *et al.* 2010; González-Moreno *et al.* 2014). Ultimately, climate changes would favor invasion success by compromising native species diversity and increasing ecosystem susceptibility to invaders (Lu *et al.* 2013). Despite all the impacts on natural ecosystems resulting from

anthropogenic activities, we can understand such scenarios as opportunities for building solid knowledge on how to cope with the challenges arising in a human-dominated world.

From all functions performed by natural and, also, restored ecosystems, in this thesis I was particularly interested in the soil nutrient dynamics (i.e. availability and retention or accumulation) in order to evaluate native and invasive plant effects on soil fertility. Therefore, it is important to state that, while native species diversity was shown to positively affect several aspects related to soil functioning (Fornara & Tilman 2008; Conti & Díaz 2013), invasive species were mostly found compromising the same functions (Weidenhamer & Callaway 2010; Vilà *et al.* 2011). Indeed, invasive plants cause several alterations on ecosystem functioning (Ehrenfeld 2010; Drenovsky *et al.* 2012). For instance, they can decrease native plant biomass by competition (Vilà and Weiner 2004; Vilà *et al.* 2011) and reduce native plant fecundity, emergence and recruitment rates, thus changing species composition in invaded communities (Ens & French 2008; Han, Buckley & Firn 2012; Gooden, French & Robinson 2014). They can also stimulate nutrient cycling and increase its availability in the soil by creating higher phosphorus turnover (Chapuis-Lardy *et al.* 2006; Vanderhoeven *et al.* 2006; Herr *et al.* 2007). Invasions alter nutrient uptake and release by plants and increase leaching losses, because native plants would acquire less nutrients due to negative effects of invader competition (Scharfy *et al.* 2009, 2010). Decomposition rates can also be affected due to changes in microbial community after invasive plant impacts (Kourtev, Ehrenfeld & Häggblom 2002; Batten *et al.* 2006). Therefore, nutrient balance in invaded terrestrial systems would be compromised in the long term, influencing nutrient dynamics and soil fertility (Ehrenfeld 2010; Corbin & D'Antonio 2011).

Therefore, more fundamental conclusions about the functioning of ecosystems might be reached by combining different levels and aspects of diversity with different stressors in experimental communities. In particular, functions related to future scenarios of land transformation, habitat loss, invasions and climate changes. In this thesis, I used three different experimental approaches to answer questions related to the effects of species number, functional diversity, phylogenetic diversity and invasive plant species on the functioning of restored ecosystems (Figure 1).

Figure 1: Conceptual diagram for the three chapters presented in this thesis. Terms in bold (center of the diagram) refer to the main topic of the thesis and to the diversity aspects used to evaluate ecosystem functioning. Plain text describes the hypotheses and experimental approaches related to each individual manuscript.

Trends and gaps in the literature on biodiversity and ecosystem functioning

The research field of biodiversity and ecosystem functioning has become increasingly common in ecology since the beginning of the 1990s (Naeem 2006; Caliman *et al.* 2010). However, its *activity index* (AI), i.e. the relative change of BEF studies compared to the general increase of scientific publications in a certain time period, has become significantly higher only after 2006 (Caliman *et al.* 2010). This trend may represent the increasing concerns of ecologists, and the society in general, about the effects of species loss on the functioning and stability of ecosystems. In fact, a recent review stated that biodiversity and ecosystem functioning studies are one of the most fundamental subjects in ecology within the 21st century (Sutherland *et al.* 2013).

Using a bibliometric approach to identify trends in BEF research and to detect potential research gaps, I searched within the Web of Science for specific terms to get the absolute and relative numbers of studies related to biodiversity and ecosystem functioning in the period 1998–2016. The motivation was to identify which diversity measures, i.e. species richness, functional diversity, phylogenetic diversity or genetic diversity, were most commonly used for explaining species effects on ecosystems. First, the search string *biodiversity near/4 ecosystem functioning (topic)* was used to obtain the absolute number of studies about BEF. Second, the string *species rich* near/4 ecosyst* (topic)* helped to obtain the absolute number of studies using species richness inside BEF. Third, the string *functional divers* near/4 ecosyst* (topic)*, to obtain the absolute number of studies using functional diversity inside BEF. Fourth, the string *phylogenetic divers* near/4 ecosyst* (topic)*, to obtain the absolute number of studies using phylogenetic diversity inside BEF; And, finally *genetic divers* near/4 ecosyst* (topic)*, to cover the absolute number of studies using genetic diversity inside BEF.
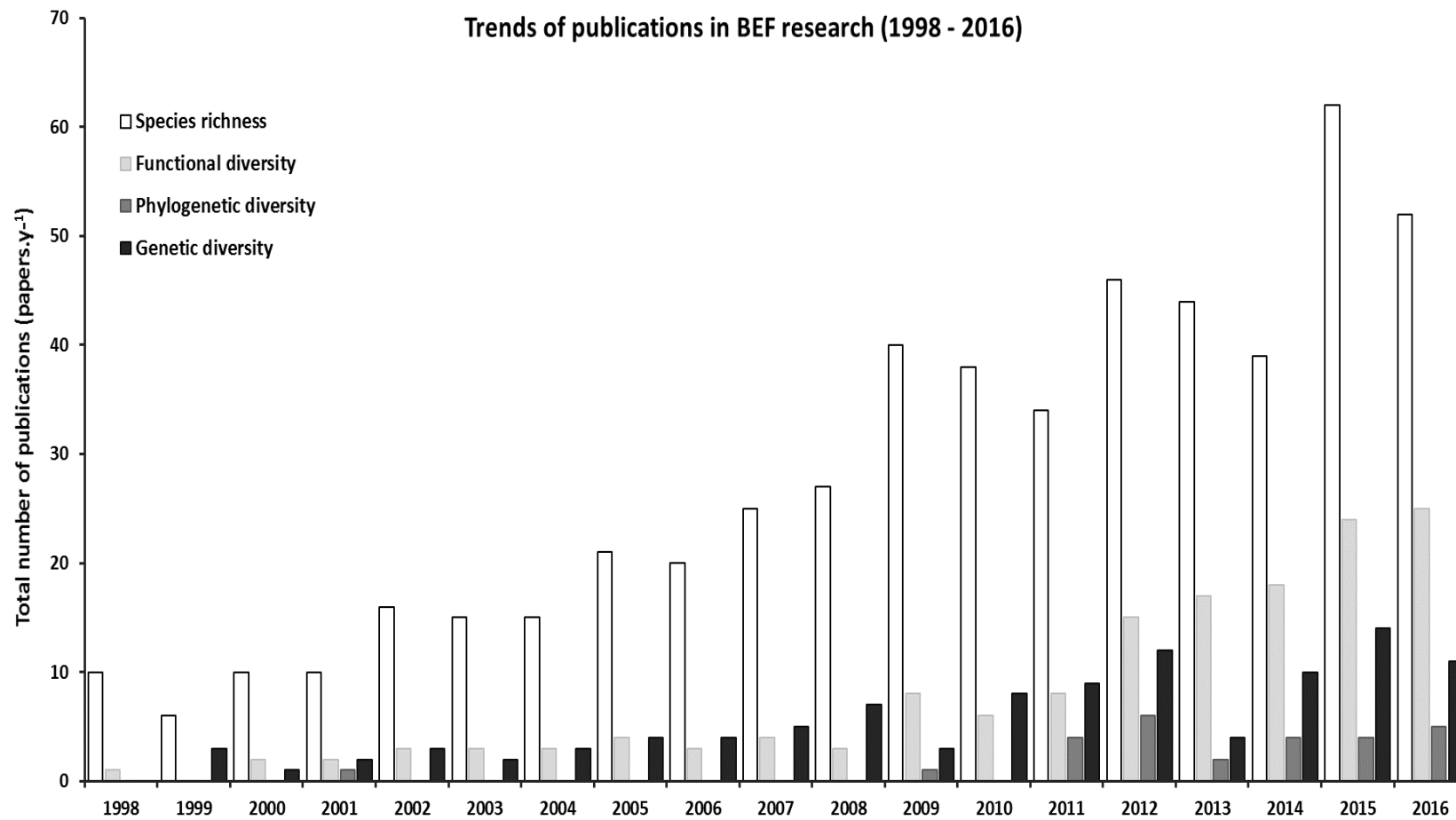
Such information cannot substitute a carefully conducted review of the respective literature, while it indicates trends and possible directions of future BEF research. Absolute numbers for general publications about biodiversity and ecosystem functioning were obtained so it was possible to calculate the relative numbers for the aspects of diversity evaluated in BEF studies along the years.

BEF publications increased by 3.5 times in 10 years (from 61 in 2006 to 212 in 2016, according to the number of publications returned by the search) indicating an increasing concern about such topics. Also, before 2006 BEF studies were not of great importance inside ecology (Caliman et al. 2010). However, it is true that most scientific publications increased exponentially in the same period. Still, this evaluation reveals that publications on biodiversity and ecosystem functioning grow at a higher rate than scientific publications englobing all science fields. According to information published in *Nature* and, also, to a recently published scienciometric study, scientific publications had a growth rate of 8–9% per year in the last decade, thus doubling every nine years (Van Noorden 2014; Bornmann & Mutz 2015).

The search in Web of Science using biodiversity and ecosystem functioning as a topic returned 1524 studies published between 1998 and 2016. From this, 530 studies were about the effects of species richness, 149 about functional diversity, 27 about phylogenetic diversity and 105 about genetic diversity, considering the same period of analysis (Figure 2). It means that during that period 34.9% of the publications in BEF were testing species richness, 9.9% functional diversity, 1.7% phylogenetic diversity and 7.1% of the studies were about genetic diversity effects on ecosystem functioning. However, the analysis was not refined by, for example, checking all papers returned from each search. Also, if we observe both total number of publications (i.e. 1524 for BEF

studies in general, and 811 considering the amount of studies using different types of diversity) are not the same. Therefore, there are still many uncertainties to be clarified before more substantial conclusions are possible.

Nevertheless, one can still observe two periods showing an increasing trend for studies using functional diversity rather than only using species richness when evaluating biodiversity and ecosystem functioning (Fig. 3a, b). Both periods might be related to key publications about functional diversity and its importance for ecosystems arising since the early 2000s (Díaz & Cabido 2001). On the other hand, this analysis shows that other aspects of species diversity are neglected by scientists. Studies on genetic diversity have decreased during the past decades despite the technology available for such purposes (Fig. 3d), while the few number of studies on phylogenetic diversity might be related to uncertainties in phylogeny datasets, and lack of proper technology for clarifying such aspects during the first years of the period considered in this analysis. However, this technology is now available and we can observe an increase of publications using phylogenetic diversity for explaining ecosystem functioning (Fig. 3c). Finally, recent studies pointed out that we do not only need to include phylogenetic diversity as predictor of ecosystem functioning, but also to design experiments orthogonally testing phylogenetic diversity as a treatment to evaluate how it would affect different functions (Cadotte 2015; Cardinale *et al.* 2015).

Figure 2: Trends in publications about BEF (1998–2016) according to the type of diversity measure used to explain biodiversity effects on ecosystem function. Bars with different shades of grey represent aspects of biodiversity adressed in the publications (in absolute numbers).

Figure 3: Relative numbers of studies published inside BEF using species richness (a), functional diversity (b), phylogenetic diversity (c) and genetic diversity (d) for explaining species diversity influences on ecosystems during the period 1998–2016. Numbers about publications were collected from Web of Science.

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Restoration projects as an opportunity for testing BEF hypotheses

Three decades ago, a review on restoration ecology stated that such studies should work as empirical tests for ecological theories rather than being only trial-and-error attempts to find the most suitable method for restoring a degraded area (Bradshaw 1987). Although the discipline of restoration ecology has increasingly benefitted from a robust theoretical framework, such projects still lack clear tests of BEF assumptions (Naeem 2006). Since Restoration Ecology can be focused on restoring not only plant communities but also ecosystem functioning, a theory-driven approach based on BEF can considerably benefit restoration projects, thus increasing their success (Wright et al. 2009).

Previous studies showed that the functional dissimilarity among species composing a plant community accounts for most of the plant positive effects on ecosystem functioning (Heemsbergen *et al.* 2004; Bowker *et al.* 2011). Therefore, for increasing resilience and better managing ecosystems facing degradation, we need to account for the differential effects of plant species on ecosystems (de Bello *et al.* 2010). Studies also showed that ecosystem multifunctionality (sensu Gamfeldt, Hillebrand & Jonsson 2008) is more susceptible to species loss when compared to single-function measurements. Additionally, we still need to understand how we can apply species diversity to achieve multifunctional ecosystem restoration.

One alternative would be the use of functional dissimilar species on restoration projects. Such approach could enhance the positive effects of diversity on ecosystem functioning and, also, could be applied to increase restoration success and reduce restoration costs (Clark *et al.* 2012; Valencia *et al.* 2015). Another alternative that had been recently proven to increase plant performance (survival and biomass production) during restoration of degraded areas, is the use of phylogenetically distant species for

setting up the communities (Verdú, Gómez-Aparicio & Valiente-Banuet 2012). Carefully considering the composition of target communities will be particularly important for restoring the functioning and the stability of degraded systems in long term, since plant species are differently affected by environmental fluctuations and, therefore, can function in a complementary manner over time (Isbell *et al.* 2011; Gamfeldt *et al.* 2013; Morin *et al.* 2014).

Therefore, by conducting restoration projects under the light of the BEF-perspective, we might be able to understand the variability, the predictability and the reliability of ecosystem functioning in restored areas (Naeem 1998; Chazdon 2008). A recent review study advocates that the monitoring of restoration projects should incorporate ecosystem functions for different trophic levels (Kollmann *et al.* 2016). Although it is important to monitor ecosystem functions and processes during restoration, we should also incorporate ecosystem functioning for better designing such projects and for increasing the functioning of restored ecosystems. In fact, since plant species normally trade-off from one function to another, restoration programs should consider complementarity across multiple functions to increase the reliability of creating self-sustainable restored systems (Wright et al. 2009).

OBJECTIVES

The overall aim of this thesis is to evaluate the effects of plants diversity on the functioning of restored systems. More specifically, the aim is to identify which characteristics of the native communities related to different types of diversity (i.e. plant traits, species richness, functional and phylogenetic diversities) would be more important

for ecosystem functions associated to productivity, soil fertility and resistance to invasions. Therefore, I investigated: (i) whether ecosystem functioning in tropical dry forests can be investigated from a trait-based approach. In terms of the trait-based perspective, I also studied whether species investing more on traits related to conservative resource-use strategy (i.e. conservative[1] traits) or more on acquisitive traits would differently affect ecosystem functions; (ii) whether we can apply the diversity-productivity relationship in terms of phylogenetic relatedness among species rather than the species number *per se* for explaining plant survival and biomass production in a recently restored forest system; and (iii) whether a functional diversity approach can be used for explaining biotic resistance during grasslands restoration, based on the diversity-invasibility hypothesis.

The final goal of this research is to generate results to support future restoration projects focusing on invasion control and on the functioning of semi-arid ecosystems, thus indicating which species are most suitable for the restoration of such areas. The different approaches presented here (see Figure 1 for an overview) can contribute with the theoretical understanding of the ecological processes occurring when the restoration of ecosystem functions is intended. Moreover, such findings can be applied for guiding the design of restoration projects to maximize species diversity effects on ecosystem functioning and increase its success.

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[1]In this thesis, I use the terms conservative and acquisitive traits referring to plants resource-use strategy. In this sense, plants with conservative resource-use strategy can be more tolerant to environmental stress by investing on traits related to resource storage and nutrient conservation such as higher wood density and leaf dry matter content at the expense of having lower growth capacity. In turn, plants with acquisitive resource-use strategy (i.e. resource exploitation strategy) would invest in traits related to leaf life span and to the ability to acquire resources like specific leaf area and specific root length, thus being considered fast-growing species. However, such species would have lower stress tolerance capacity and higher biomass turnover (Grassein, Till-Bottraud & Lavorel 2010; Prado *et al.* 2016).

THESIS OUTLINE

Study I (Chapter 2)

The study *'Linking plant traits to ecosystem multifunctionality in semi-arid ecosystems'* evaluated the effects of 15 plant species native to tropical dry forests (NE, Brazil) on ecosystem functions related to soil fertility and soil water quality maintenance. Additionally, I assessed which functional traits (six above and six below-ground plant traits) would explain the effects of plant species on the evaluated functions. This is accomplished through a greenhouse experiment with single-species treatments considering a trait-based approach and simulating rain pulses to assess plant species and trait effects on the retention of water and nutrients in the soil that would, under field conditions, reduce nutrient leaching and soil loss during the rainy season. Therefore, the importance of this study relies on the identification of the most suitable plant species for restoring ecosystem functioning in semi-arid forests.

Study II (Chapter 3)

The study *'Species richness and phylogenetic relatedness control plant growth at the individual but not at the community level during restoration of a riparian forest'* investigates the effects of species richness and phylogenetic relatedness on plants survival and growth in a recently restored riparian forest in northeastern Brazil. This study tested the diversity-productivity relationship with a phylogenetic perspective, considering the relatedness of species composing the restored communities rather than only the number of species. For accomplishing this, I performed a field experiment planting seedlings from native trees along 800 m of the two margins of a perennial stream. In this experiment, I

manipulated levels of species richness (0, 1, 3 and 9) and phylogenetic richness (closely or distantly related species). The results of this experiment can guide the design of restored systems to increase its restoration success.

Study III (Chapter 4)

The study *'Functional diversity and invasive species moderate soil water quality and soil fertility in grassland mesocosms'* investigates whether the functional diversity of a restored grassland community positively affects its resistance to invasive plants looking at native plant productivity and soil nutrient dynamics. In this study, I tested the diversity-invasibility hypothesis which explains the influence of diversity on native plant communities' resistance to invasions by complementarity effects on resources use, thus increasing the potential of plants from invaded communities to compete with the invader. For testing the diversity-invasibility hypothesis, I performed a greenhouse experiment manipulating three levels of functional composition in grassland plant communities and, also, the presence or absence of an invasive plant (*Solidago gigantea*).

Pictures of the various experiments performed in this thesis are presented in Figure 4.

Figure 4: Overview of the experiments performed in the main chapters of the thesis. In each experiment, I investigated the effects of a different measure of diversity on the functioning of restored systems.

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Chapter 2

Linking plant traits to ecosystem multifunctionality in semi-arid ecosystems[1][2]

Abstract – Restoration programs still lack focus on ecosystem functions. This is particularly urgent for semi-arid lands where the impacts of drought have been causing desertification. Here we evaluated tree species suitability for restoring degraded areas on the basis of their functional skills to modulate soil and water quality. In a greenhouse experiment, we evaluated how plant functional traits are related to soil loss, water quality, and nutrient retention for 15 tree species from the semiarid tropical forest of Brazil (Caatinga). We investigated whether the effects of plants and traits are consistent across single and multiple functions. In a greenhouse experiment we tested the effects of 15 tree species on semi-arid ecosystem functioning. Such effects were evaluated by a *one-way* ANOVA in blocks. Differences among plants were assessed by a *post-hoc* Tukey test. Twelve functional traits (six from above and six from belowground structures) were measured. Traits influence were evaluated by model selection, testing models with different trait combinations based on AIC. Only one plant species (*Mimosa tenuiflora*) consistently affected functions. Also, conservative traits controlled more functions than acquisitive ones, thus, these traits can be more important for semi-arid ecosystem functioning. Only traits related to biomass could control multifunctionality. Therefore, species with larger biomass and higher investments on conservative traits might contribute to the maintenance of multiple functions in semi-arid ecosystems.

Key words: *Caatinga, ecosystem multifunctionality, plant functional traits, green soup hypothesis, soil nutrient, tropical dry forests.*

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INTRODUCTION

Semiarid areas around the world suffer from the impacts of land use intensification which results in habitat and species loss and decreases in ecosystems stability and functional diversity (Allan *et al.*, 2015; Hautier *et al.*, 2015; van der Plas *et al.*, 2016). Therefore, the appropriated development of restoration programs is extremely important to ensure the conservation of these endangered ecosystems. The seasonally tropical dry forests in northeastern Brazil (Caatinga) is amongst the most threatened dryland area in the world, being poorly protected and very susceptible to desertification (Leal *et al.*, 2005; Manhães *et al.*, 2016; Marinho *et al.*, 2016). Additionally, the characteristic water scarcity of such regions (Pennington *et al.*, 2010) should be considered when designing restoration programs because making the restoration of degraded semiarid lands much more difficult. Water scarcity is commonly a bottleneck for the successful restoration of degraded dry lands. Therefore, the development of evidence-based restoration programs (Cooke & Suski, 2008), accounting for plants functional traits (specifically, the traits related to water uses and drought resistance) and its effects on plants performance and ecosystem functioning, would increase restoration success while reducing costs and increasing ecosystem health in terms of water and soils quality.

Functional dissimilarity among plant species in a community accounts for most of the positive effects on ecosystem functioning (Bowker *et al.*, 2011). Indeed, for better managing ecosystems in face of degradation process and increasing its resilience, we need to account for the differential effects of plant species on ecosystems (de Bello *et al.*, 2010). Therefore, functional dissimilar species should enhance the positive effects of diversity on ecosystem functioning, and could be applied to increase restoration success and reduce costs with restoration, especially when considering the multifunctionality of

tropical dry forests (Clark *et al.*, 2012; Valencia *et al.*, 2015). Such approach is particularly important for restoring the functioning of degraded systems in the long term. Indeed, a recent review advocated that restoration programs monitoring should incorporate ecosystems functions in different trophic levels (Kollmann *et al.*, 2016). Although is important to monitor ecosystems functions and processes in restoration programs, we should also incorporate ecosystem functioning for better designing such programs and for increasing the functioning of restored systems.

However, plants effects on ecosystem functioning are not consistently similar across species and/or functions (Díaz *et al.*, 2004), because species have differential investments in traits (Reich *et al.*, 2003; Westoby & Wright, 2006). The investments between above- and belowground traits can influence the coexistence and persistence of plant species in communities by differential allocation of resources to growth, reproductive or defensive traits during environmental fluctuations (Laliberté *et al.*, 2015; van Geem *et al.*, 2013; Wright *et al.*, 2010). Moreover, such differential investments should also influence the effects and the responses of plant species in different environments (De Deyn *et al.*, 2008; Diaz *et al.*, 2004; Lavorel & Grigulis, 2012). For example, plant species should invest more in defensive than in competitive traits in resource-poor environments (Lohbeck *et al.*, 2015a; Reich, 2014). The higher frequency of defensive traits in species from resource-poor communities will result in lower nutrients cycling rates. These communities would have lower complementarity and partition less resources because lower frequency of competition lead plants to explore similar parts of the available resources (Aerts, 1999). Therefore, environmental conditions will influence plant traits and plant species composition in a community, determining the rates by which plant species will affect nutrient dynamics and other ecosystem functions (Lambers *et al.*, 2008).

Despite the stressful environmental conditions that would lead to the prevalence of conservative resource-use strategies in tropical dry forests, the investment in acquisitive traits (i.e. fast-growing acquisitive species) would give plant species an advantage for acquiring nutrients in a faster rate during the transition from the dry to the wet seasons, because nutrients stocked would be more available during the first rains of the season (Schwinning & Sala, 2004; Prado-Junior *et al.*, 2016). Therefore, we can expect acquisitive plant species to play an important role in soil nutrient dynamics of tropical dry forests (Lohbeck *et al.*, 2015a). However, a recent study showed that plant species with conservative resource-use strategy play an important role in biomass production in tropical dry forests (Prado-Junior *et al.*, 2016). Hence, it is more likely that the outcome from differential investments of plants on above- and belowground traits will determine which functions should be preferentially controlled by conservative or acquisitive plant species.

Nevertheless, recent studies have shown that plant community dynamics can be affected by the initial stand biomass rather than by plant traits or species diversity (Finegan *et al.*, 2015; Lohbeck *et al.*, 2015b). The green soup (or vegetation quantity) hypothesis claims that more productive plant species are most important for ecosystem functioning than less productive ones (Prado-Junior *et al.*, 2016). Initial stand biomass was found to drive carbon storage and biomass productivity in wet and dry tropical forests (Lohbeck *et al.*, 2015; Prado-Junior *et al.*, 2016). Such strong positive relationships can be explained by the fact that individuals from high-biomass plant species are more likely to persist in the community, therefore having relatively higher contribution to biomass production over time (Lohbeck *et al.*, 2015; Prado-Junior *et al.*, 2016). Still, nutrient acquisition and storage by plants and, therefore, its influences on soil nutrient retention or exportation should also depend on soil fertility, moisture and on the balance among

different plant requirements, rather than only on plant traits and biomass (Prado-Junior *et al.*, 2016).

Aiming to contribute to the development of evidence-based restoration programs for tropical dry forests in the Northeastern Brazil, we performed a greenhouse experiment in plots comparing the effects of the functional traits from 15 tree species (native from Caatinga; Table 1) on soil and water quality maintenance. We assessed the relative effects of plant species and its functional traits on soil functioning by considering each aspect related to nutrient retention and exportation rates both individually and combined by applying a multiple functioning index (Maestre *et al.*, 2012; Zavaleta *et al.*, 2010). Here, we expected to better understand which plant species strategies (conservative or acquisitive) are more strongly correlated to semiarid soils multiple functioning. Specifically, we test whether soil functions are controlled by dissimilar plant traits or, simply, controlled by traits related to above-and belowground biomass production (green soup hypothesis; Finegan *et al.*, 2015; Lohbeck *et al.*, 2015). We expect plant traits related to acquisitive strategies to have a greater effect on nutrients retention. Higher values for such traits would allow plant species to invest more in the production of root biomass (especially fine roots), thus having more capacity to trap sediments and to acquire nutrients and water (Burylo *et al.*, 2012; Sutton-Grier *et al.*, 2013). In turn, conservative plant traits should have a smaller effect on nutrients retention because they are more correlated to strategies for increasing nutrient residence time in plants; i.e. production of stems with higher wood density or organs for water storage (Reich *et al.*, 2003; Reich, 2014).

MATERIAL AND METHODS

Plant species selection and functional traits

We selected the most common trees in the study area (FLONA Açu; LH. Teixeira, pers. observ. and field survey conducted by botanists from UFRN) to be used in the experiment (Table 1), but seed availability was also considered during species selection. Authorized and trained staff collected seeds from FLONA Açu and surrounding fragments of tropical dry forests. The fruits used for obtaining seeds were collected from (at least) ten mature and health trees. Seeds were manually extracted from the fruits (damaged seeds were discarded) and dried at 25 ± 1 °C for 24 hours. Finally, seeds were stored in a dry place at 18 ± 1°C protected from light for 10–12 weeks (Sousa, 2013).

We selected six above- and six belowground plant traits considered to be good proxies for plant competitive ability, resource exploitation and acquisition, nutrient and water storage, biomass production, stress tolerance and performance (Cornelissen *et al.*, 2003b; Cornwell *et al.*, 2008; Ebeling *et al.*, 2014; Funk *et al.*, 2008; Pérez-Harguindeguy *et al.*, 2013; Westoby *et al.*, 2002; Yannelli *et al.*, 2017). Potential functional roles are summarized in Table 2. While the majority of plant traits were determined directly from the plants used in the experiment, data on specific leaf area (SLA; mm^{-2} mg^{-1}) were collected from literature. SLA values for *Anadenanthera colubrina*, *Aspidosperma pyrifolium*, *Commiphora leptophloeos*, *Cyanophalla flexuosa*, *Libidibia ferrea*, *Mimosa tenuiflora*, *Myracrodruon urundeuva*, *Piptadenia stipulacea* and *Pseudobombax marginatum* were collected from Silva *et al.*, (2014), SLA for *Amburana cearensis*, *Combretum leprosum* and *Poincianella bracteosa* were collected from Souza et al., (2015), and SLA for *Cochlospermum regium*, *Handroanthus impetiginosus* and *Pityrocarpa moniliformis* were collected from Pinho (2014). Root length (RL) and

specific root length (SRL) measurements were performed through imagery analysis using the software IJ_RHIZO (Pierret *et al.*, 2013).

Experimental design

The plot experiment started early February 2015 by transplanting ten individuals from each one of the 15 native trees from Caatinga to the greenhouse in the study area. The experiment was conducted for 30 weeks until late August 2015. Plots were composed by plastic pots of 20 liters capacity (40 x 50 x 0.2 cm). Each plot was filled with 15 liters of natural soil collected in a partially conserved area inside the study area. Nutrient analysis with this soil revealed an average nutrient concentration of: nitrogen = 0.46 mg kg^{-1}; phosphorus = 50.2 mg kg^{-1}; potassium = 114.1 mg kg^{-1}; magnesium = 0.61 mg kg^{-1}; and calcium = 1.74 mg kg^{-1}. This soil was composed by 87.9% sand, 4.2% clay and 7.9% silt. Drylands in Northeastern Brazil have average rainfall ranging from 240 to 1500 mm per year with the dry season comprising 5 to 6 months along the year (Pennington *et al.*, 2009). The National Forest of Açu is located at 5° 34' 59.13" S and 36° 56' 42.13" W with an average altitude of 100 m. Yearly average rainfall is ca. 600 mm and yearly average temperature is 28.1 °C (Souza *et al.*, 2014).

In late February, five individuals from each plant species were planted in a single pot and arranged within five blocks inside the greenhouse. Individuals were selected based on their vitality and similar sizes. Natural light conditions were preserved inside the greenhouse, so plants received on average 12 h photoperiod per day. Plants were watered twice a day (morning and afternoon) with water from the tap to avoid desiccation and mortality.

We used an experimental design in blocks and manipulated a single factor (presence/absence of a species) with 15 levels (tree species). A control (C) treatment (i.e. bare soil) was established to verify the effects of soil particles size on the nutrient retention/exportation rates. Overall, the experiment was composed by five blocks distributed inside the greenhouse. Therefore, all treatments were replicated five times, resulting in a total of 80 experimental pots.

Measurements

Plant effects were evaluated in late July 2015, when tree saplings were five months old, by taking samples of water that had passed through the root system of plant communities. First, 100 ml of a solution enriched with nutrients for agricultural use (NPK 4:14:8) at 1% were added to each pot. The solution had 2,600 and 280 mg. L^{-1} of phosphorus and nitrogen, respectively. Then, 48 hours later, we simulate a rainfall pulse by adding two liters of deionized water (sufficient to exceed the soil field capacity) to each pot. The deionized water accumulated in buckets placed bellow the pots and samples were collected after 20 min for each single pot. We evaluated water and nutrient retention capacity for the 15 species. Suspended soil particles (a proxy for soil erosion or soil loss measurements) were also analyzed in the water accumulated in buckets. To verify the water retention in the plots, we measured the water outflow using a graduated pipet and collected 500 ml from each one of the plant species treatments. From these, 100 ml were used for analyzing soluble phosphate and 100 ml for total nitrogen. For analyzing the content of suspended solids in the water, 130 ml of each water samples were filtered with a fiberglass filter (Whatman 934-AH, 47 mm diameter, 1.5 µm porosity). Each one of the water samples and the filters were stored at –4 °C until for posterior analyses. Phosphate

(soluble reactive phosphorus, P_2O_4) analysis was performed in unfiltered water samples with a spectrophotometer using the acid ascorbic method after persulphate digestion (Murphy & Riley, 1962). Total nitrogen analysis was carried out in filtered water samples using the catalytic combustion method in a Total Organic Carbon analyzer (TOC – V, Shimadzu 2.0) with a TN analyzer attached (VNP module). Suspended soil particles (STS) were determined by gravimetry after drying the filters for two hours at 105 °C and subsequent incineration of the filters for three hours at 500 °C (APHA, 2005). One value for soil dissolved particles was found to be an outlier (*Combretum leprosum*, block 5), probably, because its weight was three times higher than all the filters from the other replicates in the same treatment; apparently some other particles had contaminated the filter. Results from this replicate were excluded from the statistical analysis.

We calculated a multifunctionality index (%) following Zavaleta *et al.* (2010) and Maestre *et al.* (2012), where for each function the plots with the higher performance were considered as reference. The functions tested were water retention, soil loss, phosphate and total nitrogen retention. First, we defined the maximum level of functioning for each one of the functions evaluated. That is, the average of the 5% (i.e. four out of 75 plots in our experiment) top-functioning plots as defined by Maestre et al. (2012). Secondly, for each one of the plots (including those used for the calculation of the maximum level of functioning), we calculated the percentage that is being performed for each one of the functions evaluated (compared to the maximum level of functioning). Finally, an average of these percentages including all evaluated functions was produced. Such average of global functioning represents the multifunctionality value for each one of the plots. Hence, the plots had different percentages of functioning for each individual function and an average of global functioning (multifunctionality). However, for soil loss (i.e. soil suspended particles) the plots with the highest values indicated more soil loss (i.e. lower

functioning). Therefore, for this function we corrected the level of functioning by subtracting 1 from the ratio of functioning performed by each single plot (% of soil loss = (1 – (soil loss / mean of the 5 % plots with highest soil loss)) * 100).

Statistical analysis

We performed a principal component analysis (PCA) to characterize the distribution of plant traits in a multidimensional space. Moreover, we compared the differences in trait values among species using a one-way block ANOVA and, subsequently, a *post-hoc* test (Tukey HSD) using the package agricolae in R (Mendiburu, 2016). Trait values were log-transformed to fulfill the assumptions of the analysis.

We applied a model selection approach (with normal error distribution) using the package bestglm in R (McLeod & Xu, 2014) including above- and belowground traits, to identify which plant traits would be most important when assessing ecosystems singles and/or multiple functions. The bestglm function works using an exhaustive search algorithm for generalized linear models (GLM) to find models with the smallest sum of squares or deviance (McLeod & Xu, 2014). We compared the effects of all traits in combination and identified the five most strong combinations of traits, based on AIC values.

Finally, we applied a one-way block ANOVA to test the effects of plants on water retention, soil loss (suspended soil particles) and nutrients retention in the soil separately or combined in the multifunctionality index. Water retention, soil loss and the multifunctionality index values were log-transformed to fulfill the ANOVA assumptions. Also, a *post-hoc* test (Tukey HSD) using the package agricolae in R (Mendiburu, 2016)

was applied to identify differences among plant species. The control treatment values were also included in the *post-hoc* analysis to evaluate if plants effects were different from the noise effect of soil granulometry on the variables we measured. Statistical analyses were performed using R Statistical Computing version 3.3.1 (R Development Core Team 2015).

RESULTS

Plant traits distribution in the Brazilian dry forest

Trees from tropical dry forests used in this study varied in trait values, including species with high and low above- and belowground biomass production. However, in general, all studied species had some degree of overlap for one or more traits (Figure 1). Such finding indicates a convergent strategy for coping with stressful environmental conditions in semi-arid areas.

Indeed, only few of the plant species show significantly divergent trait values in total (Fig. 2 and Fig. 3). While *Mimosa tenuiflora* and *Cochlospermum regium* had high root biomass (Figure 2a), and *Mimosa tenuiflora* and *Piptadenia stipulacea* had significantly high shoot and root length (Figure 2b), all other species showed similar shoot and root dry matter or water content (Figures 2c and 2d, respectively). Additionally, there is no significant differences in root water content among the trees studied here (Figure 2d).

Differently, SLA values were significantly different for all study species (Figure 3a). However, that might be related to the lack of standard deviation in the SLA data

collected from the available literature on trees from tropical dry forests. Shoot length:shoot biomass ratio and specific root length values showed, in turn, the same pattern as for the traits represented in Figure 2, with only few plant species having significant differences when compared to the other tress (Figures 3b and 3c, respectively). While *Anadenanthera colubrina*, *Cyanophalla flexuosa* and *Libidibia ferrea* exhibit significantly higher values of shoot length:shoot biomass ratio, only *Cyanophalla flexuosa* showed significantly higher values for SRL.

Plant traits control single functions but not multiple functions

Different plant traits were associated with different ecosystem functions (Table 3). Moreover, both conservative and acquisitive traits effected the different functions (Figures 4 to 7). Water retention was positively associated with SL (Estimate = 0.12, t_{69} = 4.3, p ≤ 0.001, Figure 4a), slightly positively associated with RWC (Estimate = –0.17, t_{69} = –2.4, p ≤ 0.05, Figure 4d); but negatively associated with SLA (Estimate = –0.16, t_{69} = –2.9, p ≤ 0.01, Figure 4b) and RDMC (Estimate = –0.31, t_{69} = –2.6, p ≤ 0.05, Figure 4c). Soil dissolved particles (STS, i.e. the proxy measurement for soil loss) was, in turn, marginally positively affected only by SL:SB (Estimate = 0.33, t_{72} = 2.0, p = 0.051, Figure 5). On contrary, the higher the ratio of nutrients and water accumulation in plant tissues, the lower is the effect on soil stabilization.

Phosphate retention was positively affected only by SDMC, which is a conservative trait (Estimate = 2.350e-04, t_{69} = 3.0, p ≤ 0.01, Figure 6a). Another conservative trait, RDMC, also significantly correlated with phosphate retention, but it was a negative effect (Estimate = –2.065e-04, t_{69} = –3.8, p ≤ 0.001, Figure 6c). SLA

(Estimate = –1.437e-04, t_{69} = –2.7, p ≤ 0.01) and SRL (Estimate = –9.098e-05, t_{69} = –4.0, p ≤ 0.001), both acquisitive traits, had negative effects on phosphate retention (Figures 6b and 6d, respectively). Total nitrogen retention was marginally and slightly positively affected by RWC (Estimate = –0.008, t_{69} = –1.7, p = 0.09, Figure 7c), while SL:SB (Estimate = –0.008, t_{69} = –2.3, p ≤ 0.05), RDMC (Estimate = –0.03, t_{69} = –2.9, p ≤ 0.01) and SRL (Estimate = –0.007, t_{69} = –3.5, p ≤ 0.001) negatively affect total nitrogen (Figures 7a, 7b and 7d, respectively).

In contrast, the model selection analysis revealed that ecosystem multifunctionality was not controlled by different plant traits as for the single function results (Table 3). The multifunctionality index was negatively affected by SL:SB (Estimate = –0.04, t_{72} = –2.4, p ≤ 0.05, Figure 8a) and positively by SB (Estimate = 0.04, t_{71} = 2.4, p ≤ 0.05, Figure 8b). SL had no significant effect on the multifunctionality index, despite the slightly positive trend presented (Estimate = –0.04, t_{71} = –1.6, p > 0.05, Figure 8c). However, the model selection showed only SL:SB to be included in the first-best model based on AIC comparisons. Even though, here we presented also the traits identified in the second-best model (Table 3). Despite the significant effects of SL:SB and SL on the multifunctionality index, the adjusted squared R values for both models were very low, revealing that such effects of multifunctionality should be considered non-important (Table 3).

Plant species performances for single and multiple functions

Plant species effects differed from the control treatment for all single functions evaluated, except for soil dissolved particles, i.e. soil loss ($F_{15,59}$ = 1.5, p > 0.05, Figure

9b). Plant species performances ranged from higher than the control treatment to lower than the control average effects for water and phosphate retention (Figures 9a and 9c). Additionally, effects of plant species on ecosystem functions depended mainly on the performance of a few species rather than a generalized effect of plant species (Figure 9).

Mimosa tenuiflora was the only plant species in which effects were consistent across all single functions evaluated (Figures 9a to 9d). Water retention (plant species effect: $F_{15,59} = 7.6$, $p \leq 0.001$) and phosphate (species effect: $F_{15,59} = 5.2$, $p \leq 0.001$) were significantly higher than the control treatment only for *M. tenuiflora* (Figures 9a and 9c). This suggests a stronger influence of these dominant species on these functions, since *M. tenuiflora* was the species with higher aboveground biomass (average shoot biomass = 89.5 ± 7.1 g). Although not statistically significance, this species was observed to also reduced soil loss (Figure 9b).

On the other hand, all species, in average, retained higher soil nitrogen than the control treatment (species effect: $F_{15,59} = 7.4$, $p \leq 0.001$). However, the *post hoc* test revealed that soil nitrogen retention was significantly different than the control treatment only for six plant species (Figure 9d). Indeed, *M. tenuiflora* performed better being significantly different than the control treatment and most tree species considered. In turn, *Cochlospermum regium*, *Handroanthus impetiginosus*, *Piptadenia stipulacea*, *Poincianella bracteosa* and *Pseudobombax marginatum* had significantly higher nitrogen retention in the soil when compared to the control treatment, but there were no differences among species (Figure 9d).

The multifunctionality index showed the same pattern observed for individual ecosystem functions where plant species effects ($F_{15,59} = 2.8$, $p \leq 0.01$) were significantly different than the control treatment, but such effects were mostly driven by the

performance of a single (or only a few) dominant species (Figure 10). Again, plant species performances ranged from higher to lower than the control treatment average effect, and *M. tenuiflora* had the strongest positive effect, being considered significantly different from the control and almost all other tree species (Figure 10).

DISCUSSION

Plant traits and the functioning of semi-arid ecosystems

Tree traits from tropical dry forests controlled different soil functions. While traits related to conservative strategies had positive and negative effects for all the functions evaluated, traits related to acquisitive strategies were mostly negatively correlated to the same functions (i.e. water retention, soil loss, phosphate and total nitrogen retention in the soil). Such pattern is contrary to what we hypothesized and to other findings in the literature, showing acquisitive plant traits to have a strong positive effect on soil nutrients (Díaz *et al.*, 2004; Bardgett *et al.*, 2014; Reich, 2014).

We expected SLA and SRL to positively control nutrient retention in semi-arid soils from our pot experiments, since they are both acquisitive traits and had been previously identified to influence photosynthetic rate, growth rate and nutrient storage in plant leaves (expected effects for SLA – Pérez-Harguindeguy *et al.*, 2013; Silva *et al.*, 2014; Souza *et al.*, 2015); and the rate of water and nutrient uptake (expected effects for SRL – Cornelissen *et al.*, 2003; Pérez-Harguindeguy *et al.*, 2013). However, both traits negatively affected phosphate retention, while nitrogen retention was not affected by SLA and negatively influenced by SRL. These findings could be associated to uncertainties related to our experimental approach that might have provided optimal conditions for

plant growth, while in the field those conditions are more stressful. Therefore, plants might have been more limited by light than by water, thus having their photosynthetic and metabolic rates compromised which resulted in less soil exploitation and nutrient acquisition. Also, SLA effects can be considered more strongly correlated to carbon and nitrogen storage in leaf tissues, having low influence on soil phosphate retention. Whereas, negative effects of SRL on the same nutrient retention might be because plant roots had their elongation potential limited by the size of the pots, thus resulting in a low ratio between root length and biomass and negatively affecting SRL measurements.

Additionally, plants from semi-arid environments are constantly coping with water limitation, thus a trade-off between water storage and nutrient acquisition is expect to be an important influence of plant performance on soil nutrients (Markesteijn & Poorter, 2009). The higher the water limitation, the lower would be soil nutrient exploitation by plants. In fact, such trade-off is related to the conflict between different functions, i.e. productivity and drought resistance (Diaz *et al.*, 2004; Zavaleta *et al.*, 2010). Therefore, plants from tropical dry forests would either invest on water storage for resisting during dry seasons, or would invest in strategies for acquiring as much nutrients during the rainy season, thus favoring its biomass production when conditions are favorable (Reich *et al.*, 2003; Westoby & Wright, 2006). Therefore, the positive correlation between RWC and soil nitrogen can be explained by an increase in the cationic exchange potential for plants with higher amount of water in their root systems. Also, nitrogen is a limiting resource in semi-arid ecosystems soils, thus such nutrient will be preferably exploited by plants when water is available in the system.

Ecosystem multifunctionality, in turn, was not controlled by the plant traits included in our study. Although model selection analysis had showed SL:SB and SB to

significantly affect multifunctionality index (negative and positive effects, respectively), the low values of adjusted squared R for the effects of both traits does not allow us to rely on such relationship for explaining ecosystem multifunctionality in tropical dry forest from Northeastern Brazil.

The ecosystem role of biomass-related traits: a place for the 'green soup hypothesis'?

Even though plant species studied here exhibit a convergence strategy for investments on traits, they did not influence ecosystem function similarly. This indicates that the trade-offs between different functions is influencing plant species performances and, therefore, ecosystem functioning. Indeed, only one plant species (*Mimosa tenuiflora*) had a consistent performance across different functions. Such response can be related to the higher above- and belowground biomass production presented by this tree. Such pattern can be even more important if we take in account that the model selection analysis showed that only the biomass-related traits can, at some extent, control ecosystem multifunctionality in our experiment.

Recent studies showed initial standing biomass to be the most important factor influencing plant performance on ecosystem functioning, i.e. 'the green soup hypothesis' (Finegan *et al.*, 2015; Lohbeck *et al.*, 2015). The correlation between biomass-related traits and ecosystem multifunctionality demonstrated here can indicate that more productive plant species can play a key role on the functioning of tropical dry forests. Additionally, another study argued that high productive plants can keep performing ecosystem functions even when environmental conditions are unfavorable (i.e. dry

season), thus conferring more temporal stability to semi-arid ecosystems (Prado-Junior *et al.* 2016).

However, until now, only one previous study corroborated the green soup hypothesis for Brazilian semi-arid ecosystems (Prado-Junior *et al.* 2016). Also, we argue that this is the first report for this hypothesis to affect ecosystem multifunctionality, i.e. different functions combined using an index (Zavaleta *et al.*, 2010; Maestre *et al.*, 2012). The previous studies were considering only single functions (different functions, but evaluated separately) for tropical rain forests or wet tropical forests (Finegan *et al.*, 2015; Lohbeck *et al.*, 2015, respectively). Such results showed plant biomass and/or biomass-related traits to control plant productivity, carbon storage and sequestration (Finegan *et al.* 2015) and, also, to affect rates of production and decomposition (Lohbeck *et al.*, 2015). We found biomass-related traits, both negatively (SL:SB) and positively (SB), to affect multifunctionality for tropical dry forests. We consider that our results are in accordance to these findings, but considering a plant traits approach for single species treatments in a plot experiment. Therefore, for a community level approach, under field conditions, other factors might have more importance for ecosystem multifunctionality than the ones our experimental approach can account for.

Some argue that ecosystem functions and processes would be, preferentially, controlled by the dominant plant species and/or dominant plant traits in a given community, i.e. 'the biomass ratio hypothesis' (Grime, 1998; Pakeman *et al.*, 2011). The effects of such species can be conspicuous and outperform the effects from the species that are less frequent in the community composition (Walker *et al.*, 1999; Winfree *et al.*, 2015). However, because plant species can trade-off different functions or processes (Lavorel & Grigulis, 2012; Gamfeldt *et al.* 2013), we can expect dominant plant species

to have different performances when considering different functions. Hence, instead of having redundant effects, plant species would perform unique ecosystem functions (Bowker *et al.* 2011). Additionally, studies showed that natural communities are more likely to provide higher levels for a few set of functions rather than performing similarly for several functions (Heemsbergen *et al.*, 2004). Indeed, such trade-offs can be especially important for controlling soil nutrient dynamics. Since plant species have nutrient limitations and differential functional traits, they will differently affect nutrient pools during their life cycles (Cardinale *et al.*, 2011; Conti & Díaz, 2013; Machovsky-Capuska *et al.*, 2016).

Single vs multispecies systems control function and diversity in semi-arid restoration

Based on our findings one could be tempted to disconsider possible diversity effects on ecosystem functioning while designing restoration programs for semi-arid lands. However, despite the expectation that the selection of plant species with higher performances for desired functions would increase the likelihood of successfully restoring such functions, it is important to consider that plant species performance can vary along time (i.e. different seasons) or gradients of limiting resources (Craven *et al.*, 2016). Still, a recent study evaluating grasslands ecosystem multifunctionality argue that locally rare species can also perform important ecosystem functions (Soliveres *et al.*, 2016). Therefore, the exclusion of such species from restoration programs would have a negative effect on long term ecosystem functioning that might not be compensate by the positive effects of including only the best performing species. Additionally, the literature on BEF is clear about plant trade-offs for different functions. Indeed, no single plant species can

sustain multiple ecosystem functions indefinitely, because the performance of a specific function can cost the performance of a different one (Gamfeldt *et al.* 2013).

Despite plant species can have some degree of redundancy related to their effects on ecosystem functioning, multiple redundancy is lower than single-function redundancy, thus resulting in a high level of multifunctional complementarity among different species (Gamfeldt *et al.* 2008). In other words, the unique effects from plant species on ecosystem functioning will increase with the number of functions evaluated (Petchey & Gaston, 2002). Indeed, multiple functions tend to be more susceptible to species loss and other environmental stressors compared to single functions (Gamfeldt *et al.*, 2008, 2013). Therefore, maintenance of different functions and ecosystems stability over time will tend to increase with plant diversity (Allan *et al.*, 2013, 2015; Valencia *et al.*, 2015).

Finally, we also argue that accounting for the levels of covariation and/or convergence for different traits to similarly affect different functions is crucial for the maintenance of ecosystem functioning over time and under global changing scenarios (Gamfeldt *et al.*, 2008). Here, we found plant traits to not positively affect different functions. In fact, excepting the positive effects of RWC on water and phosphate retention, only negative effects of traits were consistent across different functions, especially those affecting phosphate and total nitrogen retention in the soil. Additionally, besides the positive significant effects of SB on the multifunctionality index, multiple functioning in tropical dry forests from Northeastern Brazil might require higher levels of diversity than less stressful environments and might be more drastically compromised by anthropogenic impacts, such as land-use intensification and desertification. Therefore, functioning of such ecosystems can be more prone to disrupt under global changing scenarios.

CONCLUSIONS

Despite the limitation of our experiment, these findings are important for improving tropical dryland forests restoration and the functioning of these systems. Our results can be applied for designing plant communities (based on individual species functional roles) that might maximize soil fertility and avoid nutrient leaching losses, also contributing to the protection of adjacent water bodies. However, the difficulties in extrapolating results related to functional roles of plant traits from greenhouse experiments to field conditions hinder us from deriving further conclusions about the real functioning of tropical dry forests in Northeastern Brazil (Cornelissen *et al.*, 2003a). Therefore, future research is needed on the performance of different trees under field conditions, allowing us to investigate the effects of different stresses factors on such ecosystems functioning.

Although there are uncertainties in extrapolating results from greenhouse experiments, a recent study showed that trait diversity is the more important aspect accounting for the plants diversity effects on ecosystem functioning when considering communities composed by young trees (Tobner *et al.*, 2016). This results can be especially important when evaluating soils functioning, since plant species effects would be stronger when these plants are still young, trapping and acquiring higher amounts of nutrients and investing resources on growth rather than on reproduction (Younginger *et al.*, 2017). Nevertheless, since our results are from a pot experiment, we advise that further investigations must be conducted under field conditions to allow more general conclusions.

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TABLES AND FIGURES

Table 1: Tree species native from the Caatinga biome (tropical dry forests in the Brazilian semiarid region) used in the plots experiment to evaluate above-and belowground plant traits effects on soil ecosystems multifunctionality. Relative growth rate (RGR) is presented as the average monthly grow (± SE) for each species (adapted from Pérez-Harguindeguy *et al.* (2013) for using height measurements). Species nomenclature was used according to APG IV (2016).

Tree species from tropical dry forest (NE, Brazil)				
Scientific name	**Abb**	**Common name**	**Family**	**RGR (cm month^{-1})**
Amburana cearensis	amb.cea (AC)	Cumaru	Fabaceae	0.8 (± 0.18)
Anadenanthera colubrina	ana.col (ACl)	Angico Vermelho	Fabaceae	1.6 (± 0.15)
Aspidosperma pyrifolium	asp.pyr (AP)	Pereiro	Apocynaceae	0.8 (± 0.16)
Cochlospermum regium	coc.reg (CR)	Algodão do Mato	Bixaceae	2.0 (± 0.11)
Combretum leprosum	comb.lep (CL)	Mofumbo	Combretaceae	1.2 (± 0.13)
Commiphora leptophloeos	com.lept (CLp)	Imburana	Burseraceae	1.8 (± 0.10)
Cyanophalla flexuosa	cya.fle (CF)	Feijão Bravo	Capparaceae	1.5 (± 0.07)
Handroanthus impetiginosus	han.imp (HI)	Ipê Roxo	Bignoneaceae	0.5 (± 0.08)
Libidibia ferrea	lib.fer (LF)	Jucá	Fabaceae	0.5 (± 0.13)
Mimosa tenuiflora	mim.ten (MT)	Jurema Preta	Fabaceae	2.1 (± 0.13)
Myracrodruon urundeuva	myr.uru (MU)	Aroeira	Anacardiaceae	1.5 (± 0.07)
Piptadenia stipulacea	pip.sti (PS)	Jurema Branca	Fabaceae	3.4 (± 0.04)
Pityrocarpa moniliformis	pit.mon (PM)	Catanduva	Fabaceae	1.6 (± 0.26)
Poincianella bracteosa	poi.bra (PB)	Catingueira	Fabaceae	1.1 (± 0.12)
Pseudobombax marginatum	pse.mar (PMg)	Imbiratanha	Malvaceae	1.1 (± 0.06)

Table 2: Description of the plant traits measured (or collected from literature) during our experiment and its associated ecological roles. Ecological roles associated with the different plant traits were considered based on the literature. ***SLA** data were collected from literature available on plants from semi-arid systems (Pinho, 2014; Silva *et al.*, 2014; Souza *et al.*, 2015). ****RL** values were obtained based on imagery analysis of plants roots using the software IJ_Rhizo (Pierret *et al.*, 2013).
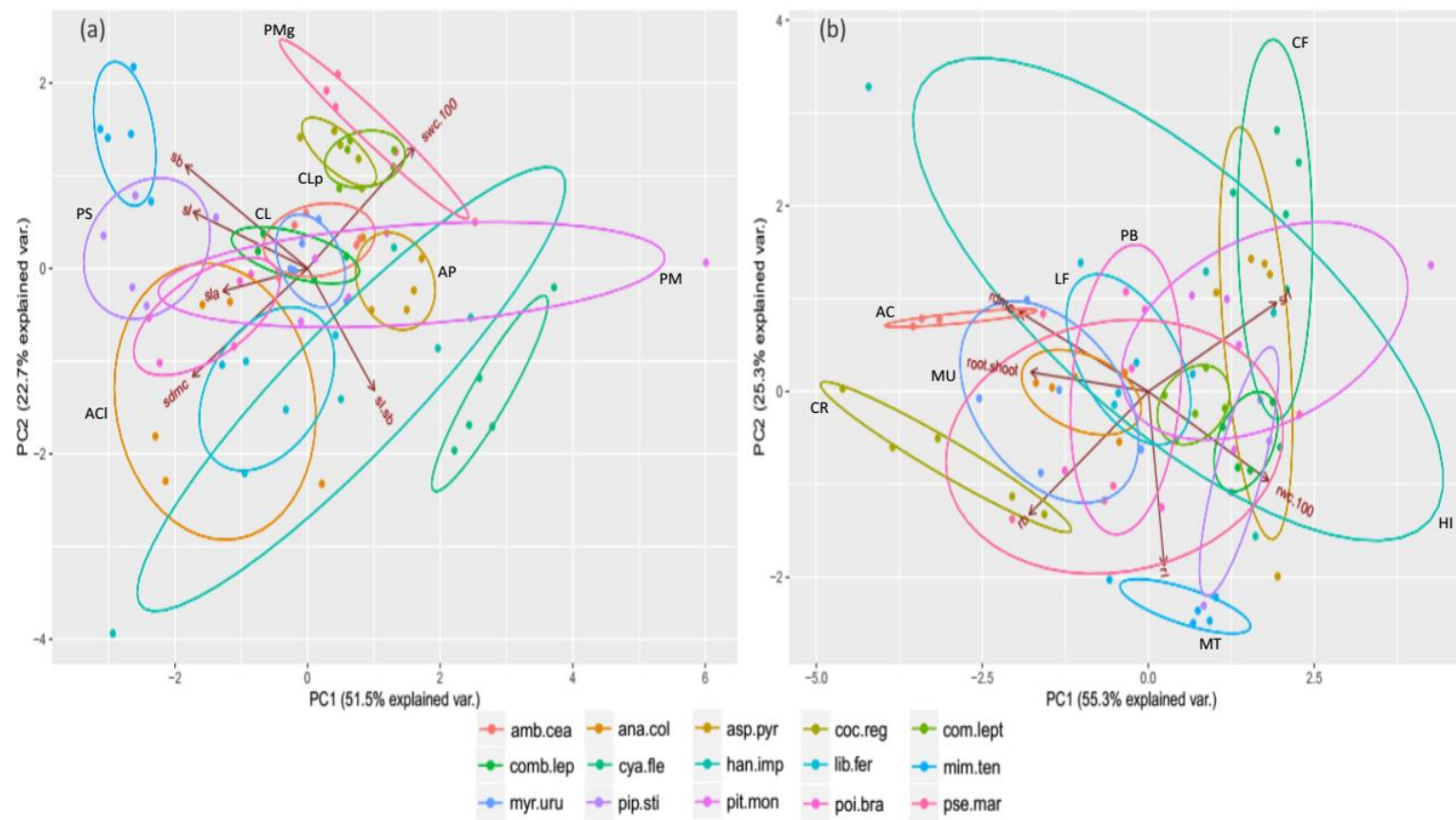
Traits	Abb	Description	Associated functional role	References
Aboveground traits				
Shoot biomass	SB	Total oven-dry mass of the aboveground part for a single plant (g)	SB can be correlated to plants fitness and performance in different systems	Markesteijn & Poorter (2009); Younginger *et al.* (2017)
Shoot length	SL	Total length of the longest shoot in the plant (cm)	SL can be a surrogate for plant height in experimental conditions and, therefore, correlated to competition for light	Markesteijn & Poorter (2009); Pérez-Harguindeguy *et al.* (2013)
Shoot dry matter content	SDMC	Proportion of shoot dry mass per unit of shoot fresh mass (%)	Higher values of SDMC indicate accumulation and conservation of carbon in the plants shoots	Poorter & Markesteijn (2008)
Shoot water content	SWC	Proportion of water per unit of shoot mass (%)	SWC indicates costs associated to the construction of shoots and, also, the potential for water storage in the plant shoot	Saura-Mas & Lloret (2007); Markesteijn & Poorter (2009)
Shoot length: shoot biomass	SL:SB	Proportion of shoot biomass produced in relation to shoot length (cm g^{-1})	This trait is analogue of SRL and SLA. Higher values of SL:SB indicate more investment in length, conferring advantage during competition for light. Lower values indicate more accumulation of water and nutrient in plant biomass	Cornelissen *et al.* (2003); Pérez-Harguindeguy *et al.* (2013)
Specific leaf area*	SLA	One-sided area of a leaf divided by its oven-dry mass (mm^2 mg^{-1})	Higher SLA values indicate potential higher growth and photosynthetic rates and higher leaf N concentrations	Cornelissen *et al.* (2003); Pérez-Harguindeguy *et al.* (2013)
Belowground traits				
Root biomass	RB	Total oven-dry mass of the roots for a single plant (g)	Higher values of RB can be related to higher drought tolerance and better performance and functioning during dry seasons	Markesteijn & Poorter (2009); Younginger *et al.* (2017)

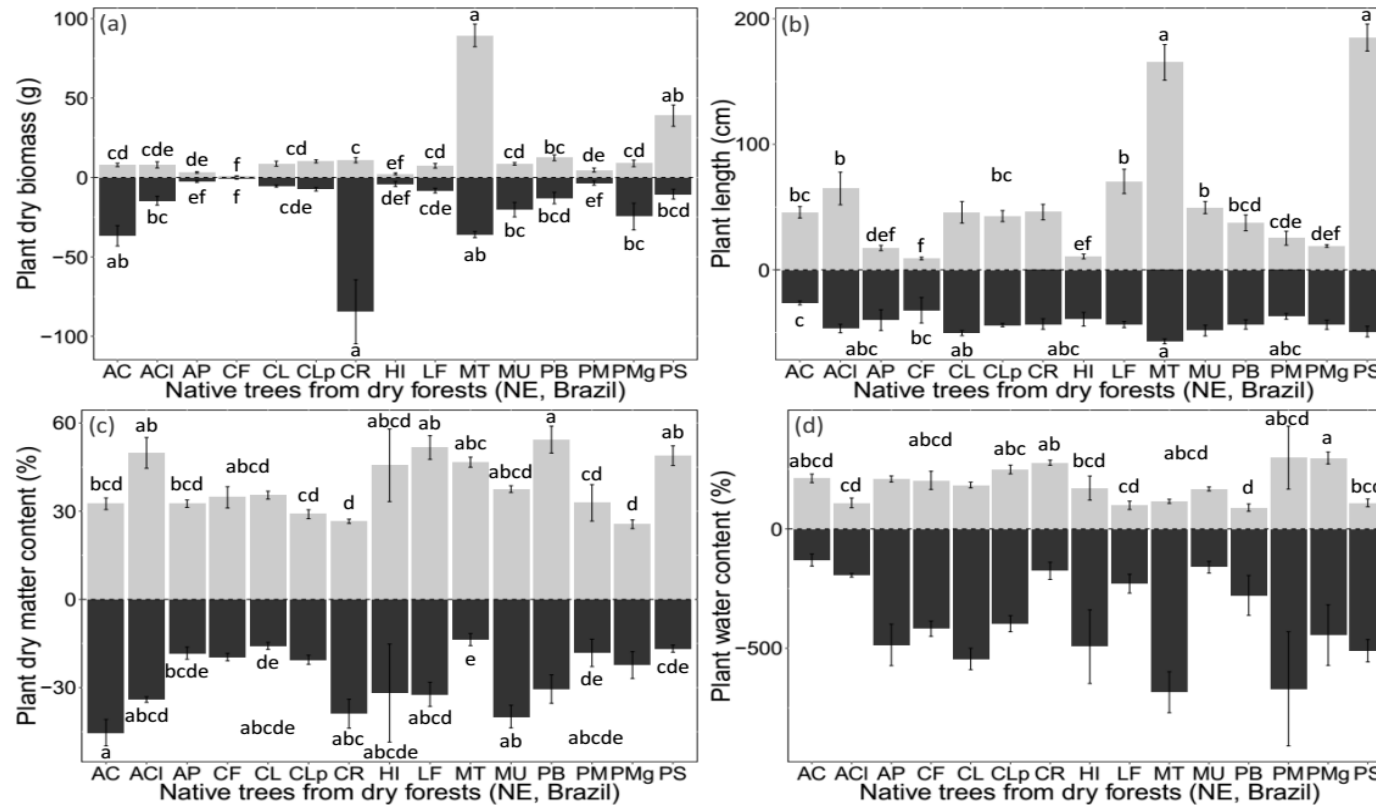| Root length	RL	Total length of fine roots length in the plant calculated by imagery analysis** (cm)	RL can influence soil exploitation by plants and it is also related to the effects of plants on soil stability	Ryser (2006); Bardgett *et al.* (2014)
Root dry matter content	RDMC	Proportion of root dry mass per unit of root fresh mass (%)	Higher values of RDMC indicate accumulation and conservation of carbon in the plants root system	Poorter and Markesteijn (2008)
Root water content	RWC	Proportion of water per unit of root mass (%)	RWC indicates costs associated to the construction of roots and, also, the potential for water storage in the root system	Saura-Mas & Lloret (2007); Pérez-Harguindeguy *et al.* (2013)
Root:shoot ratio	root:shoot	Proportion of biomass allocation for roots and shoots in a single plant	Indicates the trade-off between shade- and drought-tolerant species. Plants from semi-arid systems should allocate more biomass to their root systems and maximize water capture	Markesteijn and Poorter (2009)
Specific root length	SRL	The ratio of root length to dry mass of fine roots (cm g^{-1})	Higher values of SRL indicate higher rates of water and nutrients uptake	Cornelissen *et al.* (2003); Pérez-Harguindeguy *et al.* (2013)

Table 3: Results from the model selection analysis using the bestglm package in R. We show the five best model (traits, AIC and adjusted R^2 values) for each one of the single functions evaluated and for the index of multifunctionality.

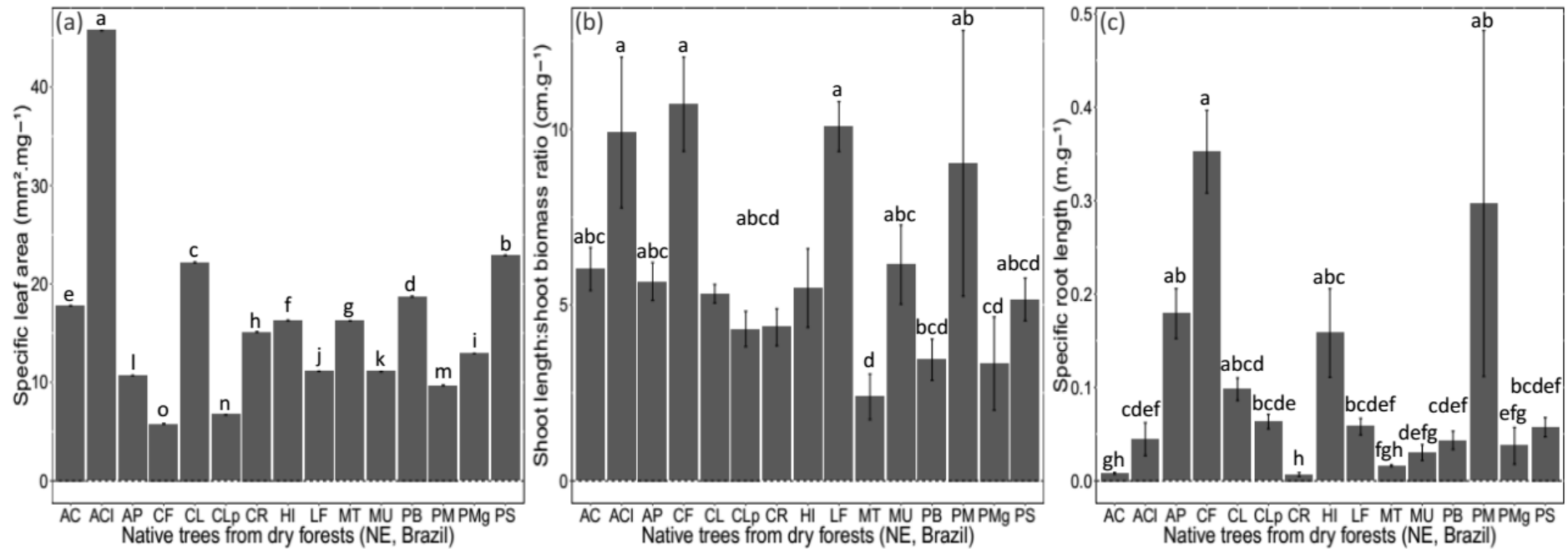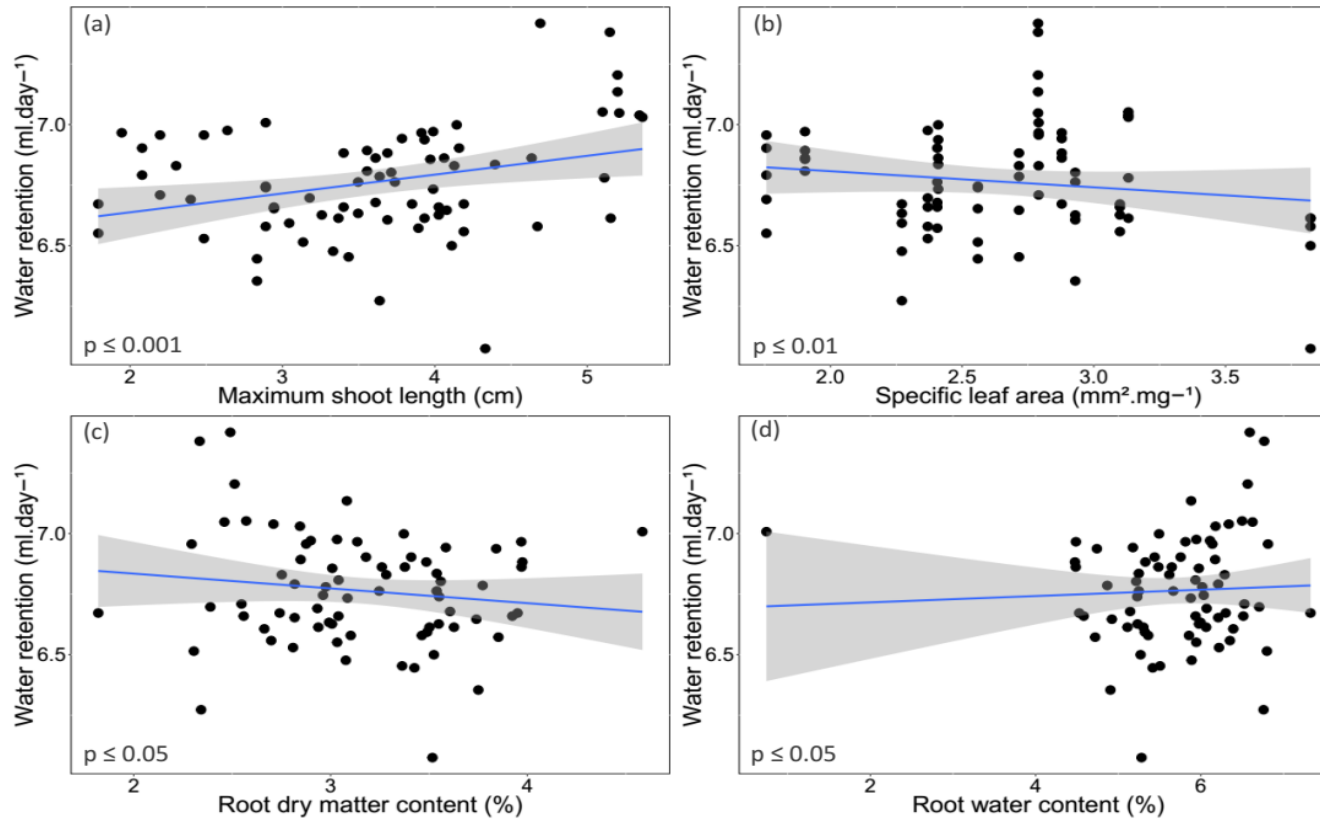| Model	Explanatory variables	AIC	R^2
Water retention			
1°	SLA + SL + RDMC + RWC	-234.01	22.4%
2°	SLA + SL + RDMC + RWC + SRL	-233.29	22.6%
3°	SLA + SL + SDMC + SWC + RDMC + RWC	-233.26	23.5%
4°	SLA + SL + RB + RDMC + RWC	-232.79	22.1%
5°	SLA + SB + SL:SB + RDMC + RWC	-232.69	22%
Phosphorus retention			
1°	SLA + SDMC + RDMC + SRL	-1261.07	22%
2°	SLA + SWC + RDMC + SRL	-1260.92	21.9%
3°	SLA + SB	-1260.65	19.6%
4°	SLA + SB + RDMC	-1260.34	20.3%
5°	SLA + SB + SWC + RDMC + SRL	-1260.33	22.2%
Total nitrogen retention			
1°	SL.SB + RDMC + RWC + SRL	-625.03	37.7%
2°	SL.SB + SWC + RDMC + SRL	-625.00	37.6%
3°	SL.SB + RB + RDMC + RWC	-624.96	37.6%
4°	SB + SL + RDMC + RWC + SRL	-624.79	38.2%
5°	SB + SL:SB + RDMC + RWC + SRL	-624.34	37.9%
Soil loss (sts - dissolved soil particles)			
1°	SL.SB	-28.96	3.8%
2°	SB + SL	-28.28	4.2%
3°	SL.SB + root:shoot	-27.95	3.8%
4°	SL.SB + RWC	-27.94	3.8%
5°	SB + SL + SL:SB	-27.70	4.7%
Multifunctionality index			
1°	SL:SB	-362.40	6.2%
2°	SB + SL	-361.13	5.8%
3°	SB + SL:SB	-360.71	5.3%
4°	SL:SB + ROOT.SHOOT	-360.68	5.2%
5°	SLA + SL:SB	-360.65	5.2%

Figure 1: Multidimensional functional space representation for above (a) and belowground (b) plant traits. Scores for axis 1 and 2 were calculated through the PCA analysis. Abbreviations represent the 15 trees from tropical dry forest (NE, Brazil). Abbreviations indicate trait distribution for the plant species used in the experiment. Scientific names can be found in table 1.
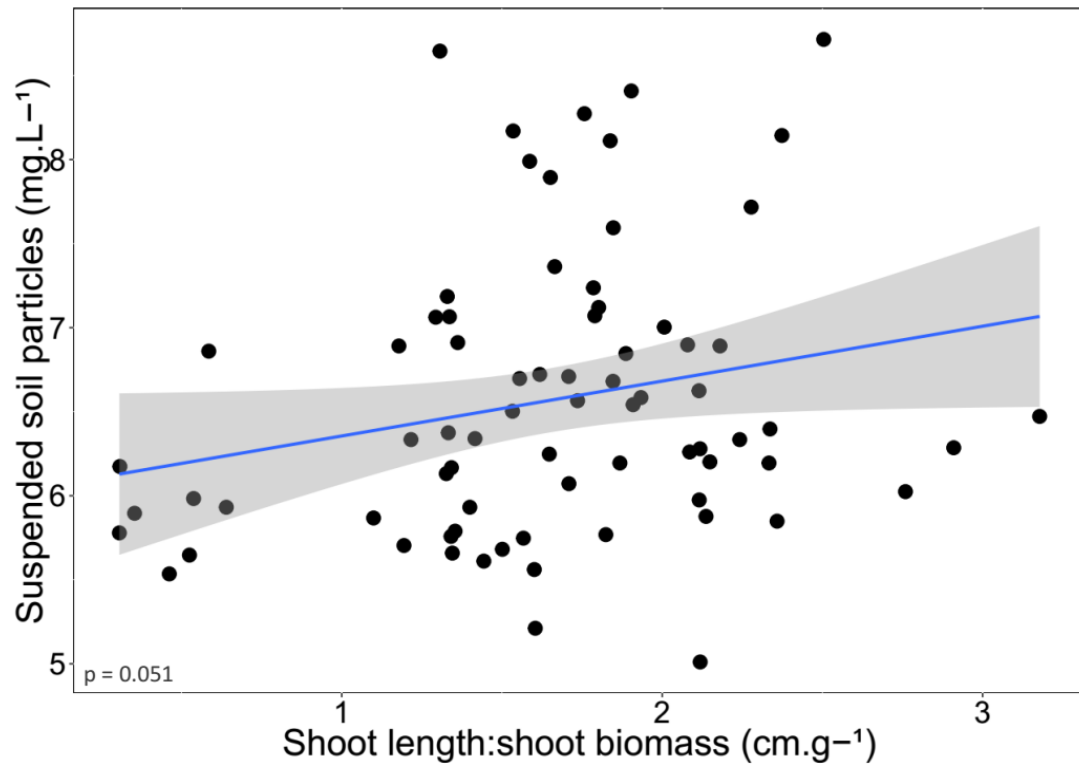
Figure 2: Functional traits comparisons among 15 trees from tropical dry forests (NE, Brazil) as a result from the Tukey HSD analysis. Barplots represent average values (±SE) for above (light grey) and belowground (dark grey) plant traits. The figure shows the results for plants shoot and root biomass (a), length (b), dry matter content (c) and water content (d). Different letters indicate that trait values are significantly different among plant species. Full species names related to abbreviations can be found in table 1.

Figure 3: Functional traits comparisons among 15 trees from tropical dry forests (NE, Brazil) as a result from the Tukey HSD analysis. Barplots represent average values (±SE) for plants SLA (a), shoot length:shoot biomass ratio (b) and SRL (c). Different letters indicate that trait values are significantly different among plant species. Full species names related to abbreviations can be found in table 1.
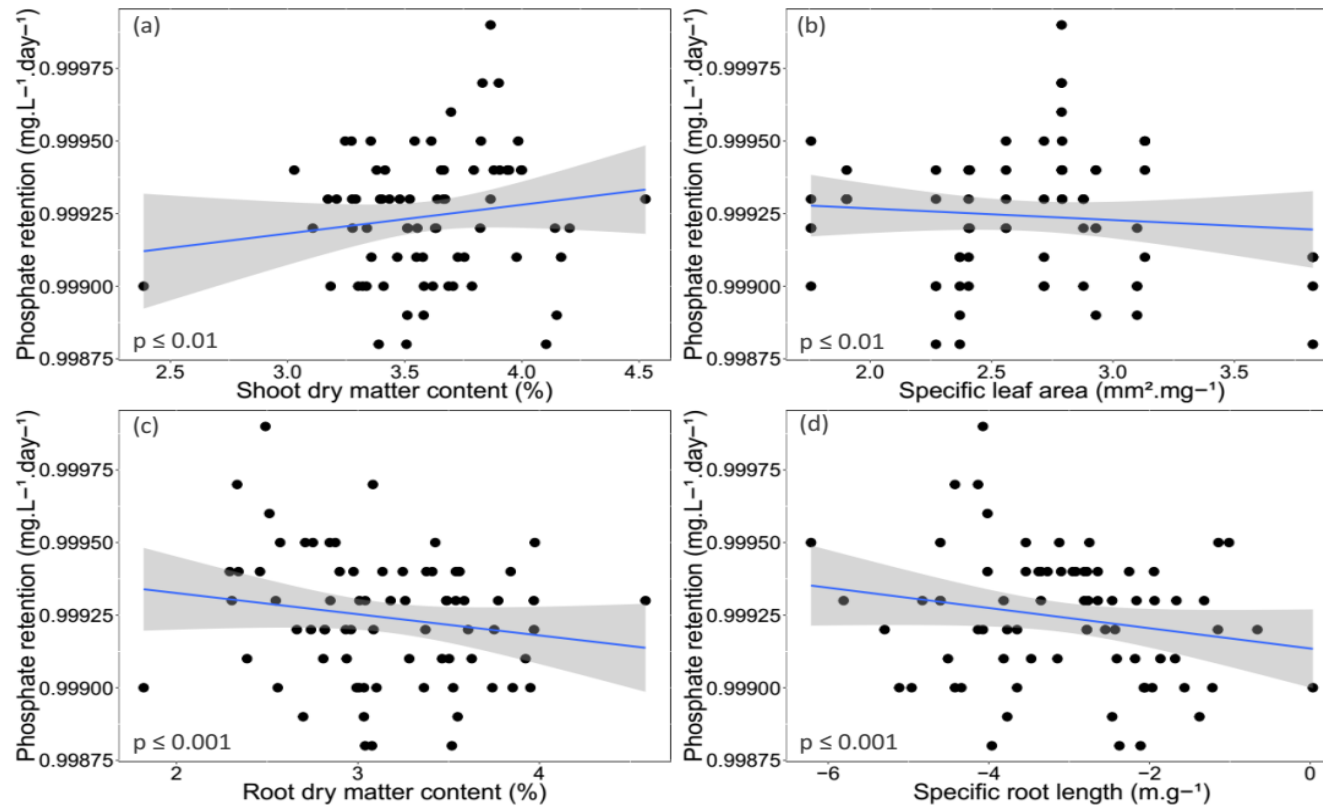
Figure 4: Plant traits affecting water retention in the soil. The plots show the results from the bestglm analysis using log-transformed values of water retention. Only the traits included in the first best model are represented. The figure shows the effects for log-transformed values of maximum shoot length (a), SLA (b), root dry matter content (c) and root water content (d). Adjusted R^2 value for the model is presented in the table 3.

Figure 5: The plot shows the results from the bestglm analysis using log-transformed values of suspended particles (STS). Only the log-transformed values of shoot length:shoot biomass ratio were found to influence soil dissolved particles (first best model). Adjusted R^2 value for the model is presented in table 3.
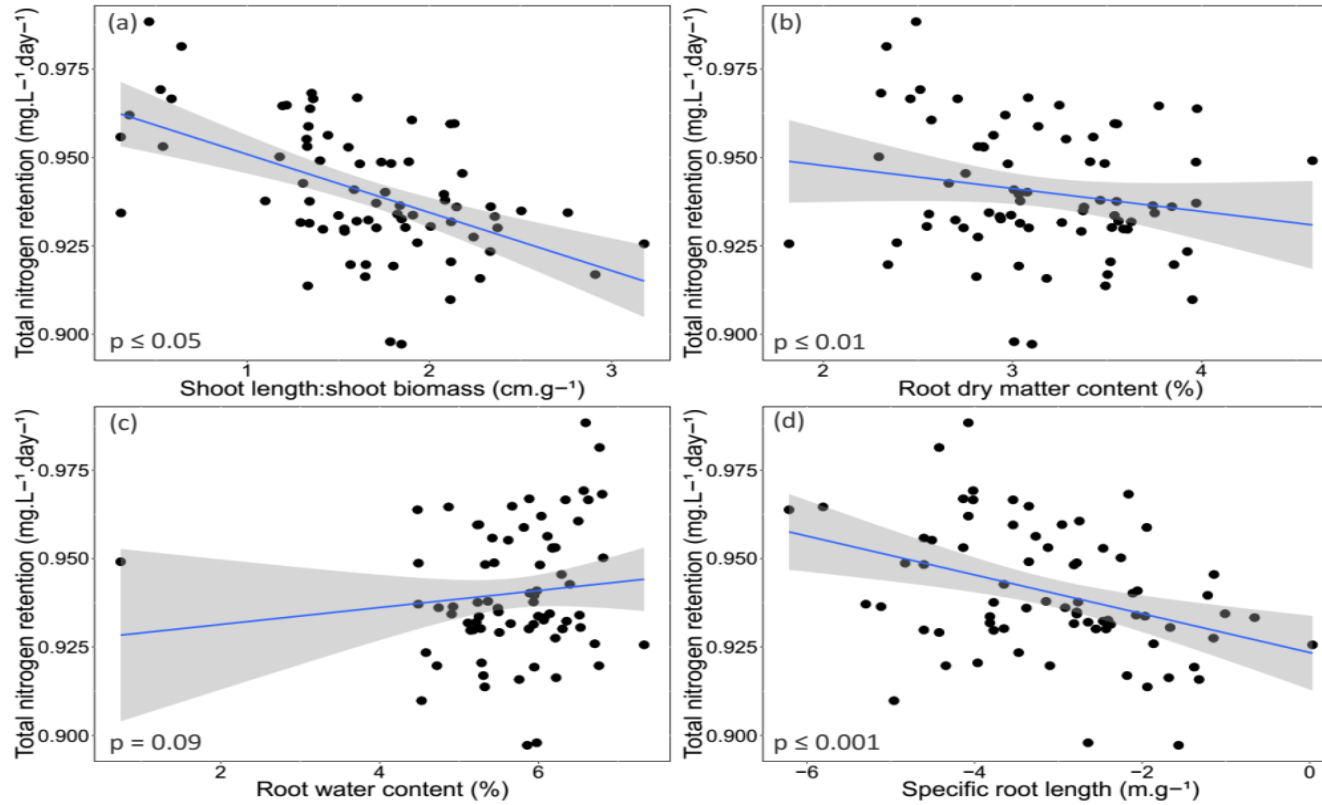
Figure 6: Plant traits affecting phosphate retention in the soil. The plots show the results from the bestglm analysis using log-transformed values of phosphate retention coefficient. Only the traits included in the first best model are represented. The figure shows the effects for log-transformed values of maximum shoot dry matter content (a), SLA (b), root dry matter content (c) and SRL (d). Adjusted R^2 value for the model is presented in table 3.

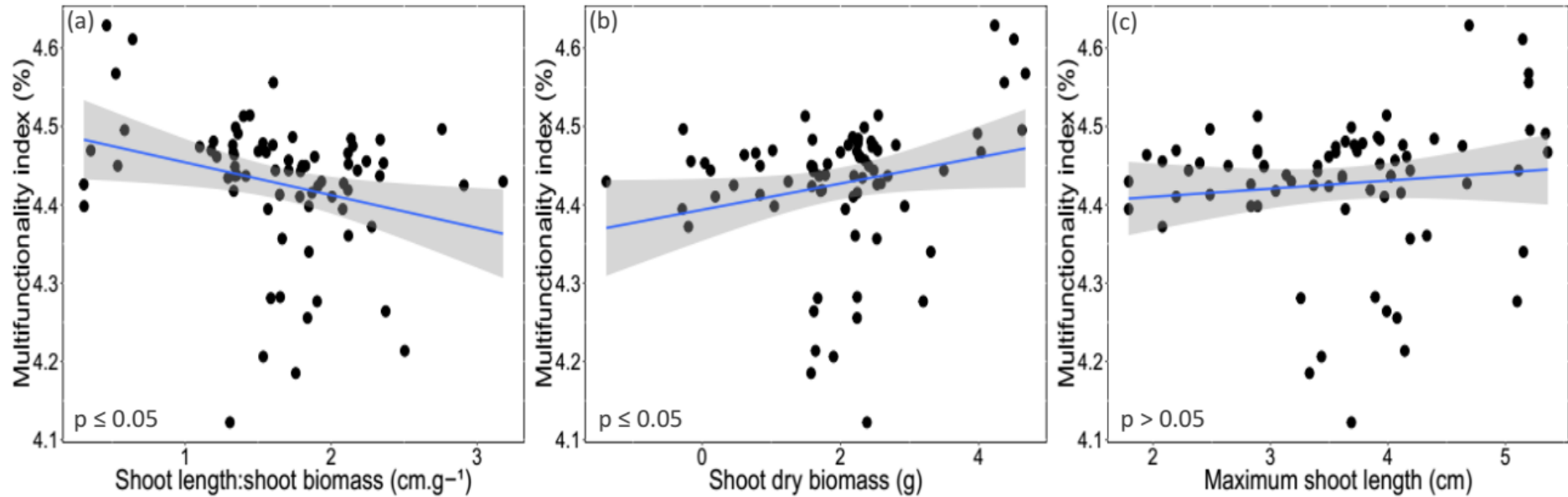**Figure 7:** Plant traits affecting total nitrogen retention in the soil. The plots show the results from the bestglm analysis using log-transformed values of total nitrogen retention coefficient. Only the traits included in the first best model are represented. The figure shows the effects for log-transformed values of maximum shoot length:shoot biomass ratio (a), root dry matter content (b), root water content (c) and SRL (d). Adjusted R^2 value for the model is presented in table 3.

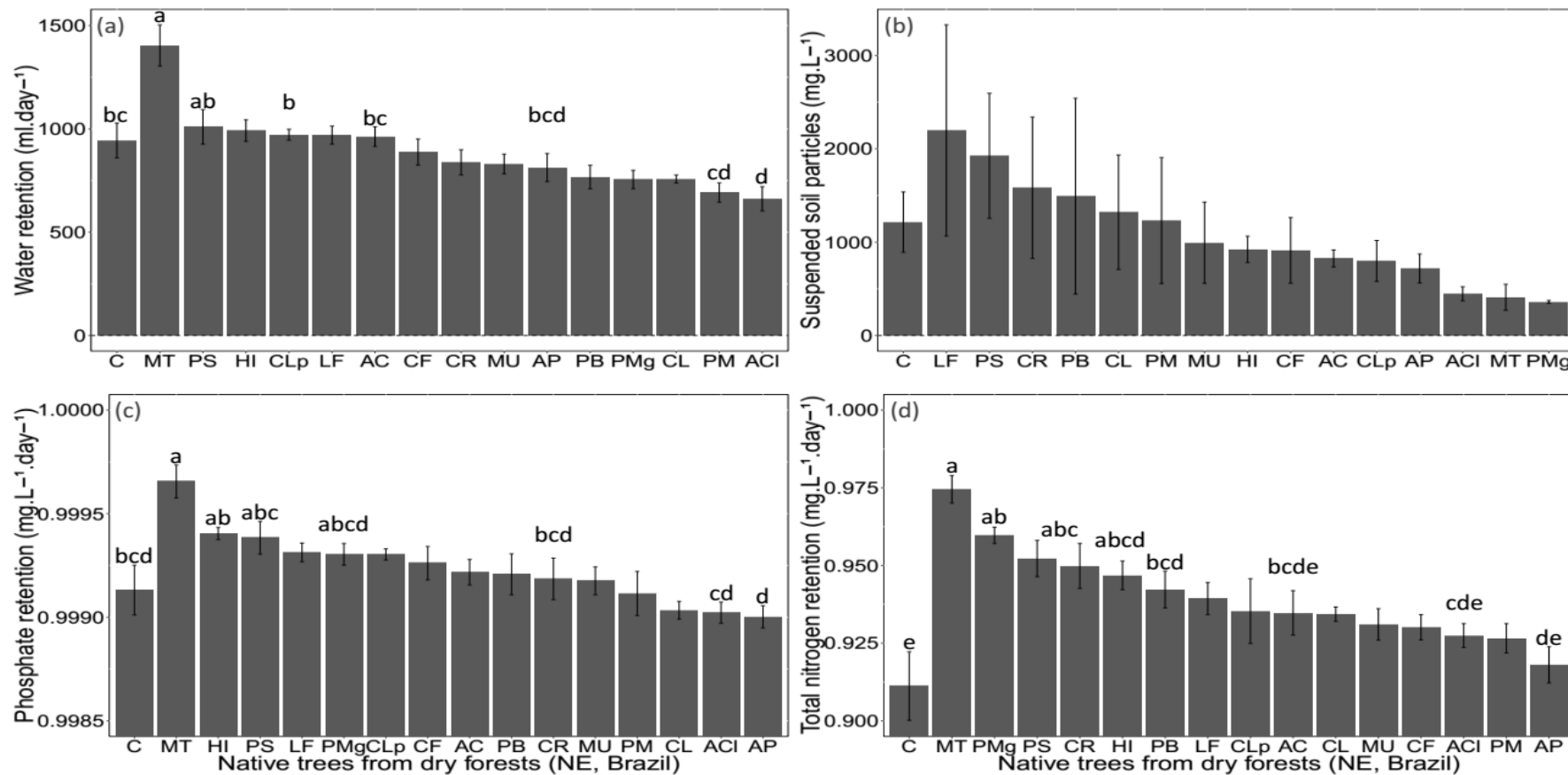**Figure 8:** Plant traits affecting the multifunctionality index. The plots show the results from the bestglm analysis using log-transformed values for multifunctionality and plant traits. Only the traits included in the two first best models are represented in the figure. The first best model (a) shows shoot length:shoot biomass ratio negatively affecting multifunctionality, while the second best model shows shoot biomass (b) and length (c) positively affecting ecosystem multifunctionality in our experiment, although only shoot biomass had a significant effect. Adjusted R^2 values for the models are presented in table 3.

Figure 9: Barplots represent average values (±SE) for the effect of plant species on water retention in the soil (a), soil loss (b), phosphate retention (c) and total nitrogen retention in the soil (d). Different letters indicate that effects are significantly different among plant species and, also, in comparison to the control treatment (i.e. bare soil) based on multiple comparisons using Tukey HSD test.

Figure 10: Barplots represent average values (±SE) for the effects of plant species on the ecosystem multifunctionality index. Different letters indicate that effects are significantly different among plant species and, also, in comparison to the control treatment (i.e. bare soil) based on multiple comparisons using Tukey HSD test.

Chapter 3

Species richness and phylogenetic relatedness control plant growth at the individual but not at the community level during restoration of a riparian forest[1][2]

Abstract – Little attention has been paid to the effects of phylogenetic diversity on the success of restoration projects. This study investigates the effects of species richness and plant phylogenetic relatedness on restoration success of a riparian forest from a region of transition between Atlantic Forest and semi-arid ecosystems in northeastern Brazil. A restoration experiment was established along a perennial stream in Monte Alegre (NE, Brazil), testing the effects of species richness and phylogenetic diversity on plant survival and growth. We used phylogenetic information on 47 plant species (trees and shrubs) occurring in the region. The resulting phylogenetic tree had a basal node with three major clades. Three species from each clade were randomly selected, resulting in nine species to settle the experiment. We defined five levels of diversity: (i) no planting (zero species), (ii) monoculture, (iii) three closely related species (same clade), (iv) three distantly related species (different clades), and (v) nine species. The experiment consists of 96 (12 x 10 m) experimental plots placed in the two margins of the stream. Overall, 1656 individuals were planted in September 2015 (184 per species). One year later, plant survival, height and community mean growth were assessed. Survival was lower but average height was higher for plants near to the stream. Plots with phylogenetically distant communities had taller plants. Community mean growth was not affected by diversity treatments. We suggest that plant phylogenetic relatedness should be considered for increasing success of future restoration projects.

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[2] In preparation to *Journal of Applied Ecology*

INTRODUCTION

Diversity-productivity hypothesis proposes that biomass production increases asymptotically with the number of species composing a community (Cardinale *et al.* 2012; Tilman, Isbell & Cowles 2014). Most of the studies addressing this issue used either species richness or functional diversity of plant communities for explaining such positive correlation, where more diverse communities would partition higher portions of available resources (Cadotte, Carscadden & Mirotchnick 2011; Cardinale 2011; Conti & Díaz 2013). However, during the last years, studies are also including information about phylogenetic diversity to explain this relationship (Cadotte *et al.* 2009; Flynn *et al.* 2011; Srivastava *et al.* 2012; Steudel *et al.* 2016). Phylogenetic distance is, normally, considered as a surrogate for ecological differences, i.e. the time since two species diverged from a common ancestral would positively correlate with the development of dissimilar functional traits (Cadotte *et al.* 2009; Cadotte 2013; Díaz *et al.* 2013). Thus, such species would complementarily affect the same ecosystem functions, as for instance biomass production, carbon sequestration and nutrient cycling (Cadotte 2013). However, it is important to keep in mind that phylogenetic diversity is not always a fully representative measure of functional dissimilarity. Since species are differently affected by evolutionary processes, they can also share similar traits because of convergent evolution. Thus, in these cases, higher phylogenetic diversity would not result in higher niche complementarity (Davies *et al.* 2016).

Another positive influence resulting from higher phylogenetic diversity in plant communities should be an increase in plant survival rates. This can be explained by the fact that diverse communities can include higher levels of species differentiation related to ecological requirements that would offset the negative effects of competition on plants

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establishment and, consequently, survival, thus allowing multiple competing species to coexist (Tilman 1999; HilleRisLambers *et al.* 2012). These effects would be possible because niche overlap among species negatively correlates with phylogenetic distinctiveness, resulting in less competition for phylogenetically diverse plant communities (Verdú, Gómez-Aparicio & Valiente-Banuet 2012).

It is well-known that positive interactions among plants will ultimately increase survival probability, especially when considering plants from harsh environments (Brooker *et al.* 2008; Paterno, Siqueira Filho & Ganade 2016; Carrión *et al.* 2017). Despite previous evidence pointing out that facilitation is more likely to produce a nested structure during community assembly resulting in a subset of species among the best benefactors which exhibit different levels of facilitation (Verdú *et al.* 2009; Verdú, Jordano & Valiente-Banuet 2010), a recent study showed that facilitative interactions will also increase with the phylogenetic distinctiveness among plants composing a community (Verdú et al. 2012). Therefore, distantly related species would have a higher degree of coexistence than expected by chance (Valiente-Banuet & Verdú 2007). Finally, since such interactions can potentially increase establishment and survival of certain species due to species-specific positive effects, i.e. improved soil conditions and microclimate, reduced seed predation and herbivory. This should drive the outcomes of ecological succession during the restoration of degraded areas (Verdú, Gómez-Aparicio & Valiente-Banuet 2012; Winter, Devictor & Schweiger 2013; Hipp *et al.* 2015).

Studies have also demonstrated that the composition (i.e. the identity of plant species in a community) is a better predictor of ecosystem functioning than species number *per se* (Mokany, Ash & Roxburgh 2008; Mouillot *et al.* 2011). Nevertheless, there are species-specific differences when considering different functions or processes

(Lavorel & Grigulis 2012), so the degree of uniqueness in a given community can be higher than previously thought. Thus, species that were supposed to be redundant would be supporting different ecosystem functions (Bowker *et al.* 2011). Additionally, while less frequent or even rare species can also perform and, thus, guarantee the maintenance of functions that could be lost in the absence of such species (Mouillot *et al.* 2013; Soliveres *et al.* 2016), it is more likely that ecosystem functioning and, especially, community biomass, should be more dependent on the species that are most abundant or dominant in the community (Roscher *et al.* 2007; Sasaki & Lauenroth 2011; Winfree *et al.* 2015). This is expected because abundant species can be more resistant to different disturbances and, therefore, have a higher contribution for the community biomass net balance (Walker, Kinzig & Langridge 1999). Therefore, for better managing ecosystems and for improving the success of restoration projects we should be able to identify species combinations that would maximize productivity in multispecies assemblages thus ensuring ecosystem functioning in the long term, since biomass production positively correlates to plants fitness and performance in ecosystems (Cadotte 2013; Younginger *et al.* 2017).

Furthermore, as predicted years ago and confirmed more recently, the inclusion of phylogenetic information of plant communities is paramount for achieving conservation or restoration goals when managing ecosystems and landscapes (Vane-Wright, Humphries & Williams 1991; Verdú, Gómez-Aparicio & Valiente-Banuet 2012; Hipp *et al.* 2015). Nowadays, phylogenetic diversity has been increasingly considered in conservation efforts due to the consensus that by conserving phylogenies we would conserve, together with the evolutionary histories of divergent species, ecosystem functions and services and, therefore, reduce future risks to human well-being (Winter *et al.* 2013; Hipp *et al.* 2015). Nevertheless, despite its potential to function as an integrative

dimension of diversity and account for different ecological strategies, phylogenetic diversity has been neglected in restoration programs (Hipp *et al.* 2015). In fact, since positive interactions among plant species were found to positively correlate with evolutionary divergence in plant communities, we could expect phylogenetic diversity to have great benefits for restoration success (Verdú *et al.* 2012; Hipp *et al.* 2015). Therefore, we should include phylogeny aspects for better designing restoration projects and for increasing the functioning of restored systems.

Nevertheless, many restoration projects still lack the inclusion of scientific evidences (Gómez-Aparicio 2009; Verdú *et al.* 2012; Hipp *et al.* 2015). This is particularly important for areas that comprises multiple uses like the riparian forests. Worldwide floodplains are continuously degraded by anthropogenic impacts resulting from uncontrolled human occupation and deforestation for the expansion of agriculture and urban developments. This is so, because the proximity with rivers or streams creates conditions that favor the development of the aforementioned activities in riparian forests, such as more fertile soils, milder climate and higher water availability (Bernhardt *et al.* 2005; Foley *et al.* 2005; Araújo 2009). Additionally, restoration of riparian forests in semi-arid climates is challenged by the need to cope with pulse dynamics drastically affecting soil conditions; i.e. from extremely dry to almost flooded soils (Williams *et al.* 2006; Collins *et al.* 2014). These dynamics can decrease plant establishment and survival, thus compromising restoration success. Therefore, the inclusion of communities with high diversity levels in the restoration of riparian forests should help to buffer flooding impacts and increase ecosystem stability (Tilman, Reich & Knops 2006; Cadotte, Dinnage & Tilman 2012).

The aim of this study is to contribute to the development of science-based restoration. As a suitable study case, we manipulate species richness and phylogenetic relatedness among plant species during restoration of a riparian forest in northeastern Brazil. We tested the following hypothesis: (i) proximity to the stream (higher water availability in an area with a semi-arid climate regime) would increase plant survival; (ii) plant survival would be higher in communities with higher species diversity; (iii) plant communities with more species would have taller plants; and (iv) plants from phylogenetically more diverse communities would also be taller.

MATERIAL AND METHODS

Study site, plant species selection and phylogenetic classification

The municipality of Monte Alegre/RN is located in the region *Agreste Potiguar*, which is a transition zone between Atlantic Forest and semi-arid areas from northeastern Brazil (Caatinga). Therefore, the region is characterized by the predominance of seasonal forests and the occurrence of plant species from both biomes (Rodal, Barbosa & Thomas 2008). The area where the experiment was implemented is a private property and comprises part of an old farm used for cattle breeding inserted in a semi-urban to rural landscape (Figure 1). The vegetation of the study site is characterized by dominance of grasses, particularly the brachiaria grass (*Brachiaria decumbens*, LHT, pers. observ.). However, a small fragment of Atlantic Forest in secondary stage of regeneration is also present. In this fragment, some plants with potential for being used in restoration projects were identified (Table 1). Still, this remnant of native vegetation does not include the riparian zone, which is highly degraded with little woody vegetation (Figure 1).

In May 2015, a field survey in the study area and its surroundings was done to identify native plant species that could be applied for restoration of the riparian zone. On that occasion, 47 woody species with potential use for restoration projects were identified, that are native in the Atlantic Forest or the Caatinga of Rio Grande do Norte (Table 1).

A phylogenetic tree based on an Angiosperm supertree was generate for the plant species identified during the field survey (Figure 2). The 47 species belong to three main clades (the superasterids clade, and within the superrosids, the malvids and fabids clades). Nine species (three from each clade) were randomly selected for the experiment. However, since the commercial availability of species is an important constraint for restoration of degraded areas in northeastern Brazil, species selection was conducted separately for each clade and repeated depending on availability from local producers. Plant species with regional provenance were acquired from two registered producers (*Viveiro de Mudas Semear LTDA – ME* & *Horto Florestal Parque do Pitimbu – NGO*) and kept in a nursery (under natural light and temperature conditions) at the study site during four weeks for acclimatization until setting up the experiment. By the moment of field transplantation, all plants were between 20 to 50 cm in height and 20 to 30 cm in root length.

Experimental design and monitoring

In July and August 2015, 96 experimental plots (12 m x 10 m) were established within 800 m on both sides of a perennial stream in Monte Alegre/RN (NE, Brazil). In each plot, 18 holes (ca. 20 cm diameter and 50 cm profundity) for receiving the study plants were prepared. Plant positions were defined using a 2 m x 3 m distance scheme,

therefore we implemented six lines with holes for receiving three plants in different distances from the stream (8, 10, 12, 14, 16 and 18 m, respectively). The experiment started in late September 2015 by transplanting 1656 saplings (184 per species and 18 per plot) from each one of the nine plant species (Figure 1).

We used a random partition design (Bruelheide *et al.* 2014) restricted to the plant species used for the construction of our phylogenetic tree, where the randomization was conducted for the plant species composing each one of the phylogenetic tree branches (Figure 2). The experiment was composed by five levels of diversity: (i) no planting (zero species, i.e. control (C) treatment), (ii) monoculture, (iii) three closely related plant species (belonging to the same branch), (iv) three distantly related species (one species from a different branch), and (v) nine species (with three species per branch). Control (i.e. no planting), monoculture, closely and distantly related species treatments were replicated four times. Polyculture treatment (all nine species used in the experiment planted together) was replicated nine times, resulting in a total of 96 experimental plots (Table 2).

In total, the experiment comprised 22 different community compositions. Besides the nine monocultures (one for each species used in the experiment) and the polyculture composition (all nine species combined), we used three compositions of closely related communities and nine compositions of distantly related communities. Therefore, we classified closely related communities in: (i) relat.A – composed by *Coccoloba latifolia*, *Tabebuia roseoalba* and *Handroanthus impetiginosus*; (ii) relat.B – *Schinus terebinthifolius*, *Tapirira guianensis* and *Myracrodruon urundeuva*; and (iii) relat.C – *Ziziphus joazeiro*, *Poincianella pyramidalis* and *Piptadenia stipulacea*. Distantly related communities were classified in: (i) dist.A – *Tabebuia roseoalba*, *Schinus terebinthifolius*

and *Piptadenia stipulacea*; (ii) dist.B – *Tabebuia* roseoalba, *Tapirira guianensis* and *Piptadenia stipulacea*; (iii) dist.C – *Coccoloba latifolia, Schinus terebinthifolius* and *Poincianella pyramidalis*; (iv) dist.D – *Tabebuia roseoalba, Myracrodruon urundeuva* and *Ziziphus joazeiro*; (v) dist.E – *Coccoloba latifolia, Tapirira guianensis* and *Ziziphus joazeiro*; (vi) dist.F – *Handroanthus impetiginosus, Myracrodruon urundeuva* and *Ziziphus joazeiro*; (vii) dist.G – *Coccoloba latifolia, Tapirira guianensis* and *Poincianella pyramidalis*; (viii) dist.H – *Handroanthus impetiginosus, Myracrodruon urundeuva* and *Poincianella pyramidalis*; and (ix) dist.I – *Handroanthus impetiginosus, Schinus terebinthifolius* and *Piptadenia stipulacea* [species nomenclature follows APG IV (2016)].

Plant survival and growth (height in cm) were the variables monitored during the first year of the experiment. We monitored survival in November 2015 and October 2016 (one year after start of the experiment). Plant growth was monitored four times after the experiment was implemented, i.e. December 2015, April 2016, June 2016 and October 2016. In November 2015, we found 157 dead plants in eight of nine species planted (i.e. 78 individuals of *Tapirira guianensis*, 23 *Piptadenia stipulacea*, 20 *Schinus terebinthifolius*, 13 *Handroanthus impetiginosus*, 11 *Tabebuia roseoalba*, nine *Poincianella pyramidalis*, two *Myracrodruon urundeuva* and one *Ziziphus joazeiro*), representing ca. 9.5% of mortality one month after the experiment was implemented. These individuals were replaced in early December by plants from the same sources; i.e. acquired from the producers before the experiment implementation and kept in the nursery at the study site. Therefore, plant height in December 2015 (instead of September 2015) was considered as the initial size for all plants used in the experiment.

Statistical analysis

For evaluating the effect of distance from the stream on plant survival and growth we re-classified the distances into two categories based on personal observations at the field site. Plants at 8, 10 and 12 m were considered near to the stream, while plants at 14, 16 and 18 m were considered far from the stream. Effects of the distance from the stream (near or far), species richness and phylogenetic relatedness on plant survival probability and on the number of surviving plants were evaluated through generalized linear mixed effects model with binomial error. Significance was determined based on likelihood ratio test (LRT) implemented by the package lmer4 (Bates *et al.* 2015). Additionally, a linear mixed-effects model with plots and species composition as random effects and the likelihood ratio test (LRT), also package lme4, was applied to test for the effects of the distance from the stream, species richness, phylogenetic relatedness and, also, the effects of community composition on plant height (i.e. plants size one year after the experiment was implemented). To correct for the differences in plant initial size, we used the initial size as a covariate in the model analyzing plant height. Thus, if height was affected only by the initial size rather than by the treatment diversity, likelihood ratio tests would show no differences when comparing the full model with the partial models (for instance, the model without interaction between diversity treatments and distance from the stream).

Community mean growth (i.e. average biomass accumulation in a given community) was calculated as the average for the absolute difference in plants size (final size – initial size) for all the communities in the experiment and used as a proxy for community biomass production. We applied the same linear mixed-effects model for assessing the effects of the distance from the stream, of the diversity treatments (i.e. species richness and phylogenetic relatedness) of the community composition on the

community mean growth. For assessing community composition effects on plant height and on the community mean growth we considered only the plots as a random effect while adjusting the mixed-effects model.

Plant height values were log-transformed, while community mean growth values were standardized by the most negative value (by adding +12.75, so all negative values would be $\geq$ zero) and, then, log-transformed [$\log(x+1)$] to fulfill the normality assumptions for the analysis. Richness values were also log-transformed before running the linear mixed-effects models. Statistical analyses were calculated using R Statistical Computing version 3.3.1 (R Development Core Team 2015).

RESULTS

Effects of diversity and distance from the stream on plant survival

Overall 1399 plants were found alive one year after the experiment was started, resulting in 84.5% overall survival probability. However, individual survival was significantly reduced for plants located near to the stream ($\chi^2 = 9.95$, df = 5, p $\leq$ 0.01; Figures 3a and 3b). Still, neither survival probability (species richness: $\chi^2 = 1.25$, df = 5, p > 0.05; phylogenetic relatedness: $\chi^2 = 0.08$, df = 5, p > 0.05; Figures 3a, b) nor the number of surviving plants were influenced by the diversity treatments (richness: $\chi^2 = 0.91$, df = 5, p > 0.05; relatedness: $\chi^2 < 0.001$, df = 5, p > 0.05; Figures 3c, d).

Overall number of plants alive one year after establishing the experiment varied from 105 for *Tapirira guinanensis* to 182 for *Piptadenia stipulacea* (out of 184 individuals planted per species; Figure 4b). Despite no statistical test was conducted, we

observed survival probability varying among plant species, from ca. 57% for *Tapirira guinanensis* to 99% for *Piptadenia stipulacea*. In fact, we observed three groups of species with different survival probabilities, ranging from low, to medium and to high survival probability (Figure 4a). Such classification in three different groups is not consistent with the species phylogenetic classification since each group had one or more species from a different branch in the phylogenetic tree (see Figure 2 for comparisons).

Effects of diversity and stream distance on plant height and on community growth

Mean plant height was 42 cm (± 0.56 SE) for monocultures, 48 cm (± 0.60 SE) for three-species communities, and 46 cm (± 1.50 SE) for nine-species communities. Thus, plants in communities composed by three species were 15.4% taller than plants in monoculture, but only 3.9% taller when comparing to plants occurring nine-species communities.

We used initial size as a covariate in the model evaluating plant height and community mean growth. Indeed, the covariate had strong effects when evaluating effects of species richness and phylogenetic relatedness on plant height (Estimate = 0.01, t = 40.8 for species richness effects; and Estimate = 0.01, t = 23.6 for phylogenetic relatedness effects). The same was observed when evaluating species richness effects on community mean growth (Estimate = –0.01, t = –2.83). However, when assessing effects of phylogenetic relatedness on community mean growth, initial size did not have a strong effect (Estimate = –0.01, t = –1.15). Finally, as shown below, initial size did not explain the complete response of plant height to the diversity treatments.

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Plant height (i.e. final size) was positively affected by species diversity in interaction with the distance from the stream, while the community mean growth was not (Figure 5). Interaction between species richness and the distance from the stream positively affected plant height, but only for three-species communities as asymptotic relationship ($\chi^2 = 4.81$, df = 8, p ≤ 0.05; Figure 5a). In turn, species richness levels and the distance from the stream by itself did not influenced plants final size ($\chi^2 = 1.02$, df = 7, p > 0.05; $\chi^2 = 0.08$, df = 7, p > 0.05 for richness and distance from the stream, respectively). The same pattern was observed when considering phylogenetic relatedness effects on plant height (Figure 5b). Similarly, the interaction between phylogenetic relatedness and the distance from the stream positively affected plant height ($\chi^2 = 20.4$, df = 8, p ≤ 0.001). Therefore, plants from distantly related communities occurring near to the stream were taller (Figure 5b). Again, treatment effects were not significant ($\chi^2 = 0.01$, df = 7, p > 0.05; $\chi^2 = 1.71$, df = 7, p > 0.05 for phylogenetic relatedness and distance from the stream, respectively). Finally, community mean growth did not respond to the effects of the interaction between stream distance and species richness ($\chi^2 = 1.62$, df = 8, p > 0.05) or phylogenetic relatedness ($\chi^2 = 2.09$, df = 8, p > 0.05; Figures 5c, d).

Community composition affecting plant height and community mean growth

Composition of distantly and closely related communities (i.e. three-species communities) significantly affected plant height ($\chi^2 = 41.9$, df = 17, p ≤ 0.001) and community mean growth ($\chi^2 = 45.9$, df = 17, p ≤ 0.001; Figure 6). It means that not only the degree of phylogenetic relatedness among species composing a given community but also the identity of such species is important for biomass production at individual and community level. However, effects of the composition of distantly related communities

on plant height and on the community mean growth were intensified according to the distance from the stream, whereas for closely related communities, the same effects were independent of the distance from the stream. We observed that, at least, one distantly related community (i.e. community dist.I) had taller plants and higher community mean growth when near to the stream (χ^2 = 73.5, df = 28, p ≤ 0.001; Figures 6a, c). In turn, in closely related communities, plant height and community mean growth were positively affected only by the composition. Therefore, the community relat.C, composed by *Piptadenia stipulacea*, *Poincianella pyramidalis* and *Ziziphus joazeiro*, had significantly taller plants and higher community mean growth (Figures 6b, d).

Average height and community mean growth varied among the different species composing the communities (Figure 7). In fact, three groups of heights were identified. The first group included the two smallest species (i.e. *Handroanthus impetiginosus* and *Tabebuia roseoalba*), while the second included the tallest species (i.e. *Piptadenia stipulacea*). The third group comprises all the other species, which presented similar intermediate average heights (Figure 7a). Indeed, community composition (χ^2 = 76.7, df = 27, p ≤ 0.001) and its interaction with distance from the stream (χ^2 = 172.1, df = 48, p ≤ 0.001) had significant effects on the height of plants from single-species communities. Height was significantly different for plants of *Handroanthus impetiginosus* (Estimate = –0.39, t = –3.26), *Tabebuia roseoalba* (Estimate = –0.25, t = –2.10) and *Piptadenia stipulacea* (Estimate = 0.82, t = 6.42). While the interaction between composition and distance from the river significantly affected plants of *Tapirira guinanensis* (Estimate = –0.20, t = –3.26), *Ziziphus joazeiro* (Estimate = –0.16, t = –2.83) and *Schinus terebinthifolius* (Estimate = –0.29, t = –5.15). In turn, community mean growth was significantly affected only by the composition (χ^2 = 79.63, df = 27, p ≤ 0.001, Figure 7b).

Moreover, we found that community mean growth was significantly different only for *Piptadenia stipulacea* (Estimate = 1.80, t = 5.85).

However, we can observe that composition effects and the positive influence from the interaction between composition and the distance from the stream on plant height were driven almost exclusively by the performance of *Piptadenia stipulacea*, whose plants were taller when located near to the stream. All the other species (excepting *Myracrodruon urundeuva* whose individuals near to the stream were slightly taller) were negatively or not affected by the proximity to the stream (Figure 7a). The same pattern was observed for community mean growth. Nevertheless, effects of the interaction between composition and the distance from the stream on *Piptadenia stipulacea* were not significant and the community mean growth for all the other monocultures was negative or nearly zero, indicating that community biomass requires more time to positively respond to diversity influences (Figure 7b).

DISCUSSION

Here we present results for the first year of a long-term restoration experiment in a riparian forest in northeastern Brazil. Our findings reveal that is possible to achieve successful restoration of degraded areas by planting phylogenetically distant species. However, not all of our expectations were confirmed. For example, despite the relatively high overall survival probability (84.5%), plants survived less when they were located near to the stream, possibly indicating that high groundwater level or flooding can affect plants adapted to semi-arid conditions more negatively than water scarcity. Also, we observed that mortality was particularly higher for three plant species (i.e. *Handroanthus*

impetiginosus, Tapirira guianensis and *Tabebuia roseoalba*). Those species had the smallest plants when the experiment was implemented. This suggests that initial plant size when restoring degraded areas can affect plant establishment and survival and, ultimately, restoration outcome.

Nevertheless, we also found important results for restoration that should be considered in future experiments. First, interactions between species richness and phylogenetic relatedness with the distance from the stream result in taller plants. Therefore, we argue that diversity effects on plant biomass are stronger when natural resources are favorable. Second, increases in biomass production are associated with particular community compositions. Hence, the inclusion of phylogeny in the design of restoration experiments allows for the identification of species combinations that would maximize biomass production, thus increasing restoration success in the long term. Third, we observed that both species richness and phylogenetic relatedness affect plant biomass at the individual but not at the community level. This indicates that broad scale measures for evaluating restoration success require more time to show the positive influence of diversity.

Species diversity, pulse dynamics and survival of plants in restored riparian forests

A recent study found that species diversity is important for increasing plant survival during the restoration of tropical forests in Malaysia (Tuck *et al.* 2016). In these areas, where logging and agricultural activities reduced tropical forest coverage thus threatening species diversity and population viability, the authors argue that by applying the so-called *enrichment planting* (i.e. multispecies mixtures inside semi-natural

fragments) they could supplement forest regeneration by overcoming recruitment limitations. Such technique can increase establishment and survival of endangered species via insurance effects, thus contributing to a successful restoration (Tuck *et al.* 2016). In fact, various studies described the potential benefits of species diversity for plant survival, thus affecting species coexistence and, also, population viability. The mechanisms responsible for this positive relationship can include reduction of competitive and an increase of facilitative interactions and, also, the dilution of herbivory effects (Tilman 1999; Lambers *et al.* 2004; Srivastava *et al.* 2012; Verdú, Gómez-Aparicio & Valiente-Banuet 2012).

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

Additionally, we also expected survival to be higher for plants located near to the stream. However, the opposite pattern was found. Plants near to the stream had lower survival probability in comparison to plants far from the stream. It seems that survival

patterns here are reflecting individual species characteristics instead of diversity effects on plants establishment. Since riparian forests are controlled by strong pulse dynamics, the ability to grow fast and reach resource patches in the soil would confer such species an advantage for establishing during initial stages of succession or regeneration (Chesson *et al.* 2004; Williams *et al.* 2006; Collins *et al.* 2014). Therefore, we can argue that fast-growing species will have higher survival during the restoration of a riparian forest. Besides, plants size when transplanted to the field and, also, the conditions in which plants were produced might have an important role for survival (Mazzochini et al. *in prep.*). In fact, this factor could have caused the low survival rates found for three species in our experiment (i.e. *Handroanthus impetiginosus*, *Tapirira guianensis* and *Tabebuia roseoalba*). All individuals of these species were smaller than other species (20–50 cm smaller height, and 30 cm shorter roots) and they were produced in greenhouse conditions (under shade and with high water availability) with restricted time for acclimatization to the field conditions.

Niche complementarity, dominance effects and diversity-productivity relationship

Previous studies showed that species diversity benefits plant productivity via complementarity effects (Cardinale *et al.* 2007; Morin *et al.* 2011; Madrigal-González *et al.* 2016). Such effects are explained by an increase in resource partitioning with diversity levels (Cadotte et al. 2009; Cardinale 2011). Niche complementarity is reported to control plant productivity in many ecosystems, from grasslands to boreal, temperate and tropical forests (Paquette & Messier 2011; Chen *et al.* 2016; Craven *et al.* 2016). Nevertheless, the significance of complementarity effects for biomass production can also be context-dependent. In fact, its strength can be determined by successional stage, tree size and,

also, the scale considered in the study (Lasky *et al.* 2014; Madrigal-González *et al.* 2016). Scale-dependence might be particularly important for complementarity effects on carbon storage in tropical forests (Sullivan *et al.* 2017). This recent study was conducted at a global scale and found no general pattern of diversity affecting carbon accumulation in tropical forests, indicating that conservation strategies must be conducted at local scales for increasing carbon sequestration while conserving species diversity (Sullivan *et al.* 2017).

Here, we expected complementarity to be the mechanism driving diversity effects on plant height. Indeed, complementarity effects must be common in ecosystems under semi-arid climate regimes when comparing to selection effects. This might be due to the strong resource limitation (i.e. water and nutrient availability) and to the pulse dynamics that make resources available, thus leading plant species to adapt their fundamental niche for exploiting different parts of the same resources (Chesson *et al.* 2004; Perroni-Ventura, Montaña & García-oliva 2006; Conti & Díaz 2013). However, in some cases, when resource conditions are changed there is a decrease in complementarity effects (Craven *et al.* 2016). In these cases, enhances in productivity may reflect dominant species effects (Roscher *et al.* 2007; Sasaki & Lauenroth 2011; Winfree *et al.* 2015). In fact, dominance effects (i.e. selection effects) might be, temporarily, responsible for the patterns in plant height found in our experiment. We argue so, because of the results presented by *Piptadenia stipulacea*. This species had the tallest individuals after one year; it outperformed other species for all types of community composition and, also, for the monocultures. Such results indicate that this species can perform better during initial successional stages compared to the other plants studied here. A possible explanation would be its relatively higher growth rate that allowed the species to capitalize on resources and to produce more biomass. This pattern enabled *P. stipulacea* to establish

better than other species used in our restoration experiment (Chesson *et al.* 2004; Williams *et al.* 2006; Collins *et al.* 2014).

We observed plant height to be positively affected by the interaction between species richness and stream distance, as plants from three-species communities close to the stream were significantly taller than plants from monocultures. We also observed a decrease in plant height when comparing plants from three-species communities with those from nine-species communities. This pattern confirms the asymptotic relationship between diversity and ecosystem functioning (Cardinale *et al.* 2012; Tilman *et al.* 2014). However, since we are presenting only the initial results of a long-term experiment we cannot ensure that plants from polycultures will still be smaller than plants from communities with three species as community dynamics continue. Therefore, we argue that long-term ecosystem responses to species diversity will tend to reflect complementarity effects, thus increasing diversity importance and functioning reliability across scales and functions and, also, when facing extreme events (Cardinale *et al.* 2007; Isbell *et al.* 2011, 2015; Gamfeldt *et al.* 2013; Tilman, Isbell & Cowles 2014). The need for conducting long-term monitoring so we could be able to identify diversity complementarity effects would be even more important for BEF studies conducted in forest ecosystems, since the time scale for such ecosystem to maturate and represent the full spectrum of responses requires decades or even centuries in some special cases (Brassard *et al.* 2013).

Furthermore, the composition of our experimental communities also significantly influenced plant height. We observed four compositions to have the most important effects on plant height (three for distantly related and one for closely related communities). All of these compositions had the presence of *P. stipulacea*. This pattern

underlines the strong dominance effect of this species. These findings are consistent with previous studies evaluating the effects of plant community compositions on ecosystem functioning (Mokany, Ash & Roxburgh 2008; Mouillot *et al.* 2011). Most of the previous studies were conducted in grasslands (Brassard *et al.* 2013), however, more recently, studies found that forests structure and composition are also important drivers of the diversity-productivity relationship (Zhang, Chen & Reich 2012; Sullivan *et al.* 2017). Therefore, we can argue that, independently of the diversity levels being considered, the identity of the species can also determine diversity effects on plant growth. This pattern can be particularly important when restoring degraded forests and affect outcomes related to plant survival and establishment, thus influencing the restoration success.

Additionally, community mean growth was not affected by species richness or its interaction with stream distance. Community mean growth was used here as a proxy for community biomass production, and it is positively responding to species diversity as described by Cardinale *et al.* (2013) and Tilman *et al.* (2014). However, we found no positive correlation between species diversity and community mean growth. Such pattern can indicate that responses at the community-level require more time to be perceived. We also observed stronger composition effects on the community mean growth, with communities in which *P. stipulacea* was absent having negative or close to zero mean growth. However, since species responses to environmental factors are asynchronous, we can argue that subordinate species can compensate dominance effects in case of disturbances as predicted by the insurance hypothesis (Morin *et al.* 2014). Hence, species diversity will still be important for maintaining ecosystem functioning over time regardless the dominance effects found for *P. stipulacea* (Isbell *et al.* 2011; Gamfeldt *et al.* 2013; Morin *et al.* 2014).

Phylogenetic relatedness controlling restoration success

Plant interactions can determine the course of ecological succession in different communities (HilleRisLambers *et al.* 2012). Such influence is equally important when considering plant community dynamics in restored or regenerating systems (Gómez-Aparicio 2009; Tuck *et al.* 2016). Therefore, the inclusion of positive interactions among plants (i.e. nurse-based restoration) contributed to launch restoration projects during the past years (Gómez-Aparicio 2009; Castillo, Verdú & Valiente-Banuet 2010; Verdú, Gómez-Aparicio & Valiente-Banuet 2012). Here we assessed the effects of phylogenetic relatedness on plant height and community mean growth during the restoration of a riparian forest in northeastern Brazil. We found phylogenetic relatedness to significantly increase plant height (only when plants occurred close to the stream), but not community mean growth. Such significant interaction indicates that the positive relationship between diversity and productivity is stronger when environmental conditions are favorable. These findings are in accordance with previous studies showing that creating phylogenetically distant communities can enhance plants performance while restoring a degraded area, thus contributing to the restoration success (Castillo, Verdú & Valiente-Banuet 2010; Verdú *et al.* 2012).

However, is important to reinforce the strong effects of community composition on plant growth (discussed above), thus indicating that new species combinations should be tested in future experiments so we can identify compositions that will maximize effects of positive interactions on restoration outcomes (Verdú *et al.* 2012; Cadotte 2013). Additionally, the results presented here did not account for the effects from the imbalance of abundance among clades (IAC). This measure can be calculated as the deviation of abundances at internal nodes from a null distribution (Cadotte *et al.* 2010). High values

of IAC indicate that some clade, family or genus is disproportionally represented in the phylogenetic tree in comparison to others (Cadotte 2013). In fact, high IAC values were found to be associated with strong selection effects, indicating that this measure account for the effects of close related species (Cadotte 2013). The phylogenetic tree obtained with the species used in our experiment included nine species belonging to five different families (i.e. Anacardiaceae, Bignoniaceae, Fabaceae, Polygonaceae, Rhamnaceae). Anacardiaceae plants dominated our experimental design (three species), therefore controlling for IAC can allow us to separate the effects of phylogenetic relatedness from those of the dominant family in our experiment.

CONCLUSION

As first results of a long-term study, we observed that the inclusion of phylogenetic information while designing restoration experiments can significantly increase the likelihood of success. The relatively cheap and easy application of such approach make it a promising strategy for restoring degraded areas in semiarid environments. Since phylogenetic relatedness (in this case the phylogenetic distinctiveness among plants) can positively affect the performance of plants, we recommend the use of phylogenetically distant plant communities in order to maximize cost-effective restoration activities.

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TABLES AND FIGURES

Table 1: Native plants identified during field survey in the study site (Monte Alegre, RN, NE Brazil – Figure 1). Species' natural occurrence in the surroundings of the experimental area (transition zone from Atlantic Forest to Caatinga) was confirmed by a niche modeling analysis. Plant species are also classified according to its successional stage (i.e. ES = early successional; IS = intermediate successional; LS = late successional; NC = not classified) and adaptability to dry and wet conditions (i.e. H = hygrophytes; SH = selective hygrophytes; X = xerophytes). Successional stages were obtained from (Brandão *et al.* 2009; Oliveira *et al.* 2012; Sousa *et al.* 2014). Species nomenclature were used according to APG IV (2016).
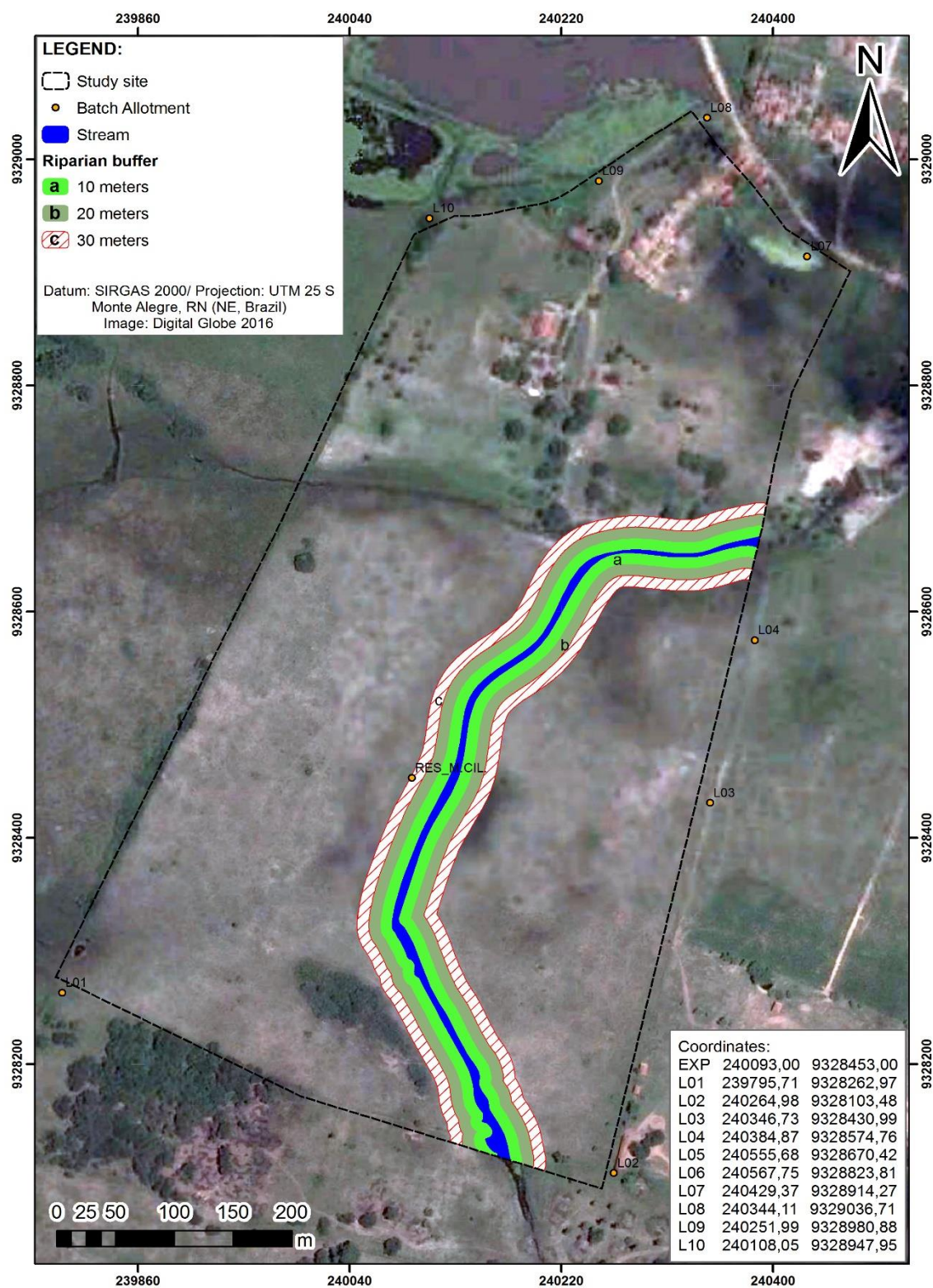
Native plant species naturally occurring in the study site				
Family	**Species**	**Common name**	**Life form**	**Successional stage**
Anacardiaceae	*Anacardium occidentale*	Cajueiro	Tree	IS / LS
Anacardiaceae	*Schinus terebinthifolius*	Pimenta-rosa	Tree	ES
Anacardiaceae	*Tapirira guianensis*	Cupiúva	Tree	ES / IS (H)
Anacardiaceae	*Myracrodruon urundeuva*	Aroeira	Tree	IS
Bignoniaceae	*Handroanthus impetiginosus*	Pau D'arco	Tree	IS
Bignoniaceae	*Tabebuia roseoalba*	Ipê-rosa	Tree	IS
Bixaceae	*Cochlospermum vitifolium*	Algodão-do-mato	Tree	LS
Burseraceae	*Commiphora leptophloeos*	Imburana	Tree	LS
Cactaceae	*Cereus jamacaru*	Cardeiro	Tree	ES (X)
Cactaceae	*Pilosocereus catingicola*	Facheiro	Tree	ES (X)
Dilleniaceae	*Curatella americana*	Lixeira	Tree	ES
Erythroxylaceae	*Erythroxylum revolutum*	--	Shrub	LS
Erythroxylaceae	*Erythroxylum* sp.	--	Shrub	NC
Euphorbiaceae	*Croton sonderianus*	Marmeleiro	Shrub	IS
Fabaceae	*Andira fraxinifolia*	Pau-angelim	Tree	IS (H)
Fabaceae	*Bauhinia pentandra*	Pata-de-vaca	Tree	ES

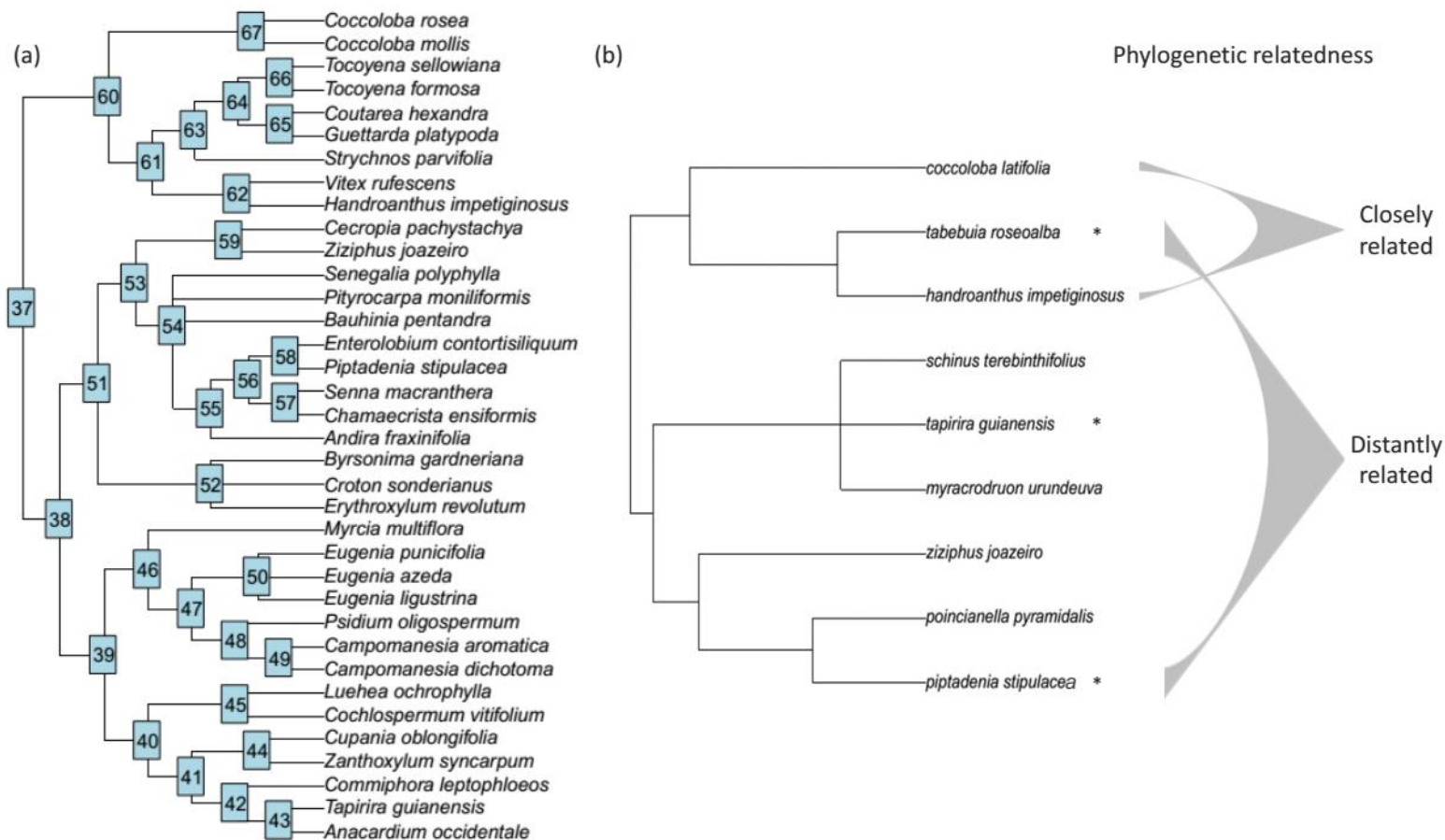|				
Fabaceae	*Chamaecrista ensiformis*	Pau-ferro	Tree	ES / IS
Fabaceae	*Piptadenia stipulacea*	Jurema-branca	Tree	ES / IS
Fabaceae	*Pityrocarpa moniliformis*	Catanduva	Tree	ES / IS
Fabaceae	*Poincianella pyramidalis*	Catingueira	Tree	ES / IS
Fabaceae	*Senegalia polyphylla*	--	Tree	ES
Fabaceae	*Senna macranthera*	--	Shrub	ES
Lamiaceae	*Vitex rufescens*	Maria-preta	Tree	IS
Loganiaceae	*Strychnos parvifolia*	--	Shrub	ES / IS
Malpighiaceae	*Byrsonima gardneriana*	Murici	Tree	IS
Malvaceae	*Luehea ochrophylla*	--	Tree	NC
Myrtaceae	*Campomanesia dichotoma*	Guabiraba	Shrub	LS
Myrtaceae	*Campomanesia aromatica*	--	Shrub	LS
Myrtaceae	*Eugenia ligustrina*	--	Shrub	ES / IS
Myrtaceae	*Eugenia azeda*	Ubaia-azeda	Shrub	ES / IS
Myrtaceae	*Eugenia punicifolia*	--	Shrub	ES / IS
Myrtaceae	*Myrcia multiflora*	Pau-mulato	Shrub	IS / LS
Myrtaceae	Myrtaceae sp.	--	Shrub	NC
Myrtaceae	*Psidium oligospermum*	Araçá	Shrub	IS / LS
Olacaceae	*Ximenia americana*	Ameixa	Shrub	ES / IS
Polygonaceae	*Coccoloba mollis*	Cauaçú	Tree	IS
Polygonaceae	*Coccoloba latifolia*	Cauaçú	Tree	IS
Polygonaceae	*Coccoloba rosea*	Cauaçú	Tree	IS
Rhamnaceae	*Ziziphus joazeiro*	Juazeiro	Tree	ES / IS (SH)
Rubiaceae	*Coutarea hexandra*	--	Shrub	NC
Rubiaceae	*Guettarda platypoda*	--	Tree	IS / LS
Rubiaceae	*Tocoyena formosa*	Jenipapo-bravo	Tree	NC
Rubiaceae	*Tocoyena sellowiana*	Jenipapo-bravo	Tree	NC
Rutaceae	*Zanthoxylum syncarpum*	--	Tree	ES
Sapindaceae	*Cupania oblongifolia*	--	Tree	IS
Simaroubaceae	*Simarouba* sp.	Cajarana	Tree	NC
Urticaceae	*Cecropia pachystachya*	Embaúba	Tree	ES

Table 2: Design of the restoration experiment implemented in Monte Alegre (RN, Brazil), including treatments, number of combinations and plots. The experiment was established along 800 m on both sides of a perennial stream manipulating five levels of diversity: i. zero species (control treatment), ii. one species (monocultures), iii. three closely related species (plant species from the same branches in the phylogenetic tree), iv. Distantly related species (plant species from different branches in the phylogenetic tree), and v. nine plant species (polycultures).

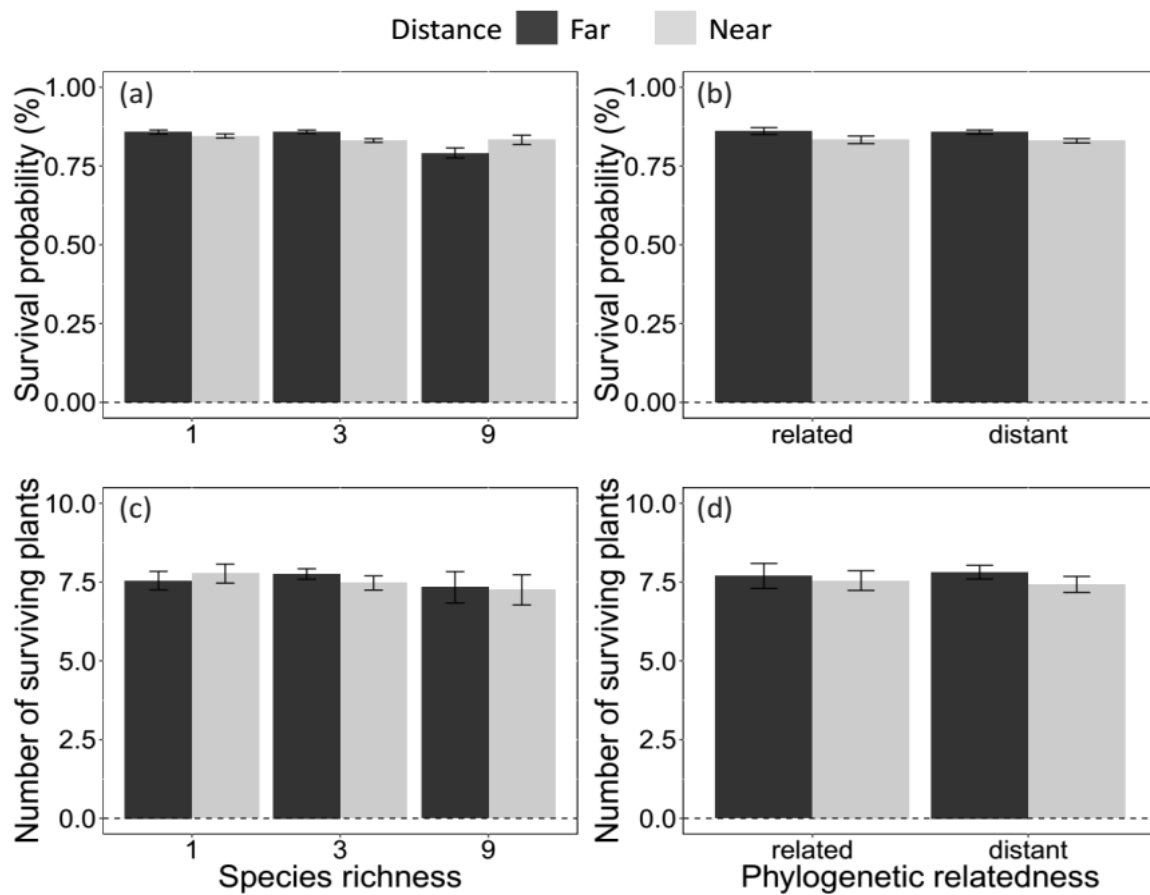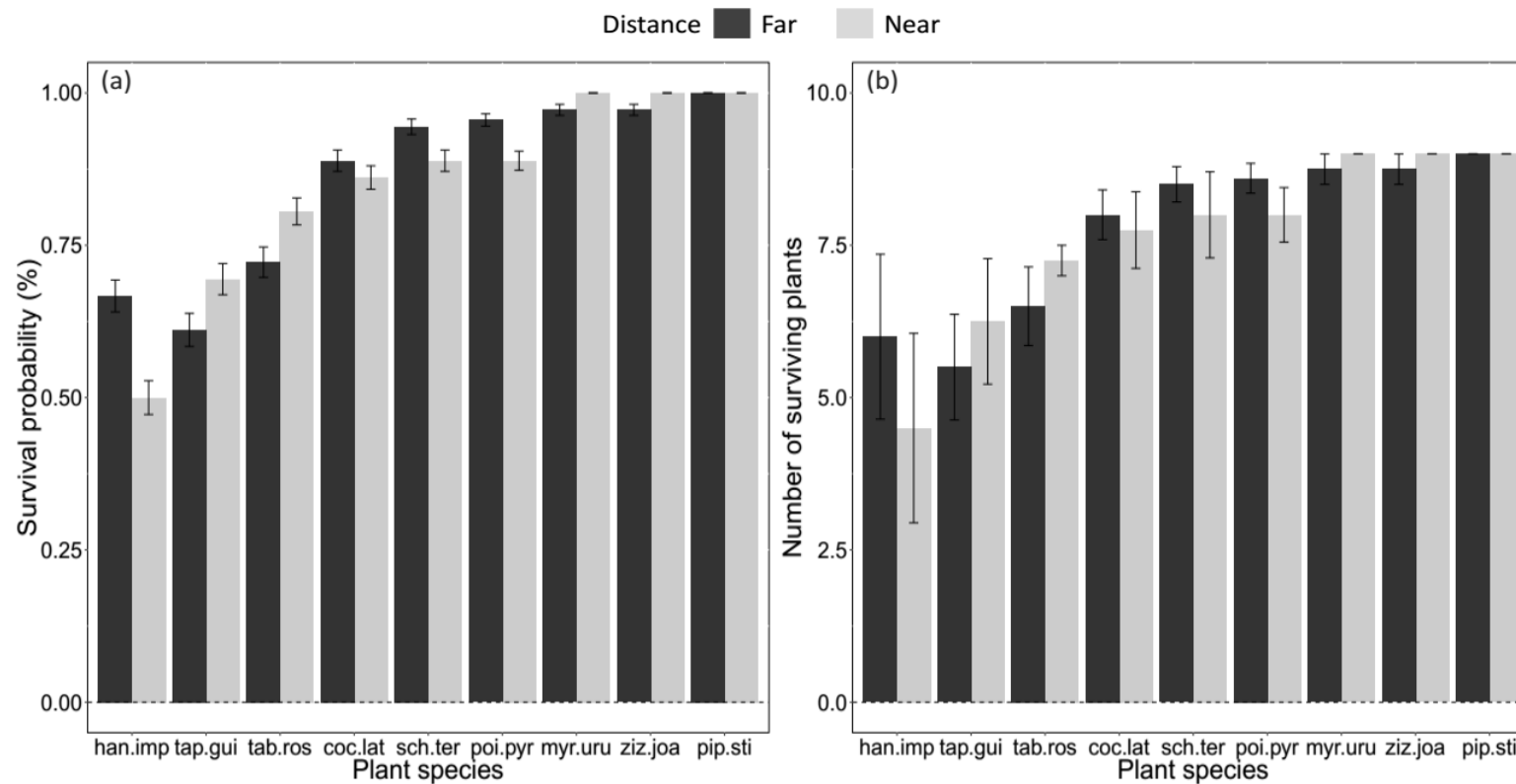| Treatment	Composition *	Replicates =	N Plots
0 spp. Control	1	4	4
1 spp. Monoculture	9	4	36
3 spp. Closely related	3	4	12
3 spp. Distantly related	9	4	36
9 spp. Polyculture	1	8	8
		Total number of plots	**96**

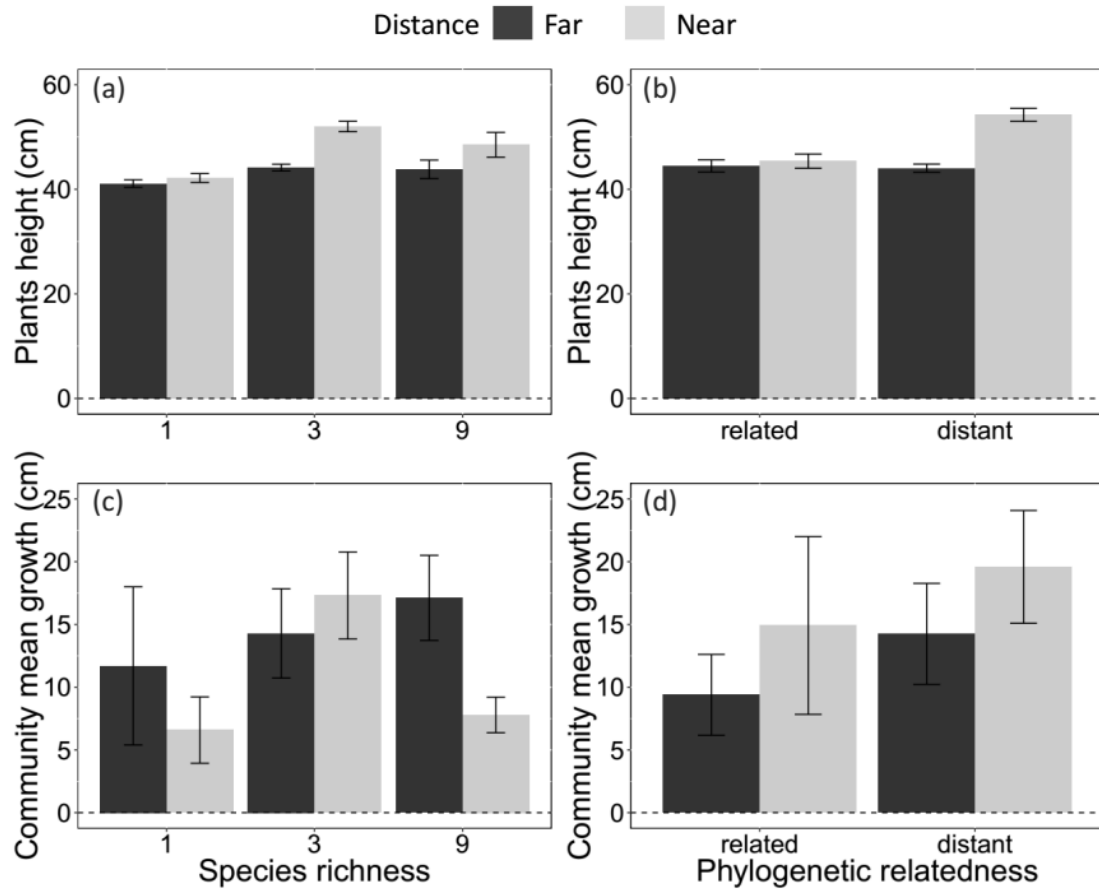**Figure 1:** Map of the study site in Monte Alegre (RN, Brazil).

Figure 2: Phylogenetic trees for plant species native from Atlantic Forest and Caatinga (NE, Brazil) and naturally occurring at the experimental site surroundings (**a**) and for the nine species randomly selected for composing our experimental communities (**b**).
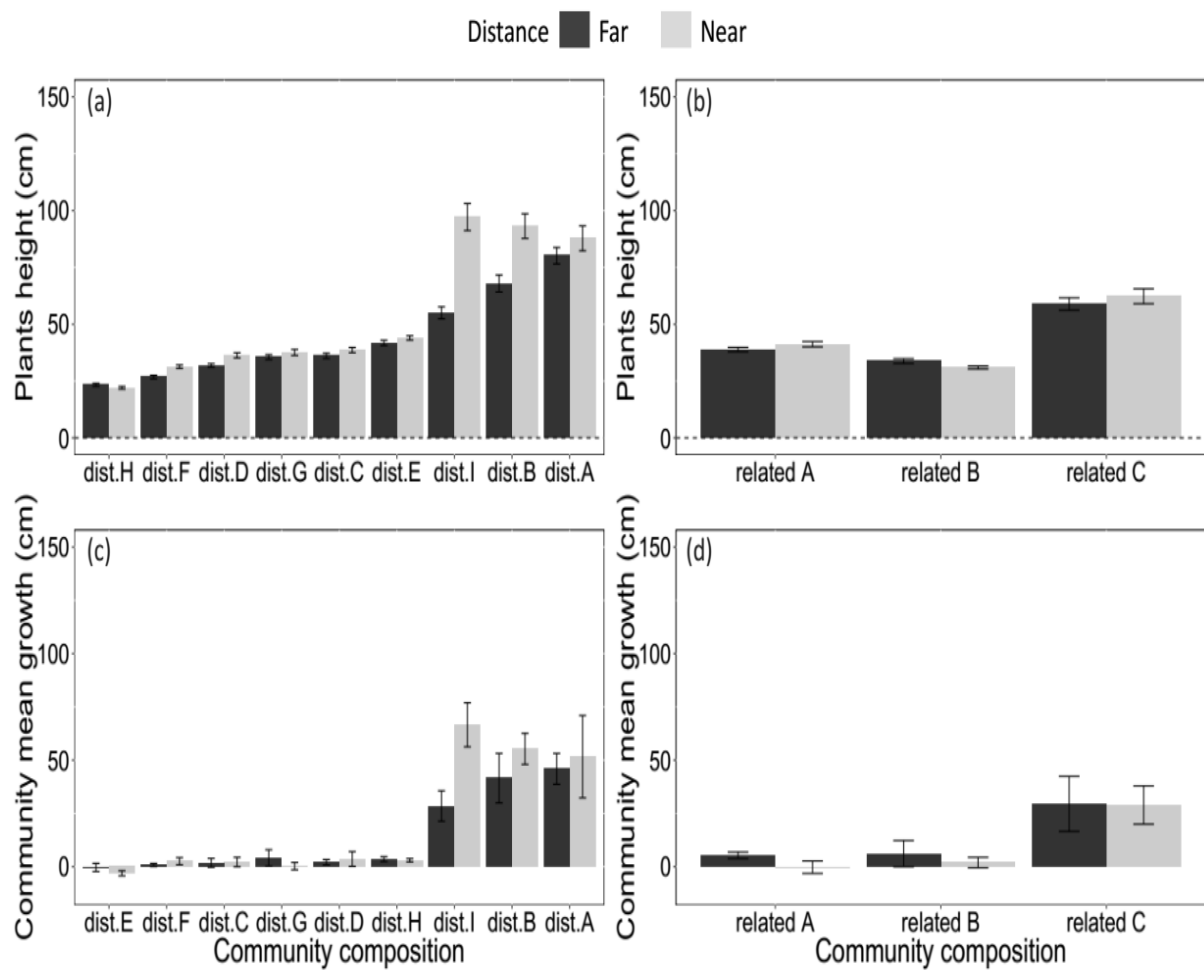
Figure 3: Effects of the distance from the stream, of the species richness and the phylogenetic relatedness on plant survival probability (**a** and **b**) and on the number of surviving plants (**c** and **d**). Barplots show mean values (±SE) for plant survival one year after the restoration experiment was established in a riparian forest in northeastern, Brazil. Survival probability was negatively affected by the proximity with the river, while diversity treatments had no effect on both, the probability, or the number of surviving plants.

Figure 4: Survival probability (**a**) and the number of surviving plants (**b**) one year after the restoration experiment was implemented in a riparian forest in northeastern, Brazil. Barplots show the mean values (±SE) for plant survival separated by all the species used in the experiment. No statistical analysis was conducted for assessing species-specific probabilities of survival and its interaction with the diversity treatments manipulated in the experiment.

Figure 5: Effects of the distance from the stream, of the species richness and the phylogenetic relatedness on plant height (**a** and **b**) and on the community mean growth (**c** and **d**). Barplots show mean values (±SE) for plant growth one year after the restoration experiment was implemented. Plant height was positively affected by the interaction between species richness and the distance from the stream and, also, by the interaction between phylogenetic relatedness and the distance from the stream. Community mean growth was, in turn, not significantly influenced by any of the treatments.

Figure 6: Effects of the distance from the stream and of the community composition on plant height (**a** and **b**) and on the community mean growth (**c** and **d**). Barplots show mean values (±SE) for plant height in communities composed by distantly (**a**) or closely (**b**) related species and, also, for the community mean growth in distant (**c**) and related communities (**d**). Plant species forming each one of the distantly or closely related communities are: relat.A – *Coccoloba latifolia*, *Tabebuia roseoalba* and *Handroanthus impetiginosus*; relat.B – *Schinus terebinthifolius*, *Tapirira guianensis* and *Myracrodruon urundeuva*; and relat.C – *Ziziphus joazeiro*, *Poincianella pyramidalis* and *Piptadenia stipulacea*; dist.A – *Tabebuia roseoalba*, *Schinus terebinthifolius* and *Piptadenia stipulacea*; dist.B – *Tabebuia* roseoalba, *Tapirira guianensis* and *Piptadenia stipulacea*; dist.C – *Coccoloba latifolia*, *Schinus terebinthifolius* and

Poincianella pyramidalis; dist.D – *Tabebuia roseoalba*, *Myracrodruon urundeuva* and *Ziziphus joazeiro*; dist.E – *Coccoloba latifolia*, *Tapirira guianensis* and *Ziziphus joazeiro*; dist.F – *Handroanthus impetiginosus*, *Myracrodruon urundeuva* and *Ziziphus joazeiro*; dist.G – *Coccoloba latifolia, Tapirira guianensis* and *Poincianella pyramidalis*; dist.H – *Handroanthus impetiginosus*, *Myracrodruon urundeuva* and *Poincianella pyramidalis*; and dist.I – *Handroanthus impetiginosus*, *Schinus terebinthifolius* and *Piptadenia stipulacea* [species nomenclature follows APG IV (2016)].

Figure 7: Plant height (**a**) and the community mean growth (**b**) one year after the restoration experiment was implemented in a riparian forest in northeastern, Brazil. Barplots show the mean values (± SE) for plant growth separated by all the species used in the experiment. Linear mixed-effects model revealed a strong dominance effect of *Piptadenia stipulacea* on plant height. Community mean growth exhibited the same pattern, despite no statistical significance was detected.

Chapter 4

Functional diversity and invasive species moderate soil water quality and soil fertility in grassland mesocosms[1][2]

Abstract – Ecosystem functioning can be positively affected by plant functional diversity, whereas compromised by invasive alien plants. We performed a mesocosm study to test if functional diversity of native grassland plants could constrain the impact of an invasive alien plant on soil nutrient and plant community biomass. The factorial experiment included three levels of functional diversity, and two levels of plant invasion (with and without *Solidago gigantea*). Response variables were soil nutrient, soil water nutrient and aboveground biomass. We applied a structural equation model to evaluate if diversity effects directly control soil nutrient or indirectly via plant biomass and soil water quality. Functional diversity indirectly affected soil and soil water nutrient via plant biomass, soil water pH and conductivity, whereas the invasive species negatively influenced native plant biomass and disrupts the effects of diversity on nutrients. We found little evidence for functional diversity preventing plant invasions in restored grasslands. Also, long-term functioning of grasslands may be compromised by invasive plants, since they modify plant biomass, soil water quality and nutrient dynamics. Restoration of grasslands should include a higher variety of plant traits in attempt to reduce the successful establishment of invasive plants and to ensure ecosystem functioning.

Key words: *Aboveground biomass, biotic resistance, competition, structural equation model, soil water nutrient, Solidago gigantea*

INTRODUCTION

Studies showed that diversity measurements other than the usual species number approach could be better predictors of ecosystem functioning (de Bello *et al.* 2009; Lavorel *et al.* 2011; Balvanera *et al.* 2014). In fact, plant functional diversity or the number of functional groups composing a given plant community can positively affect nutrient cycling and storage (Fornara & Tilman 2008; Conti & Díaz 2013), increase soil fertility (Burylo *et al.* 2012; Sutton-Grier, Wright & Richardson 2013), and enhance plant productivity (Roscher *et al.* 2012; Zhu, Jiang & Zhang 2016). The control of nutrient fluxes is an important ecosystem function and it is, directly and/or indirectly, related to plant traits controlling nutrient acquisition, above- and below-ground biomass production (Bardgett, Mommer & De Vries 2014). Nutrient fluxes are, in turn, intrinsically related to soil and water quality as well as plant productivity (Cardinale *et al.* 2012; Balvanera *et al.* 2014). Such function is frequently compromised by the impacts of invasive plant species (Ehrenfeld 2010; Pyšek *et al.* 2012).

Previous results showed that, when plant diversity cannot prevent invasion, it can at least reduce growth and spread of invasive populations (Levine *et al.* 2004). Although plant functional diversity can increase biotic resistance of communities by exhaustively depleting limiting resources as a result of higher biomass production (Brym *et al.* 2011; Byun, de Blois & Brisson 2013), invasive plants can still compromise ecosystem functioning in invaded communities, both in short and long term (Elgersma *et al.* 2011; Pyšek *et al.* 2012). Invasive species reduce native plant biomass by competition (Vilà et al., 2011; Vilà and Weiner, 2004), and alter nutrient cycling by increasing soil nutrient availability, e.g. due to higher phosphorus turnover (Chapuis-Lardy *et al.* 2006; Herr *et al.* 2007). Additionally, they can indirectly decrease nutrient uptake of native plants

(Weidenhamer & Callaway 2010) that could result in increased leaching losses. Therefore, affecting nutrient balance and soil productivity in invaded terrestrial ecosystems in the long term (Ehrenfeld 2010; Corbin & D'Antonio 2011).

Several studies indicate that the effects of invasive alien species on ecosystem functioning might depend on site conditions instead of only relying on the invader characteristics (Vicente *et al.* 2013). In many regions, changes in land use have altered grassland community composition leading to alien plant invasion (Habel *et al.* 2013; Diekmann *et al.* 2014). Therefore, controlled experiments with model grasslands are needed for improving restoration methods and for designing plant communities that would be most efficient in restoring invaded grasslands (Daehler 2003; Scharfy *et al.* 2010). Such experiments should test different functional diversity levels of seed mixtures, and could identify species that reduce plant invasions (Staab *et al.* 2015).

The invasive perennial plant, *Solidago gigantea* (Asteraceae), originally native from North America, is a widely spread and successful invader in central Europe (Jakobs, Weber & Edwards 2004; Vanderhoeven *et al.* 2006; Herr *et al.* 2007). The species invades a broad range of habitats in Europe, from drylands to wetlands and from nutrient-poor to nutrient-rich sites (Güsewell et al., 2006; Scharfy et al., 2010). *S. gigantea* also successfully invades restored grasslands, while the species composition in such systems can be determined by species dispersion, the availability of niches for being occupied and its invasibility resistance (Poschlod *et al.* 1998; Funk *et al.* 2008b). Therefore, we might expect *S. gigantea* to colonize restored grasslands where the invader could benefit from the susceptibility of the environment, such as recent disturbance, presence of non-local species and lower diversity of traits (Didham et al., 2007; Funk et al., 2008; Staab et al., 2015).

Ultimately, the capacity of invasive plants to produce more biomass than native species could be related to the successful invasion of plant communities (Laungani & Knops 2009). For achieving this, the invader should change nutrient conditions in the invaded sites, thus limiting native plants growth while increasing its own biomass production. However, the influence of plant functional diversity on ecosystem functioning can buffer such impacts (Levine *et al.* 2004; Byun *et al.* 2013). Increased biotic resistance would be expected due to strong competition and depletion of limiting resources that would otherwise be used by the invader (Brym *et al.* 2011; Byun *et al.* 2013). Nevertheless, although *S. gigantea* can be more efficient in capturing available resources than native plant species (Scharfy *et al.* 2010), it can also significantly reduce native plants biomass. Hence, invaded communities would have overall less biomass and, in turn, more nutrient could be lost by leaching.

Based on this, we designed a mesocosm experiment manipulating levels of functional diversity (represented by the number of functional groups making up our experimental communities) and invasion by *S. gigantea*. We tested if grassland plant communities with a higher number of functional groups would be more resistant to impacts of invasive plants on productivity and soil fertility. Therefore, we hypothesized: **i.** Functional diversity will increase native plant biomass by complementarity and, consequently, increasing biotic resistance of grassland communities and reducing nutrient leaching by increasing its retention in the plant-soil system. **ii.** Invasion by *S. gigantea* would increase nutrient leaching loss and reduce soil nutrient accumulation. The responses of functionally diverse communities would contribute to soil fertility, thus moderating the impacts of invasive plants on ecosystem functioning.

Besides increasing biomass production of native plants, functional diversity would reduce soil acidity (higher pH) and soil dissolved salts (lower conductivity). These factors would, in turn, have stronger effects on soil and soil water nutrient. However, invasive plants can alter pH values and phosphorus availability in invaded soils (Herr et al., 2007; Scharfy et al., 2009). Therefore, we investigated if the effects of plant functional diversity and *S. gigantea* would be either direct on soil and soil water quality or indirectly mediated by plant aboveground biomass and soil water micronutrients availability, represented by measurements of pH and conductivity. Finally, we evaluated if the direct and indirect effects of functional diversity on nutrients are negatively affected by *S. gigantea*. In other words, we investigated if the control exerted by plant diversity would remain the same or would be disrupted when comparing invaded and non-invaded communities.

MATERIAL AND METHODS

Plant traits selection and functional groups

Functional group classification was performed according to Yannelli et al. (2017) and resulted in three different functional groups (FG 1–3; Figure S1). We used trait information from a set of 54 native grassland species (Table S1). We selected eight traits found to be good proxies for species dispersal, establishment success, growth, persistence and competitive ability (Westoby et al., 2002; Cornelissen et al., 2003; Funk et al., 2008), i.e. specific leaf area (SLA; $g\ cm^{-2}$), leaf dry matter (mg), life form, shoot morphology, morphology of other vegetative organs, canopy height at maturity (m), seed mass (g) and longevity. While SLA, canopy height at maturity and seed mass can be correlated with

competition (Garnier & Navas 2012) and invasiveness (Hamilton *et al.* 2005); longevity (i.e. annual or perennial plants) can be related to temporal niche overlap (Yannelli *et al.* 2017) or temporal resources acquisition (Ebeling *et al.* 2014). Leaf dry matter, in turn, can account for rates of nutrient mineralization (Cornwell *et al.* 2008; Pérez-Harguindeguy *et al.* 2013). Furthermore, we consider that morphological traits can be associated to interference competition and to water and nutrient trapping. Functional trait information was obtained from the BiolFlor (Klotz et al., 2002) and LEDA databases (Kleyer *et al.* 2008). Details on how functional groups were clustered can be found in the supplementary material (Appendix S1, Table S1, Figure S1).

Experimental design

The mesocosm experiment started in late November 2013 and ran over 16 weeks within the Centre of Greenhouses and Laboratories Dürnast, at the School of Life Sciences Weihenstephan of the Technical University of Munich (48°24'N, 11°41'E). The experiment was conducted in a heated greenhouse using plastic trays with an area of 0.14 m^2 and 0.0098 m^3 of volume. The pots were filled with 9.8 l of gardening soil consisting in a mixture of peat, quartz sand and clay powder (2:1:1), arranged within five blocks. Artificial light was provided during 16 h per day (4–15 ± 0.5 lux); daily temperatures were 16–21 °C. The trays were watered every two days using tap water with the following anion content, i.e. 38.7 µg l^{-1} chloride, 0.0001 µg l^{-1} nitrate, 15.9 µg l^{-1} phosphate and 28.9 µg l^{-1} sulfate.

The experimental design was full factorial and consisted of eight treatment combinations: communities with three levels of functional diversity (FG 1–3), with and

without the invasive alien species *Solidago gigantea* (+S, –S), communities with only *S. gigantea* plants (+S) and a control (C) treatment, i.e. bare soil. The native grassland communities were designed by randomly selecting nine species from the regional pool of native plants according to the number of functional groups in each treatment. The functional group composition was also selected randomly for each replicate. If two species from the same genus were selected by chance, one was replaced by another species from the same group (see Appendix S1 for plant community composition). The sowing was carried out at a density of 3 g m^{-2} for the native target community and 1 g m^{-2} for *S. gigantea.* Densities for the native species correspond to common practice in grassland restoration for central Europe (Kiehl et al., 2010). All treatment combinations were replicated five times, with a total of 40 trays. In this study, functional diversity refers to the number of functional groups composing each community.

Measurements

Treatment effects were evaluated by taking samples of soil, leachate water and soil water during the experimental period. A mixed soil sample from potting substrate was collected at the beginning of the experiment to establish the initial conditions. Five subsurface soil samples (0–5 cm depth) were extracted from each mesocosm combination 5 weeks after sowing and mixed up to a single bulk. One sample was taken at each corner and one sample at the center of the mesocosms as suggested by Vanderhoeven et al. (2006). After collection, all soil samples were kept frozen at –4 °C for 3 weeks when they were dried at 75 °C for 48 hours, before preparing the samples for analysis. The analysis was performed by taking 5-g subsamples from the collected soil and diluting them in 100 ml of distilled water (1:20 dilution), from this 10 ml of the solution was centrifuged during

a 10-minute period. Furthermore, 8 ml from the centrifuged soil solutions was pipetted into plastic polyvials and frozen again for later analysis. Soil nutrient loss or accumulation resulting from the diversity and/or invasive species effects in each mesocosm was determined by reducing the final concentrations (5 weeks after sowing) from the initial concentrations, obtained at the beginning of the experimental period.

Leachate water samples were collected 7 weeks after sowing. We watered the plant communities until field capacity was exceed (2.1 l tap water) and collected the samples after 20 min of water accumulation. Leachate samples were filtered with a glass-fiber filter and 8 ml from each replicate were stored at –4 °C for further analyses. Additionally, one water sample (taken directly from the tap) was collected before watering the plant communities to determine water ion concentrations. For each sample, conductivity and pH values were measured by a pH meter (pH 196 – WTW). These leachate samples were collected after passing through the root system of the plant communities. While conductivity can be used as a proxy for micronutrients availability, leachate water pH represents the potential for ions exchange between soil and plants.

Soil water samples for each treatment combination were collected 8 weeks after sowing using suction cups (2.5 mm diameter mini plastic suction cups – ecoTech GmbH). Soil water was collected during a 70-hour period with the assistance of a vacuum pump. These samples were also analyzed for their ions content. For soil and soil water samples, the contents of ammonium, calcium, chloride, magnesium, phosphate, potassium, sodium and sulfate were determined using the Dionex ICS-1600 Ion Chromatography System (Thermo Fisher Scientific Inc.).

Native and *S. gigantea* plants emergence were evaluated one week after sowing. A rectangular grid (30.5 X 46 cm) divided by three columns and five rows (15 plots) was

placed above the trays and five plots of this grid were randomly selected. We then counted the number of emerged plants for each one of the selected plots. Competition effects among plants were evaluated 16 weeks after seed sowing by collecting aboveground biomass of both native and invasive species. This was done by harvesting all aboveground plants (from 1 cm above soil surface), then placing native and invasive species in different paper bags. All samples were dried at 65 °C during 48 hours and weighted immediately after this period.

Statistical analysis

A linear mixed-effects model with block and species composition as random effects and the likelihood ratio test (LRT) implemented by the package lme4 (Bates et al., 2015) were applied to test for effects of functional diversity, invasive species presence and the interaction between them on native plants aboveground biomass and emergence (Appendix S4, Figure S8). Functional diversity was converted into a numeric variable and log-transformed ($\log(x+1)$) before running the linear mixed-effects models. Native plants biomass values were also log-transformed to fulfill the normality assumptions for the analysis. The effect of the different levels of functional diversity on biotic resistance was tested against *S. gigantea* aboveground biomass (log-transformed values) and emergence (Appendix S4, Figure S8) by applying a linear mixed-effects model with block and species composition as random terms using package nlme under the version 3.1-128 in R (Pinheiro et al., 2016).

Finally, to test if effects of functional diversity and *S. gigantea* on resource capture of the plant communities were direct or indirect, we calculated a structural equation model

(SEM) according to the package piecewiseSEM in R (Lefcheck 2016). We evaluated if diversity effects would cascade through plants biomass, water pH and conductivity before it affects soil and soil water nutrient. This analysis allows statistically testing the causal relationships among variables by multilevel path models (Shipley 2009; Oliveira *et al.* 2016). SEM models were implemented using mixed-effects structure of analysis (LME) to incorporate block as a random effect (Lefcheck 2016). Statistical analyses were performed using R Statistical Computing version 3.3.1 (R Development Core Team, 2015).

RESULTS

Effects on plant emergence and aboveground biomass

Emergence of native plants was negatively affected by *S. gigantea* presence, but the increasing levels of functional diversity did not influence invasive plant emergence by competition. More information can be found within the supplementary material (Appendix S4, Figure S8).

Aboveground biomass of native plants was not influenced by the levels of functional diversity ($\chi^2 = 0.2$, df = 5, p > 0.05). Still, a positive trend was found in terms of biomass production, and native plants had in average 22% more aboveground biomass in more functionally diverse communities. On the other hand, native plants biomass was negatively affected by the presence of *S. gigantea* ($\chi^2 = 12.2$, df = 5, p ≤ 0.01). In fact, the presence of the invasive species reduced aboveground biomass of native plants by 68% across all treatments (Figure 1a). The opposite way of the competitive interaction was not observed. Despite no statistical significance, there was a positive trend for *S.*

gigantea aboveground biomass to increase with increasing the levels of functional diversity (F = 1.7, df = 14, p > 0.05, Figure 1b).

Direct and indirect effects of functional diversity and S. gigantea *on nutrients*

Structural equation models indicated that functional diversity controlled soil and soil water nutrient both, directly (only for soil nutrient) and indirectly via plant biomass, pH and conductivity (Figures 2 and 3), although direct effects of functional diversity on aboveground biomass ($\beta = 0.09$, p > 0.05) and water pH ($\beta = 0.15$, p > 0.05) were weak. Contrastingly, aboveground biomass had positive effects on water pH ($\beta = 0.85$, p ≤ 0.001), while water pH had negative effects on water conductivity ($\beta = -0.99$, p ≤ 0.05). Moreover, *S. gigantea* altered the effects of functional diversity, water pH and conductivity on nutrients (Figures 4c, d, 5c, d). *S. gigantea* apparently reduced the strength of aboveground biomass effects on water pH ($\beta = 0.84$, p ≤ 0.001), but increased pH effects on conductivity ($\beta = -1.80$, p ≤ 0.001). In the presence of *S. gigantea*, there was also a strong positive effect of aboveground biomass on conductivity ($\beta = 1.20$, p ≤ 0.01).

In non-invaded communities, functional diversity did not directly affect soil water nutrient (Figure 2). Aboveground biomass had negative effects on chloride ($\beta = -1.12$, p ≤ 0.05), while water pH and conductivity had strong positive effects on the availability of the same micronutrient ($\beta = 1.03$, p ≤ 0.05; $\beta = 0.87$, p ≤ 0.01, respectively). Also, water pH had negative effects on phosphate ($\beta = -0.73$, p ≤ 0.05), while conductivity had marginally positive effects on sulfate ($\beta = 0.50$, p > 0.05, Figure 2a). Additionally, water pH had marginally negatively affected calcium availability ($\beta = -0.85$, p > 0.05), while

conductivity marginally positively affected sodium availability ($\beta = 0.64$, $p > 0.05$, Figure 2b). For invaded communities, none of the previous effects on chloride, phosphate or sulfate were detected (Figure 2c). On the other hand, presence of *S. gigantea* created a negative effect of aboveground biomass on potassium ($\beta = -1.13$, $p \leq 0.05$) and a positive effect of conductivity on ammonium concentrations ($\beta = 0.74$, $p \leq 0.05$) showing that *S. gigantea* can completely change native plant communities control over soil water nutrient (Figure 2d).

Nutrients stocked in the soil were directly affected by functional diversity in non-invaded communities, both for anions and cations (Figure 3). Functional diversity positively affected phosphate ($\beta = 0.61$, $p \leq 0.05$) and marginally positively affected sulfate concentrations in the soil ($\beta = 0.49$, $p > 0.05$; Figure 3a), while water pH had marginally positive effects on chloride ($\beta = 1.00$, $p > 0.05$, Figure 3a). Ammonium in the soil was, in turn, marginally negatively affected by functional diversity ($\beta = -0.42$, $p > 0.05$; Figure 3b). For invaded communities, there was no effect of functional diversity on the concentration of chloride, phosphate or sulfate in the soil (Figure 3c). In turn, conductivity negatively affected chloride ($\beta = -0.71$, $p \leq 0.05$) and marginally negatively affect sulfate in the soil ($\beta = -0.63$, $p > 0.05$). Most importantly, *S. gigantea* changed the signal for the effect of functional diversity on ammonium concentrations, from marginally negative in non-invaded communities to significantly positive in the invaded ones ($\beta = 0.34$, $p \leq 0.05$). Also, there was a trend for aboveground biomass positively affecting calcium in the soil of the mesocosms ($\beta = 1.00$, $p > 0.05$, Figure 3d).

DISCUSSION

Effects on plant emergence and aboveground biomass

We found no support for the idea that plant functional diversity could prevent invasion by increasing competitive interaction with invasive plants or by constraining invasive plant biomass production due to an exhaustive use of the limiting resources (Levine et al., 2004; Brym et al., 2011; Zeiter and Stampfli, 2012). In fact, we showed that the presence of *S. gigantea* negatively affects native plants biomass, independently of functional diversity levels. Competitive effects of invasive plants on native species can are stronger than the effects of native plants on the invader (Vilà et al., 2004; Vilà and Weiner, 2004). Our results confirm these observations, since *S. gigantea* negatively affected native plants, but the opposite was not observed. Therefore, we argue that *S. gigantea* is a stronger competitor than native grassland plant species. The same pattern was observed for plant emergence. Native emergence was compromised by the presence of the invasive plants, but the functional diversity of native plants in the invaded communities could not reduce *S. gigantea* emergence, despite the slight trend of reduction in the communities with higher functional diversity levels (Appendix S3, Figure S6). In fact, previous studies found that invasive plants can emerge earlier and alter the conditions in the invaded soils, thus effectively preventing native plants emergence and recruitment rates (Davis, Grime & Thompson 2000; Han *et al.* 2012; Gooden *et al.* 2014).

S. gigantea can suppress native species due to higher aboveground biomass production and higher P uptake which can create positive feedbacks for further invasions (Herr *et al.* 2007; Scharfy *et al.* 2009; Weidenhamer & Callaway 2010). Here, communities with higher functional diversity levels (i.e. number of functional groups) were not able to prevent *S. gigantea* successful invasion. Although native and invasive alien plants were sown with different seed densities (3 g m^{-2} and 1 g m^{-2}, respectively),

we found native plants average biomass to not differ from *S. gigantea* for invaded communities with one or two levels of functional diversity (FG1: 4.9 g for native and 5.8 g for *S. gigantea*; FG2: 9.6 g for native and 7.8 g for *S. gigantea*). Our results agree with other studies showing that *S. gigantea* produce more biomass than native species in invaded sites (Jakobs *et al.* 2004; Güsewell, Jakobs & Weber 2006; Vanderhoeven *et al.* 2006).

Lower production of biomass for native plants in communities with higher functional diversity might reflect a stronger competition between native species, or/and that *S. gigantea* is occupying an empty niche (Brym et al. 2011). Nevertheless, the hump-shaped pattern (i.e. reduced biomass production when comparing communities composed by two functional groups with those composed by three functional groups) observed for native plants aboveground biomass in both, invaded and non-invaded communities, can be also explained by the nutrient limitation in our mesocosms (Yannelli et al., 2017). While the asymptotic productivity-diversity relationship observed in nature can be explained by functional redundancy among plant species composing a given community (Balvanera et al., 2014; Cardinale et al., 2012), in our experiment such pattern reflects mostly the artificial conditions of the mesocosms. Though our functional diversity treatments were not able to increase biotic resistance to prevent invasions of *S. gigantea*, there is ample evidence in the literature that justifies the inclusion of functional diversity measures in grassland restoration (Funk et al. 2008; Byun et al. 2013).

Direct and indirect effects of functional diversity and S. gigantea *on nutrients*

Our results indicate that plant functional diversity decreases phosphate and potassium concentrations in the soil water solution, potentially reducing exportation rates and leaching losses of such nutrients (Appendix S2, Figure S4). Such a trend is consistent with other studies showing the complementarity effects of plant diversity on nutrient use and reinforces the importance of restoring functional diversity in degraded grasslands (Funk *et al.* 2008b; Clark *et al.* 2012). Additionally, plant functional diversity appears to contribute to higher phosphate and sulfate concentrations in the soil of the experimental communities (Appendix S2, Figure S5). This pattern might occur because functional diversity results in different strategies for resources acquisition (spatially and temporally) which is fundamental to increase nutrient retention and storage and to sustain soil quality (De Bello et al., 2010; Burylo et al., 2012; Sutton-Grier et al., 2013).

We found that invasion of *S. gigantea* can be mediated by its impact on soil nutrient. The structural equation models showed that functional diversity does not directly control nutrients in soil water. Instead, nutrients were indirectly controlled via the effects of aboveground biomass on water pH and conductivity. This is consistent with previous studies showing plants to control nutrient availability (i.e. by CO_2 inputs) which, in turn, affect pH and soil cationic exchange (Chapuis-Lardy *et al.* 2006; Vanderhoeven *et al.* 2006). In non-invaded communities, aboveground biomass decreased chloride concentrations, while water pH and conductivity increased. Several studies reported that plants can increase soil pH values which will increase phosphate availability (Scharfy *et al.* 2009; Weidenhamer & Callaway 2010). However, we found a different pattern with functional diversity increasing pH values but reducing phosphate availability.

Presence of *S. gigantea* caused direct and indirect effects on soil water nutrient. It seems that this invasive species can rely on its effects on potassium and ammonium

availability (Wang *et al.* 2015). Indeed, we observed that this species reduced potassium concentrations and seems to compromise native plant biomass production. On the other hand, *S. gigantea* increased ammonium which might affect native plant root production (Liu et al. 2013). Invasive plants were shown to perform better when the soil of the invaded sites is rich in nitrogen (Funk & Vitousek 2007; Wang *et al.* 2015). In fact, one of the mechanisms by which invasive plants increase its invasion success is by affecting nitrogen concentrations in the soil (Weidenhamer and Callaway 2010; Wang et al. 2015). Despite the low values observed, the increased soil ammonium concentrations resulting from invasion would have a more pronounced negative effect on native plants than on invasive ones, since native plants might not be able to cope with increased levels of ammonium.

Soil nutrient showed different patterns than nutrients in soil water. In non-invaded communities, functional diversity directly increased phosphate in the soil, possible through changes in pH and roots exudation (Herr *et al.* 2007; Scharfy *et al.* 2009), while ammonium suffered direct reductions. In invaded communities, however, the interaction between native plants and *S. gigantea* resulted in less consumption of ammonium by plants, increasing its concentrations in the soil of the mesocosms. Thus, the invasive species altered soil nutrient potentially favoring further invasions (Ehrenfeld 2010; Weidenhamer & Callaway 2010; Wang *et al.* 2015).

Our work shows the initial impacts (i.e. short-term effects) of plant invasions on grassland communities. Nevertheless, scientific literature has demonstrated that short-term and long-term impacts of invasive alien species on ecosystem functioning are different. In fact, studies report invasive plants short-term effects to ecosystems as being less pronounced than long-term effects (Strayer *et al.* 2006; Elgersma *et al.* 2011; Vilà *et*

al. 2011). Therefore, long-term assessment is needed to fully understand how invasive plants are influencing ecosystem functioning in restored grasslands. Despite this, we showed that *S. gigantea* can disrupt the controls exerted by plant functional diversity on soil and soil water nutrient. Hence, we can also argue that invasion success, besides the competitive advantages, relies on affecting nutrient dynamics in the soil which, in turn, will reduce the vigor and even the persistence of native species in the invaded communities (Vila & Weiner 2004; Vilà *et al.* 2011).

Conclusions

Our results indicate that plant functional diversity partially promotes water cleaning and soil fertility in grassland communities. However, plant functional diversity did not prevent the negative impact of the invasive *S. gigantea* on the plant community. The invasive species can compromise grassland long-term functioning since it interferes with community biomass, soil water quality and nutrient dynamics. Therefore, further experiments should be performed testing different plant traits and species to match and/or overcome the ecological strategies of *S. gigantea* in order to reduce its invasion success. Performing experiments with similar approach is important for improving restoration methods of invaded grasslands, contributing to increase native plant diversity, reducing invasive plants and maintaining soil fertility and other ecosystem functions.

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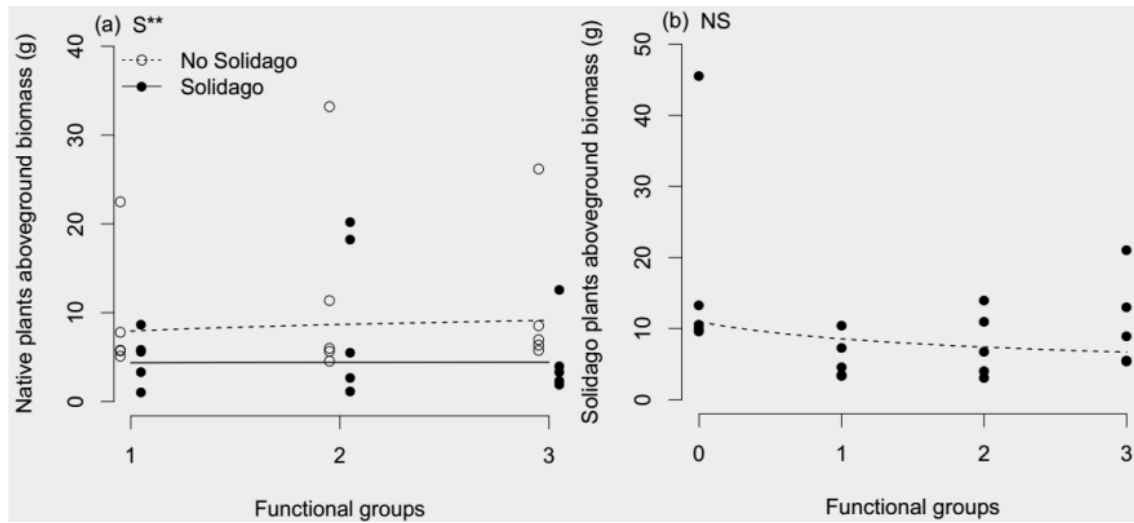
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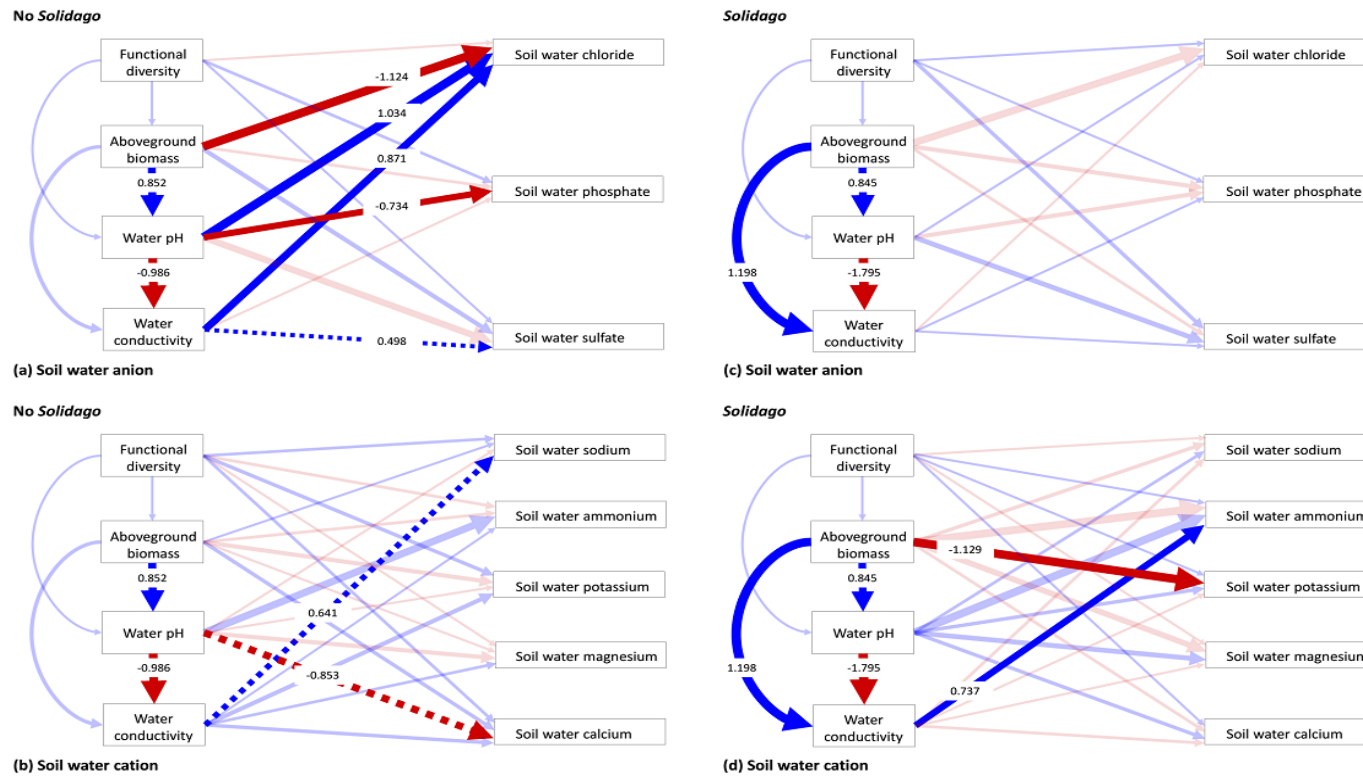
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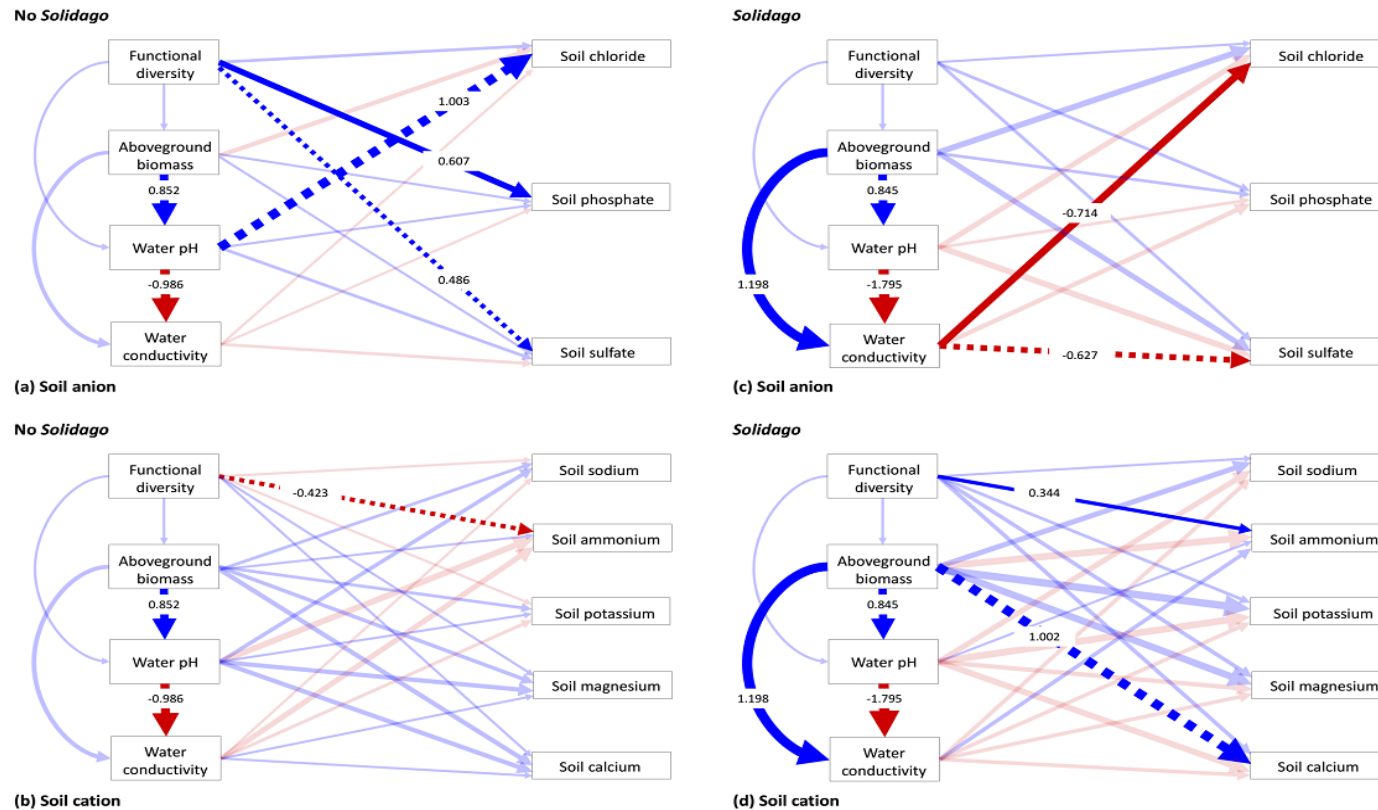
Figure 1: Effects of functional diversity (represented by the number of functional groups, FG) and *Solidago gigantea* (S) on plant aboveground biomass. Figure **(a)** shows native plants biomass production in six combinations of functional diversity (levels 1, 2, 3) and presence or absence of the invasive alien plant. Figure **(b)** represents results for *S. gigantea* under four levels of functional diversity (0, 1, 2, 3); FD 0 was a monoculture of *S. gigantea*. Aboveground biomass for all the plant communities was collected at the end of the experimental period (16 weeks). For native plants, we informed chi-squared values of dependent variables. For *S. gigantea* plants, F-values are presented (*** $p \le 0.001$; ** $p \le 0.01$; * $p \le 0.05$; . $p \le 0.10$). NS means non-significant effects.

Figure 2: Structural equation model (SEM) for the effects of functional diversity (1, 2, 3) and *Solidago gigantea* (presence or absence) on nutrients in the soil water fraction (**a–b**, anions; **c–d**, cations). Partial correlations are represented by the arrows, and path coefficients indicate the strength of the correlations (standardized β-coefficients calculated by using piecewise SEM according to Lefcheck 2016). Arrow thickness reflects the values of β-coefficients and solid arrows represent significant effects (p ≤ 0.05). Blue arrows show positive effects, while red arrows show negative ones. Dotted arrows show marginally significant effects, while transparent arrows show non-significant effects.

Figure 3: Structural equation model for the effects of functional diversity (1, 2, 3) and *Solidago gigantea* (presence or absence) on soil nutrient stocks (**a–b**, anions; **c–d**, cations). Partial correlations are represented by the arrows, and path coefficients indicate the strength of the correlations (standardized β-coefficients calculated by using piecewise SEM according to Lefcheck 2016). Arrow thickness reflects the values of β-coefficients and solid arrows represent significant effects (p ≤ 0.05). Blue arrows show positive effects, while red arrows show negative ones. Dotted arrows show marginally significant effects, while transparent arrows show non-significant effects.
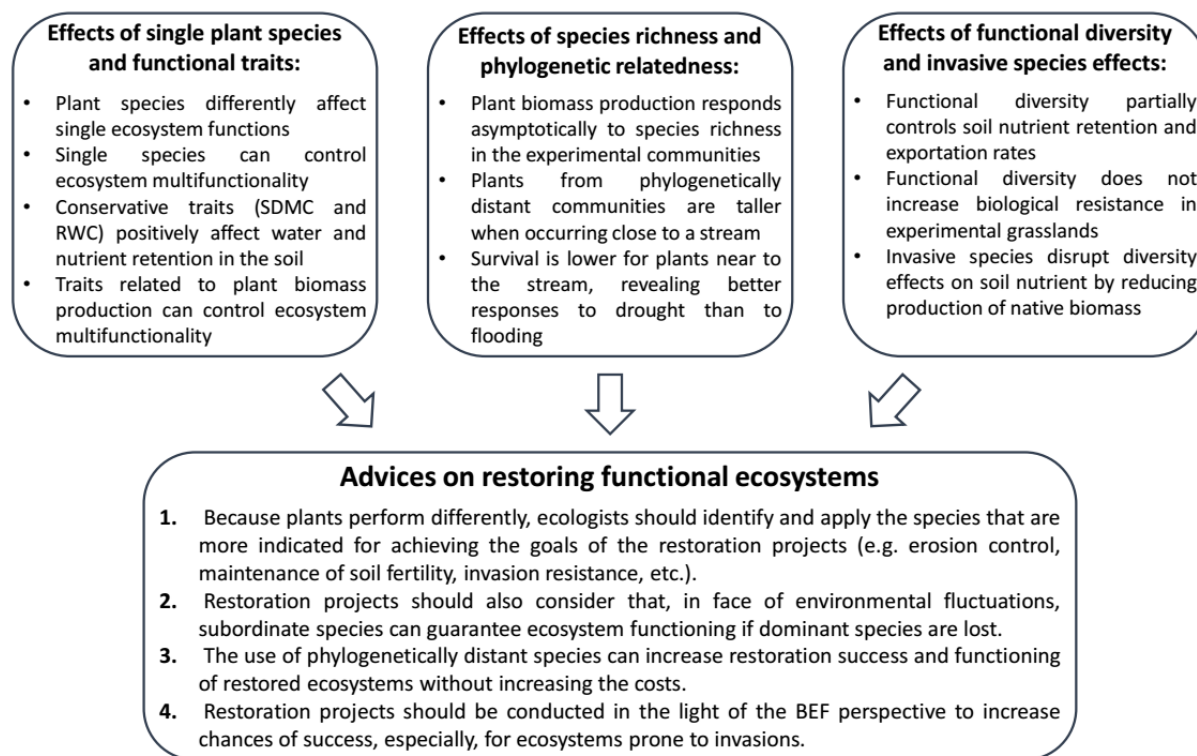
Chapter 5

GENERAL DISCUSSION

Summing up the main results of the thesis

The aims of this thesis were to improve the understanding about the effects of plant diversity on the functioning of restored ecosystems and to generate knowledge on how to design functional and self-sustainable restored ecosystems to increase restoration success. For this purpose, I developed three experimental studies testing different measures of plant diversity (i.e. functional trait diversity, species richness, functional and phylogenetic diversities) in face of different stressors, according to the ecosystems under investigation. Therefore, I consider that this thesis presents a complementarily perspective about the effects of plant diversity on biomass production, soil fertility and soil water quality in restored ecosystems.

As summed up in Figure 1, the thesis assessed the effects of plant functional traits on single and multiple ecosystem functions (Chapter 2); the effects of species richness and phylogenetic relatedness on the restoration success of a riparian forest (Chapter 3); and the effects of functional diversity on the biological resistance of a restored grassland (Chapter 4). By applying a theoretical approach based on the BEF perspective during restoration experiments, I tested how we can use plant diversity to effectively restore ecosystem functioning. In the following section, I discuss the main results related to the factors found to influence functioning of restored ecosystems and that should be considered for the design of

future restoration projects. Furthermore, I point out some challenges that must be overcome for achieving the successful restoration of semi-arid ecosystems in Brazil.

Figure 1: Main findings of the thesis and consequences for the restoration of functional ecosystems.

On the different aspects of diversity influencing ecosystem functioning

Plants both respond to and modulate environmental conditions by processing different types of natural resources. The different investments of plants for resource acquisition and metabolization influence ecosystem functions and processes, resulting in a positive relationship between plant diversity and ecosystem functioning (Diaz *et al.* 2004). Nonetheless, the extent of such relationship can also depend on the aspect of diversity being considered when assessing

ecosystem functioning. Hundreds of studies were conducted on the effects of species number on ecosystem functions. Some of the most investigated questions are (i) the diversity-productivity, (ii) the diversity-stability and (iii) the diversity-invasibility relationships (Levine, Adler & Yelenik 2004; Hooper *et al.* 2012; Cardinale *et al.* 2012; Tilman, Isbell & Cowles 2014). Moreover, functional diversity, species identity and community composition were found to play important roles for the relationships mentioned above (Mokany, Ash & Roxburgh 2008; Mouillot *et al.* 2011; Roscher *et al.* 2012; Byun, de Blois & Brisson 2013). More recently, phylogenetic diversity was shown to explain most of the variation in ecosystem productivity (Cadotte, Dinnage & Tilman 2012; Cadotte 2013, 2015).

Despite all these efforts for understanding diversity effects on the variability, predictability and reliability of the functions performed by ecosystems, there is still no consensus on which aspect of diversity would have higher influence on ecosystem functioning by consistently controlling functions across temporal and spatial scales (Cadotte 2015; Cardinale *et al.* 2015; Venail *et al.* 2015). In fact, it seems that the relative importance of the different levels of plant diversity varies according to study systems. Therefore, more species diversity would always be desirable for maintaining ecosystem functioning in face of environmental fluctuations (Cardinale *et al.* 2007; Isbell *et al.* 2011, 2015; Gamfeldt *et al.* 2013; Tilman *et al.* 2014). Given these considerations, I conducted experimental studies to contribute with the understanding on at which extent different aspects of plant diversity would be important for the functioning of restored ecosystems.

The first study of this thesis (Chapter 2) used an experimental approach to examine how plant species from tropical dry forests in northeastern Brazil affect single and multiple ecosystem functions related to soil and soil water quality. Additionally, this experiment

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compared the effects of above-and below-ground functional traits on the same functions. I found that the studied species present a high degree of trait convergence. However, within species the variability in the functional space was high. Also, only one plant species (*Mimosa tenuiflora*) consistently performed best across single and multiple functions, positively affecting water and nutrient retention in the soil and, therefore, avoiding nutrient leaching losses. Moreover, only traits related to plant biomass were found to control ecosystem multifunctionality.

The finding that initial stand biomass (i.e. vegetation quantity or green soup hypothesis) is important for controlling ecosystem multifunctionality in Brazilian tropical dry forests provides an insight on how to restore ecosystem functioning of semi-arid areas by designing plant communities that maximize biomass production. Such approach would increase plant survival and establishment, thus enhancing the reliability of maintaining functioning in the long term. In fact, recent studies found that initial stand biomass could drive early stages of ecological succession in forests (Carreño-Rocabado *et al.* 2012; Rozendaal & Chazdon 2015). Therefore, biomass production can be a crucial factor for the restoration of tropical dry forests. Additionally, selecting adequate plant species and traits would allow for less biomass turnover and larger standing biomass over time, thus enhancing carbon sequestration and soil nutrient retention by plants, while increasing reliability for successfully restoring these areas (Conti & Díaz 2013; Prado-Junior *et al.* 2016; Buzzard *et al.* 2016). Nevertheless, the experiment presented in Chapter 2 was conducted in a greenhouse with, relatively, well controlled conditions; i.e. enough water availability, no species interactions and no environmental fluctuations. Therefore, conducting studies under field conditions is a necessary next step for achieving more robust conclusions about the effects of plant traits on the multifunctionality of

Brazilian semi-arid ecosystems. These studies should also investigate the applicability of plant traits for the restoration of ecosystem functions in such degraded areas.

To investigate if restoration success is enhanced when using phylogenetically distant species, the second study (Chapter 3) assessed plant survival and growth in communities with different levels of species richness and phylogenetic distance during the restoration of a riparian forest. The results show that plants from phylogenetically distant communities had better growth, but only when environmental conditions were favorable (i.e. when having water availability by occurring near to the stream). Therefore, designing restoration projects in the light of the BEF perspective is a suitable alternative for maximizing restoration success and the functioning of restored ecosystems (Naeem 2006; Chazdon 2008). In fact, when restoring riparian forests, ecologists have to deal with high environmental fluctuations from pulse dynamics (Williams *et al.* 2006; Collins *et al.* 2014). Such scenario is particularly critical for riparian forests from transition zones between Atlantic Forest and Caatinga in northeastern Brazil. These areas can have considerably high precipitation rates concentrated in part of the year, but also suffer from the severity of the semi-arid climate regime (Schwinning *et al.* 2004; Schwinning & Sala 2004; Rodal, Barbosa & Thomas 2008). Therefore, due to the constant variation of the environmental conditions, restoration of these riparian forests should focus on achieving functioning temporal stability. Indeed, if attempts to restore these areas do not consider temporal species redundancy (Naeem 2006), productivity and nutrient retention in the soil of such areas will have a high variability. Consequently, we can expect high rates of nutrient leaching loss during the rainy season. This will further create a positive feedback that compromises plant biomass production and survival and, finally, restoration success in the long term (Suding, Gross & Houseman 2004).

However, when restoring degraded ecosystems, ecologists also have to deal with impacts derived from other sources than environmental fluctuation. In this sense, one of the most widespread stressors is the presence of invasive species (MEA 2005; CBD 2010). Invasive species can reduce native species abundance and occurrence by competition (Vilà, Williamson & Lonsdale 2004; Vilà *et al.* 2011) and alter important processes like decomposition and nutrient cycling (Chapuis-Lardy *et al.* 2006; Herr *et al.* 2007; Weidenhamer & Callaway 2010), thus compromising native species colonization and facilitating further invasions (Ehrenfeld 2010; Simberloff *et al.* 2013; Wang *et al.* 2015). Therefore, the third study of this thesis (Chapter 4) investigated whether by increasing the functional diversity of restored grasslands one could enhance biological resistance to invasion while maintaining native diversity effects on soil ecosystems. For this, I performed a greenhouse experiment manipulating the number of functional groups and the presence of an invasive plant found to be a successful invader in calcareous grasslands. The main results show that grassland functional diversity was not able to prevent invasions nor to reduce the impacts of invasive species on native plants biomass production and on soil nutrient dynamics. Further investigations based on long term community dynamics are needed to confirm the importance of these findings for grassland restoration.

An important first step in this direction has recently been made by Yannelli et al. (2017) who, based on the limiting similarity and on the Darwin's naturalization hypotheses, suggested that by applying plant species that are functionally and phylogenetically similar to potential invaders, is possible to reduce invaders successful establishment by increasing the competitive ability of restored grasslands. Therefore, future studies should investigate other aspects of grassland diversity (e.g. genetic or phylogenetic diversity) and the levels of similarities between native and invasive plants in order to reduced ecological niche availability for invaders in restored ecosystems. This approach would increase biological resistance, while allowing for the

performance of other ecosystem functions (Funk *et al.* 2008; Staab *et al.* 2015; Yannelli *et al.* 2017). Also, it is important to further investigate different community compositions (e.g. by manipulating relative abundances of dominant and subordinate species), because the most important roles for the biological resistance of native communities seem to be performed by dominant species, i.e. the dominance hierarchy hypothesis (Thuiller *et al.* 2010; Yannelli *et al.* 2017). These further investigations can support management plans for degraded and invaded sites, thus contributing to the reduction of invasive species prevalence and its impacts on grasslands ecosystem functioning.

On the challenges for restoring semi-arid ecosystems

The results presented in this thesis confirm that applying the BEF perspective when conducting restoration projects can significantly improve functioning of restored ecosystems and increase restoration success. Therefore, restoration ecology can benefit from applying such approach. The development of evidenced-based designs and problem-oriented techniques and, also, the identification of species combination that will exhibit the best performance in face of environmental fluctuations are more likely to be achieved when restoration experiments incorporate BEF hypotheses and premises (Aerts & Honnay 2011; Bullock *et al.* 2011). However, despite its recognized benefits and importance, the BEF perspective or even the monitoring of ecosystem functions other than biomass production had been barely applied in restoration projects conducted in the Brazilian semiarid.

Finally, restoration of semi-arid degraded areas need to cope with a myriad of constraining factors. These factors include (i) the high demand of natural resources for

agriculture or livestock activities resulting in constantly high impacts on ecosystems; (ii) the absence of management plans adequate to the multiple uses of natural resources in these regions; (iii) the lack of water availability during most of the year requiring the implementation of irrigation systems and, considerably, elevating restoration costs; (iv) the occurrence of desertification processes that compromise soil quality and jeopardize plant establishment and survival, thus drastically reducing restoration success; and (v) the total absence of producers that consider recently developed techniques appropriate to the restoration of semi-arid ecosystems during plant production, thus increasing mortality rates in the dry season and reducing chances of success. Steps in the direction of solving these problems are being taken, however, we still have a long way ahead for developing programs that will effectively restore ecosystem functioning in the Brazilian semiarid biome.

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Appendix

A1. Supporting information to Teixeira *et al.* 'Functional diversity and invasive species moderate soil water quality and soil fertility in grassland mesocosms'

Appendix S1: Material and methods extended

Plant species and functional traits selection

Solidago gigantea (Asteraceae) was used as a model species, given that is known to be problematic in disturbed areas such as roadsides and newly re-vegetated areas (Kowarik 2003). Seeds from S. gigantea were collected from seven clones and within seven stands along River Isar near Freising, southern Germany (48°24'N, 11°41'E). Before the experiment, the seeds were tested for viability under controlled conditions consisting in an 8 h night at 12 °C and a 16 h day at 20 °C and resulting in a germination success of $73.6 \pm 4.5\%$. The experimental pool of native species was based on a set of 54 native grassland species occurring with a frequency $\geq 10\%$ in a dataset comprising more than 100 surveys of calcareous grasslands in the agricultural landscape north of Munich, Germany (Conradi & Kollmann 2016). The native seed material was obtained from the local seed producer Johann Krimmer (Pulling, Germany).

Functional group classification was performed using trait information for the set of 54 native grassland species (Table S1, Figure S1). For doing so, eight traits found to be good proxies for species dispersal, establishment success, growth, persistence, and competitive

ability (Cornelissen et al., 2003; Funk et al., 2008; Westoby et al., 2002) were selected. That is, specific leaf area (SLA), leaf dry matter, life form, shoot morphology, morphology of vegetative organs, canopy height at maturity, seed mass and longevity (Table S1, Figure S1). Furthermore, SLA, canopy height at maturity and seed mass have been found to be correlated with invasiveness (Hamilton *et al.* 2005). Some of these traits are correlated to competition among plant species (i.e. SLA, seed mass, and canopy height at maturity). However, during functional groups clustering, is important to use also traits related to resource acquisition and uptake, because they can affect niche partitioning and community processes differently than those influencing plants competitive ability (Yannelli et al., 2017). We collected the functional traits information from the BiolFlor (Klotz et al. 2002) and LEDA databases (Kleyer *et al.* 2008).

Functional groups clustering

Statistical analyses for the functional grouping were performed using Infostat software (Di-Rienzo et al. 2013). Previous to clustering analysis, all non-numerical functional traits were transformed into dummy variables (binary values). Subsequently, the trait information was converted to continuous values using a principal coordinate analysis using Jaccard's distance measure and saving the first five principal coordinates (Pla et al. 2012). Based on the collected data for all functional traits, a cluster analysis was conducted using Gower's similarity coefficient among species and Ward as the linkage method (Podani 1999; Rostagno et al. 2006).

The classification of all species led to three statistically different functional groups (Figure S1). To prove that clusters were significantly different, a multivariate analysis of

variances was performed with the same variables. Null hypothesis of equal vector means was rejected (F = 13.6, p < 0.0001) and mean vector comparisons showed significant differences among the clusters (Table S1). For more details on the significance of the functional groups clustering, check the results of the MANOVA analysis below. Finally, for making sure that the functional composition of our experimental plots (FG 1–3) resulted in plant communities with increasing levels of functional diversity, we calculated functional diversity indexes according to Laliberté and Legendre (2010) and correlated such indexes to our functional groups classification using a linear regression model (Appendix S1.4, Figures S2 and S3).

MANOVA results for functional groups classification

Analysis of variance table (Lawley-Hoteling)

S.V.	Statistic	F	df(num)	df(den)	p
Cluster	14.02	29.6	18	76	<0.0001

Hotelling test (Bonferroni adjustment) Alpha = 0.05

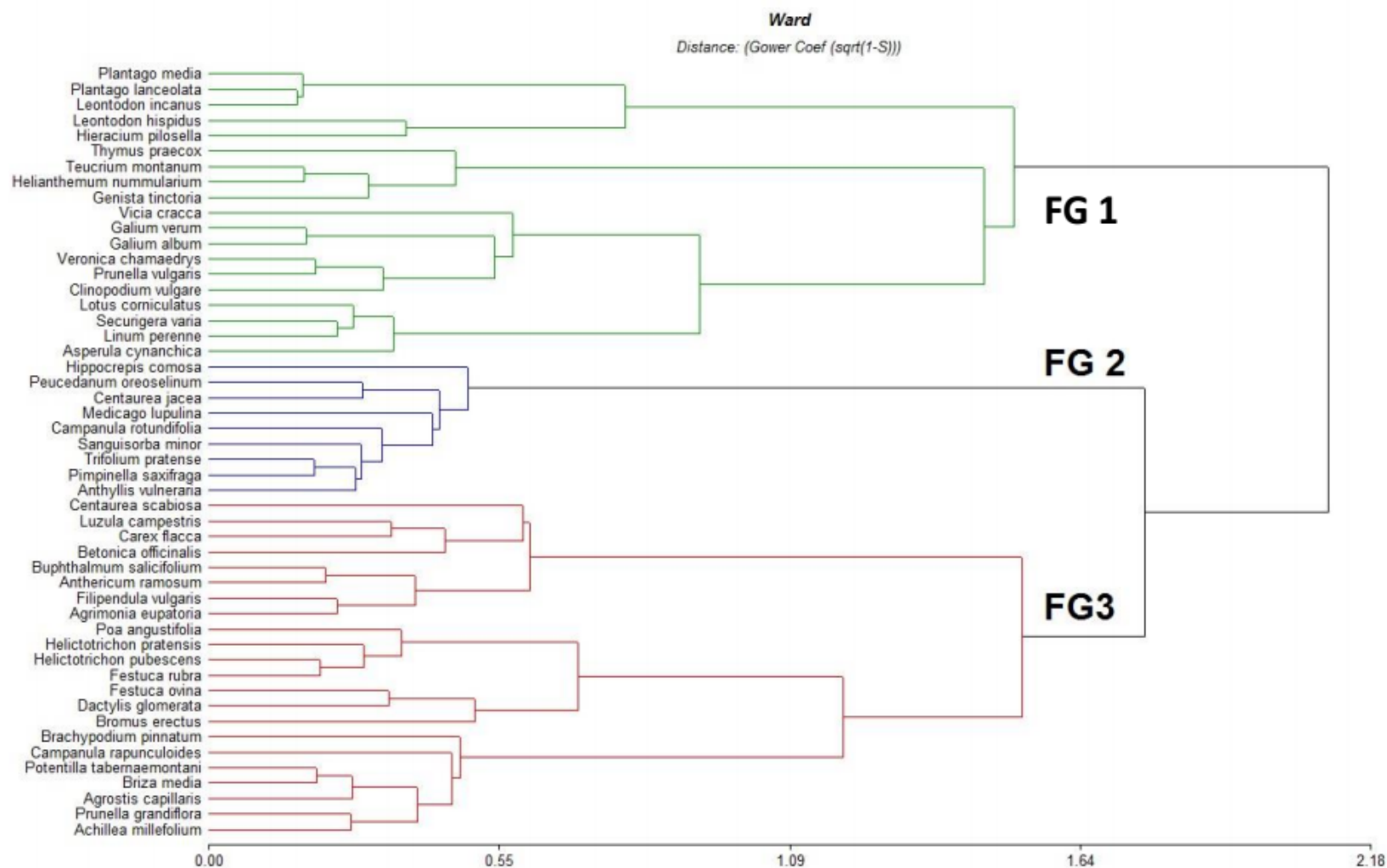| Cluster	Seed. mass .med	Can. height .med	SLA	dry leaf mass	PCO_1	PCO_2	PCO_3	PCO_4	PCO_5	n	
3	1.97	0.27	23.17	202.84	0.29	0.04	-0.01	-0.05	0.04	19	**A**
2	2.44	0.33	21.45	240.07	-0.08	-0.31	-0.1	0.11	-0.07	9	**B**
1	1.6	0.37	22.58	268.19	-0.21	0.09	0.05	-0.01	-2.10E-03	22	**C**

Means with a common letter are not significantly different (p > 0.05)

Table S1: Functional trait characteristics for each functional group. Values of numerical functional traits represent mean (± SD).

Functional traits	Functional group FG 1	FG 2	FG 3
Longevity	Perennial	Perennial + biannual + annual	Perennial
Life form	Hemicryptophytes, geophytes, chamaephytes	Hemicryptophytes	Hemicryptophytes, chamaephytes
Shoot morphology	Hemi-rosette, erosulate	Hemi-rosette	Erosulate, rosette
Morphology of vegetative organs	Runner, rhizome, tuft, pleicorm	Pleiocorm, runner	Pleiocorm, rhizome, runner
Seed mass (g)	1.60 ± 1.72	2.44 ± 1.64	1.97 ± 3.27
Canopy height (m)	0.37 ± 0.18	0.33 ± 0.22	0.27 ± 0.19
SLA (g.cm^{-2})	22.6 ± 9.2	21.5 ± 7.2	23.2 ± 6.0
Dry leaf mass (mg) *	268 ± 78 (b)	240 ± 44 (ba)	203 ± 52 (a)

Numerical functional traits were significantly different (ANOVA test; $F = 5.34$; $p \leq 0.05$). Means with a common letter are not significantly different ($p > 0.05$).

Figure S1: Functional classification for a set of 54 grassland plant species by trait similarity into three functional groups.

Composition of the plant communities

One functional group

Replica 1 = FG1

Nr	Species	Family	FG
1	*Prunella vulgaris*	Lamiaceae	1
2	*Plantago media*	Plantaginaceae	1
3	*Helianthemum nummularium*	Cistaceae	1
4	*Genista tinctoria*	Fabaceae	1
5	*Asperula cynanchica*	Rubiaceae	1
6	*Veronica chamaedrys*	Scrophulariaceae	1
7	*Lotus corniculatus*	Fabaceae	1
8	*Hieracium pilosella*	Asteraceae	1
9	*Vicia cracca*	Fabaceae	1

Replica 2 = FG2

Nr	Species	Family	FG
1	*Anthyllis vulneraria*	Fabaceae	2
2	*Campanula rotundifolia*	Campanulaceae	2
3	*Centaurea jacea*	Asteraceae	2
4	*Hippocrepis comosa*	Fabaceae	2
5	*Medicago lupulina*	Fabaceae	2
6	*Peucedanum oreoselinum*	Apiaceae	2
7	*Pimpinella saxifraga*	Apiaceae	2
8	*Trifolium pratense*	Fabaceae	2
9	*Sanguisorba minor*	Rosaceae	2

Replica 3 = FG3

Nr	Species	Family	FG
1	*Betonica officinalis*	Lamiaceae	3
2	*Poa angustifolia*	Poaceae	3
3	*Festuca rubra*	Poaceae	3
4	*Agrimonia eupatoria*	Rosaceae	3
5	*Prunella grandiflora*	Lamiceae	3
6	*Helictotrichon pubescens*	Poaceae	3
7	*Agrostis capillaris*	Poaceae	3
8	*Achillea millefolium*	Asteraceae	3
9	*Potentilla tabernaemontani*	Rosaceae	3

Replica 4 = FG3

Nr	Species	Family	FG
1	*Helictotrichon pubescens*	Poaceae	3
2	*Dactylis glomerata*	Poaceae	3
3	*Agrostis capillaris*	Poaceae	3
4	*Anthericum ramosum*	Anthericaceae	3
5	*Potentilla tabernaemontani*	Rosaceae	3
6	*Helictotrichon pratense*	Poaceae	3
7	*Brachypodium pinnatum*	Poaceae	3
8	*Festuca rubra*	Poaceae	3
9	*Buphthalmum salicifolium*	Asteraceae	3

Replica 5 = FG 1

Nr	Species	Family	FG
1	*Teucrium montanum*	Plantaginaceae	1
2	*Helianthemum nummularium*	Cistaceae	1
3	*Galium album*	Rubiaceae	1
4	*Asperula cynanchica*	Rubiaceae	1
5	*Genista tinctoria*	Fabaceae	1
6	*Linum perenne*	Linaceae	1
7	*Vicia cracca*	Fabaceae	1
8	*Prunella vulgaris*	Lamiaceae	1
9	*Veronica chamaedrys*	Scrophulariaceae	1

Two functional groups

Replica 1 = FG 1 + FG 3

Nr	Species	Family	FG
1	*Leontodon incanus*	Asteraceae	1
2	*Achillea millefolium*	Asteraceae	3
3	*Linum perenne*	Linaceae	1
4	*Plantago media*	Plantaginaceae	1
5	*Brachypodium pinnatum*	Poaceae	3
6	*Lotus corniculatus*	Fabaceae	1
7	*Genista tinctoria*	Fabaceae	1
8	*Festuca ovina*	Poaceae	3
9	*Bromus erectus*	Poaceae	3

Replica 2 = FG 1 + FG 3

Nr	Species	Family	FG
1	*Helictotrichon pubescens*	Poaceae	3
2	*Teucrium montanum*	Plantaginaceae	1
3	*Agrostis capillaris*	Poaceae	3
4	*Veronica chamaedrys*	Scrophulariaceae	1
5	*Hieracium pilosella*	Asteraceae	1
6	*Genista tinctoria*	Fabaceae	1
7	*Prunella grandiflora*	Lamiceae	3
8	*Vicia cracca*	Fabaceae	1
9	*Brachypodium pinnatum*	Poaceae	3

Replica 3 = FG1+FG2

Nr	Species	Family	FG
1	*Veronica chamaedrys*	Scrophulariaceae	1
2	*Sanguisorba minor*	Rosaceae	2
3	*Clinopodium vulgare*	Lamiaceae	1
4	*Teucrium montanum*	Plantaginaceae	1
5	*Lotus corniculatus*	Fabaceae	1
6	*Medicago lupulina*	Fabaceae	2
7	*Anthyllis vulneraria*	Fabaceae	2
8	*Leontodon incanus*	Asteraceae	1
9	*Trifolium pratense*	Fabaceae	2

Replica 4 = FG2+FG3

Nr	Species	Family	FG
1	*Helictotrichon pratense*	Poaceae	3
2	*Anthyllis vulneraria*	Fabaceae	2
3	*Achillea millefolium*	Asteraceae	3
4	*Prunella grandiflora*	Lamiceae	3
5	*Medicago lupulina*	Fabaceae	2
6	*Sanguisorba minor*	Rosaceae	2
7	*Trifolium pratense*	Fabaceae	2
8	*Festuca ovina*	Poaceae	3
9	*Bromus erectus*	Poaceae	3

Replica 5 = FG 1 + FG 2

Nr	Species	Family	FG
1	*Sanguisorba minor*	Rosaceae	2
2	*Genista tinctoria*	Fabaceae	1
3	*Asperula cynanchica*	Rubiaceae	1
4	*Clinopodium vulgare*	Lamiaceae	1
5	*Peucedanum oreoselinum*	Apiaceae	2
6	*Linum perenne*	Linaceae	1
7	*Prunella vulgaris*	Lamiaceae	1
8	*Pimpinella saxifraga*	Apiaceae	2
9	*Anthyllis vulneraria*	Fabaceae	2

Three functional groups

Replica 1 = FG 1 + FG 2 +FG 3

Nr	Species	Family	FG
1	*Festuca rubra*	Poaceae	3
2	*Dactylis glomerata*	Poaceae	3
3	*Poa angustifolia*	Poaceae	3
4	*Hippocrepis comosa*	Fabaceae	2
5	*Campanula rotundifolia*	Campanulaceae	2
6	*Medicago lupulina*	Fabaceae	2
7	*Leontodon incanus*	Asteraceae	1
8	*Hieracium pilosella*	Asteraceae	1
9	*Teucrium montanum*	Plantaginaceae	1

Replica 2 = FG 1 + FG 2 +FG 3

Nr	Species	Family	FG
1	*Festuca rubra*	Poaceae	3
2	*Poa angustifolia*	Poaceae	3
3	*Centaurea scabiosa*	Asteraceae	3
4	*Sanguisorba minor*	Rosaceae	2
5	*Pimpinella saxifraga*	Apiaceae	2
6	*Anthyllis vulneraria*	Fabaceae	2
7	*Asperula cynanchica*	Rubiaceae	1
8	*Lotus corniculatus*	Fabaceae	1
9	*Vicia cracca*	Fabaceae	1

Replica 3 = FG 1 + FG 2 +FG 3

Nr	Species	Family	FG
1	*Centaurea scabiosa*	Asteraceae	3
2	*Dactylis glomerata*	Poaceae	3
3	*Potentilla tabernaemontani*	Rosaceae	3
4	*Medicago lupulina*	Fabaceae	2
5	*Campanula rotundifolia*	Campanulaceae	2
6	*Anthyllis vulneraria*	Fabaceae	2
7	*Galium album*	Rubiaceae	1
8	*Leontodon incanus*	Asteraceae	1
9	*Helianthemum nummularium*	Cistaceae	1

Replica 4 = FG 1 + FG 2 +FG 3

Nr	Species	Family	FG
1	*Betonica officinalis*	Lamiaceae	3
2	*Potentilla tabernaemontani*	Rosaceae	3
3	*Poa angustifolia*	Poaceae	3
4	*Trifolium pratense*	Fabaceae	2
5	*Sanguisorba minor*	Rosaceae	2
6	*Anthyllis vulneraria*	Fabaceae	2
7	*Galium album*	Fabaceae	1
8	*Teucrium montanum*	Plantaginaceae	1
9	*Leontodon incanus*	Asteraceae	1

Replica 5 = FG 1 + FG 2 +FG 3

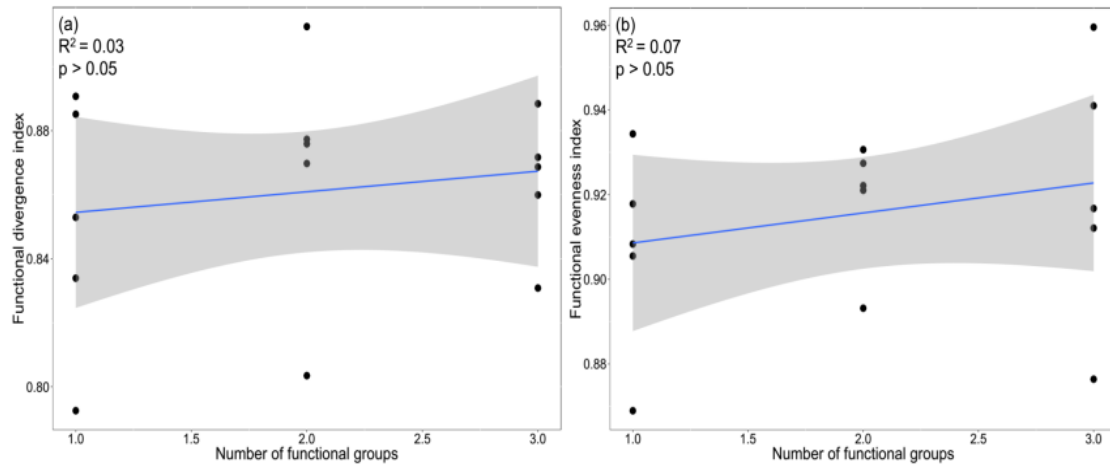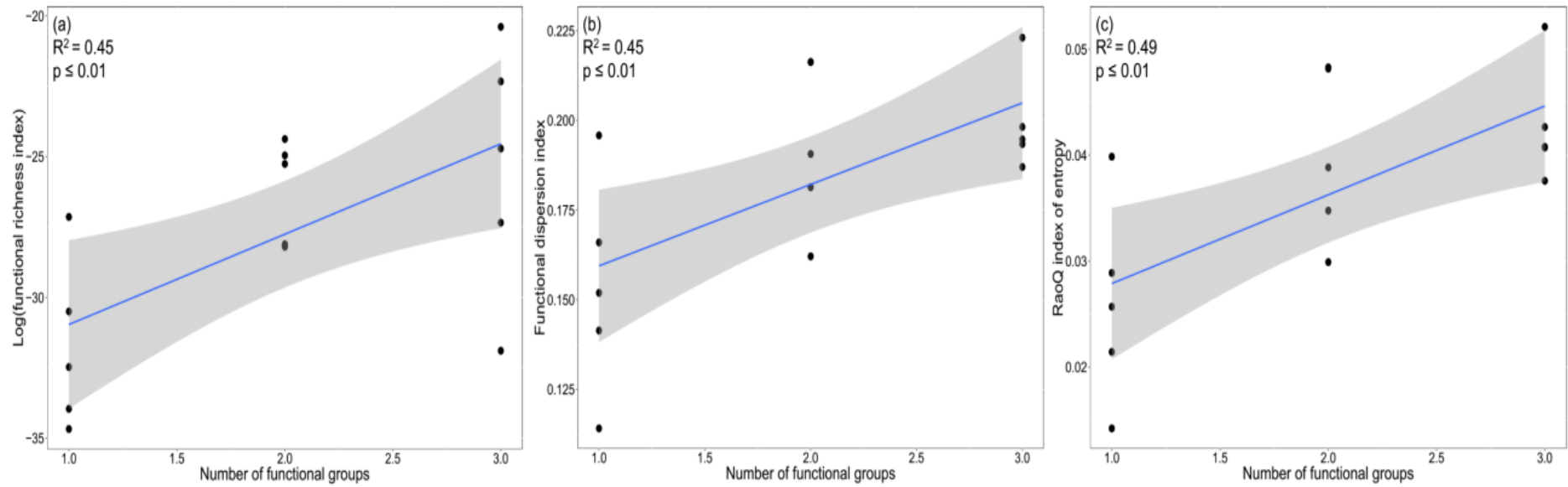| Nr	Species	Family	FG
1	*Festuca ovina*	Poaceae	3
2	*Brachypodium pinnatum*	Poaceae	3
3	*Agrostis capillaris*	Poaceae	3
4	*Campanula rotundifolia*	Campanulaceae	2
5	*Pimpinella saxifraga*	Apiaceae	2
6	*Centaurea jacea*	Asteraceae	2
7	*Leontodon incanus*	Asteraceae	1
8	*Genista tinctoria*	Fabaceae	1
9	*Prunella vulgaris*	Lamiceae	1

Does the number of functional groups positively affect functional diversity of plant communities?

We calculated five indexes of functional diversity (i.e. functional divergence – Fdiv; functional evenness – Feve; functional richness – Fric; functional dispersion – Fdis; and the RaoQ index of entropy) using the FD package in R, according to Laliberté and Legendre (2010). Afterwards, we correlated these functional diversity indexes to the functional diversity levels resulting from the cluster analysis based on plant traits using a linear model. The index of functional richness (calculated using the FD package) and our functional diversity levels were log-transformed prior to the analysis to fulfill the linear model assumptions.

This analysis shows that three from the five index of functional diversity we have calculated are significantly correlated to the levels of functional diversity determined by the cluster analysis using plant traits and were found to increase with the number of functional groups composing the plant communities. Functional richness (Fric), functional dispersion (Fdis) and the RaoQ index of entropy were positively related to the levels of functional diversity in the plant communities (Figure S3), while functional divergence (Fdiv) and functional evenness (Feve) were not (Figure S2).

Figure S2: No correlation between the number of functional groups and the functional divergence (**a**) and functional evenness (**b**) indexes, calculated according Laliberté and Legendre (2010).

Figure S3: Significant positive correlation between the number of functional groups and the functional diversity indexes following Laliberté and Legendre (2010). The figures show the functional richness index (**a**), the functional dispersion index (**b**) and the RaoQ index of entropy (**c**).

Statistical analysis for the effects of functional diversity and S. gigantea on nutrients
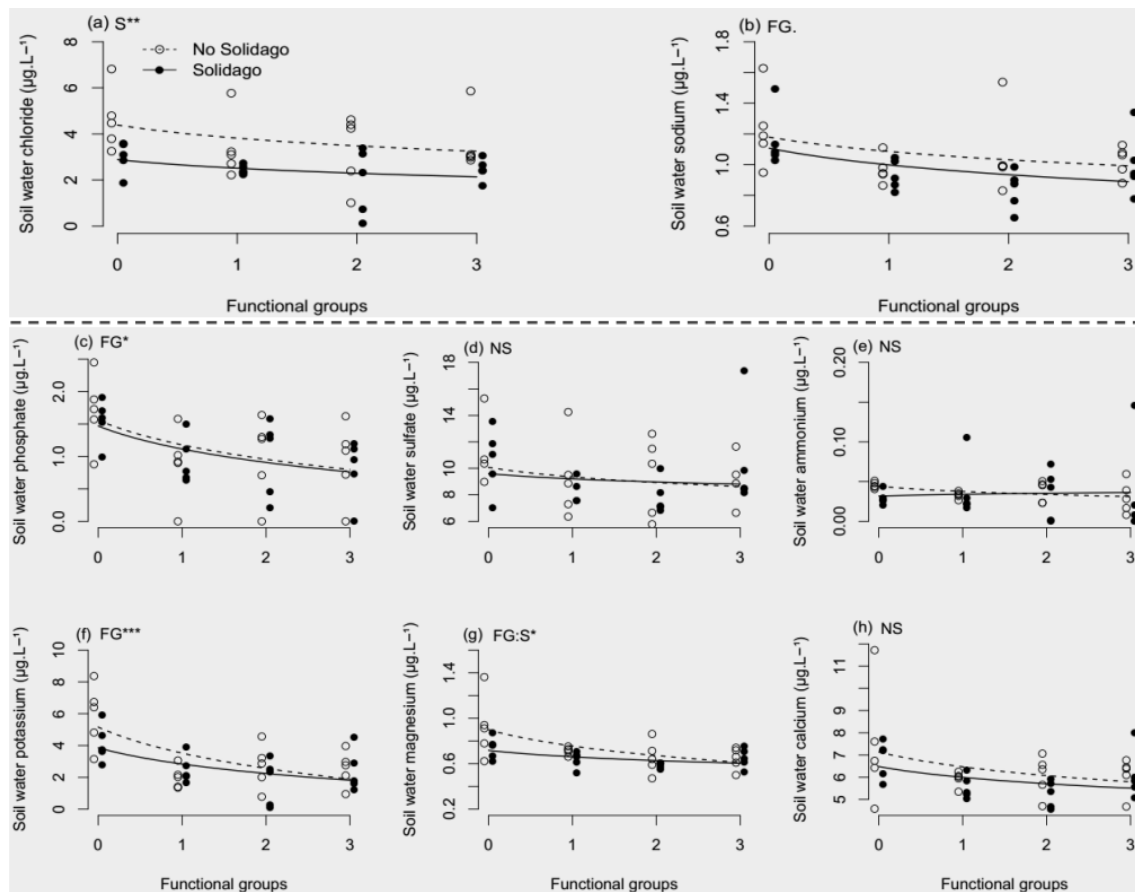
A linear mixed-effects model with block and species composition as random effects and the likelihood ratio test (LRT) implemented by the package lme4 (Bates et al., 2015) were applied to test the effects of functional diversity, invasive species presence and the interaction between them on the soil and soil water sample nutrients. Functional diversity was converted into a numeric variable and log-transformed ($\log(x+1)$) before running the linear mixed-effects models.

For ensuring that the functional diversity levels effects were different when comparing communities composed by different functional groups (FG 1–3) a *two-way* ANOVA block was performed using functional diversity as a categorical variable. Posteriorly, a *post-hoc* test (Tukey HSD for multiple comparisons) was applied for evaluating the influence of the three levels of functional diversity on soil water and soil nutrient. These results are presented in Appendix S2. Statistical analyses were performed using R Statistical Computing version 3.3.1 (R Development Core Team, 2015).

Appendix S2: Functional diversity and S. gigantea effects on nutrients
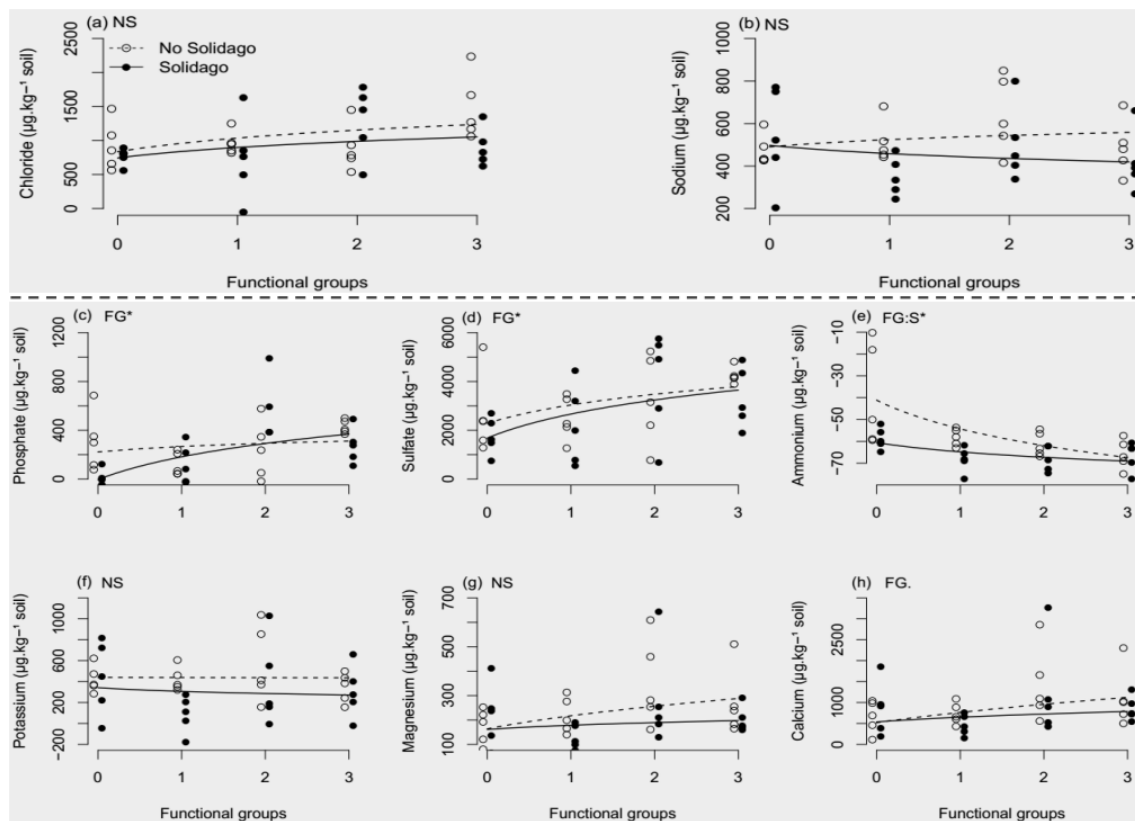
Soil water nutrient

Nutrient concentrations in soil water were reduced by functional diversity treatments by 25.2% on average, independently whether they were invaded or not (Figure S4). However, from the eight ions analyzed in the soil water samples, functional diversity significantly affected only two macronutrients and marginally affected one of the micronutrient (Figure S4). Soil water phosphate was reduced by 43.5% under increasing functional diversity of native plants ($\chi^2 = 7.8$, df = 5, p ≤ 0.05, Figure S4c), while soil water potassium was reduced under functional diversity by 54% ($\chi^2 = 14.8$, df = 5, p ≤ 0.001, Figure S4f). Soil water magnesium was significantly affected by the interaction between functional diversity and *S. gigantea* and it was reduced by 22% ($\chi^2 = 4.2$, df = 6, p ≤ 0.001, Figure S4g). Also, functional diversity was found to slightly reduce soil water sodium by 18.8% ($\chi^2 = 4.9$, df = 5, p = 0.084, Figure S4b), while the concentrations of sulfate ($\chi^2 = 0.9$, df = 5, p > 0.05), ammonium ($\chi^2 = 1.0$, df = 5, p > 0.05) and calcium ($\chi^2 = 4.0$, df = 5, p > 0.05) were not affected (Figures S4d, S4e and S4h, respectively). On the other hand, *S. gigantea* significantly affected only one micronutrient (Figure S4). Soil water chloride was reduced at 34% under presence of *S. gigantea* ($\chi^2 = 12.3$, df = 5, p ≤ 0.01, Figure S4a).

Figure S4: Effects of functional diversity (represented by the number of functional groups - FD) and the invasive alien *Solidago gigantea* (S) on chemical parameters of soil water in mesocosms grassland communities. Dashed lines separate the two micronutrients that are not directly controlled by plants (**a**, chloride; **b**, sodium). The figures below show macronutrients that are important for plant growth and are directly controlled by plants (**c**, phosphate; **d**, sulfate; **e**, ammonium; **f**, potassium; **g**, magnesium; **h**, calcium). For the dependent variables, chi-squared values are presented in the text (*** $p \leq 0.001$; ** $p \leq 0.01$; * $p \leq 0.05$; . $p \leq 0.10$). NS means non-significant effects.

Soil nutrient

There was no clear pattern for plant functional diversity controlling soil nutrient in the mesocosms (Figure S5). Despite no significant effects, we observed a trend for chloride concentration to increase with functional diversity ($\chi^2 = 4.4$, df = 5, p > 0.05, Figure S5a), while sodium concentration was reduced at higher levels of functional diversity; i.e. in the communities with three different functional groups ($\chi^2 = 1.3$, df = 5, p > 0.05, Figure S5b). Differently, functional diversity was found to significantly increase concentrations of phosphate ($\chi^2 = 8.4$, df = 5, p ≤ 0.05, Figure S5c) and sulfate ($\chi^2 = 6.8$, df = 5, p ≤ 0.05, Figure S5d) both in invaded and uninvaded communities. Ammonium concentration was reduced under high functional diversity (Estimate = –18.9, $\chi^2 = 18.0$, df = 5, p ≤ 0.001) and in the presence of *S. gigantea* (Estimate = –19.4, $\chi^2 = 14.8$, df = 5, p ≤ 0.001). However, the interaction between functional diversity and presence of *S. gigantea* had a positive effect on ammonium concentration decreasing the rate by which it was consumed in the mesocosms (Estimate = 12.8, $\chi^2 = 6.3$, df = 6, p ≤ 0.05, Figure S5e). Potassium (for FG effects: $\chi^2 = 0.2$, df = 5, p > 0.05; for *S. gigantea* effects: $\chi^2 = 2.7$, df = 5, p > 0.05) and magnesium (for FG effects: $\chi^2 = 4.1$, df = 5, p > 0.05; for *S. gigantea* effects: $\chi^2 = 3.2$, df = 5, p > 0.05) concentrations in the soil of the mesocosms were not affected by functional diversity nor *S. gigantea* (Figures S5f and S5g), while calcium concentration slightly increased with functional diversity ($\chi^2 = 5.2$, df = 5, p = 0.075, Figure S5h). Although no statistical differences were detected, invaded communities had 14% less nutrients in the soil than the native ones.

Figure S5: Effects of functional diversity (represented by the number of functional groups - FD) and *Solidago gigantea* (S) on nutrient stocks in the soil of mesocosms with synthetic grassland communities. As in Figure 1, micronutrients are presented above the dashed line (**a**, chloride; **b**, sodium) and macronutrients below the dashed line (**c**, phosphate; **d**, sulfate; **e**, ammonium; **f**, potassium; **g**, magnesium; **h**, calcium). For the dependent variables, chi-squared values are presented in the text (*** $p \leq 0.001$; ** $p \leq 0.01$; * $p \leq 0.05$; . $p \leq 0.10$). NS means non-significant effects.

Appendix S3: Multiple comparisons for the effects of functional diversity on nutrients: a post-hoc analysis

Soil water nutrient

Despite the described effects of plant functional diversity on soil water nutrient, a *post-hoc* test revealed no effects of the different levels of functional diversity on such nutrients. The Tukey HSD for multiple comparisons showed no differences when comparing the three functional groups among themselves (FG 1–3). The reported effects are rather to be considered the influence of the presence of vegetation when compared to the bare soil treatment, regardless the number of functional groups composing the plant communities (Table S2, Figure S6).

Soil nutrient

Similar to the soil water nutrient measurements, the *post-hoc* test revealed no significance of increasing the levels of functional diversity on the nutrient concentration in the soil of the mesocosms. Again, the Tukey HSD for multiple comparisons showed no differences when comparing the three functional groups among themselves (FG 1–3). Therefore, we argue that the effects of plant functional diversity appear only when comparing the nutrient concentration in the soil of the mesocosms with plants against the nutrient concentrations in the bare soil treatment (Table S3, Figure S7).

Table S2: Results of the Tukey HSD *post-hoc* test evaluating the effects of the number of functional groups on soil water nutrient in the mesocosms.

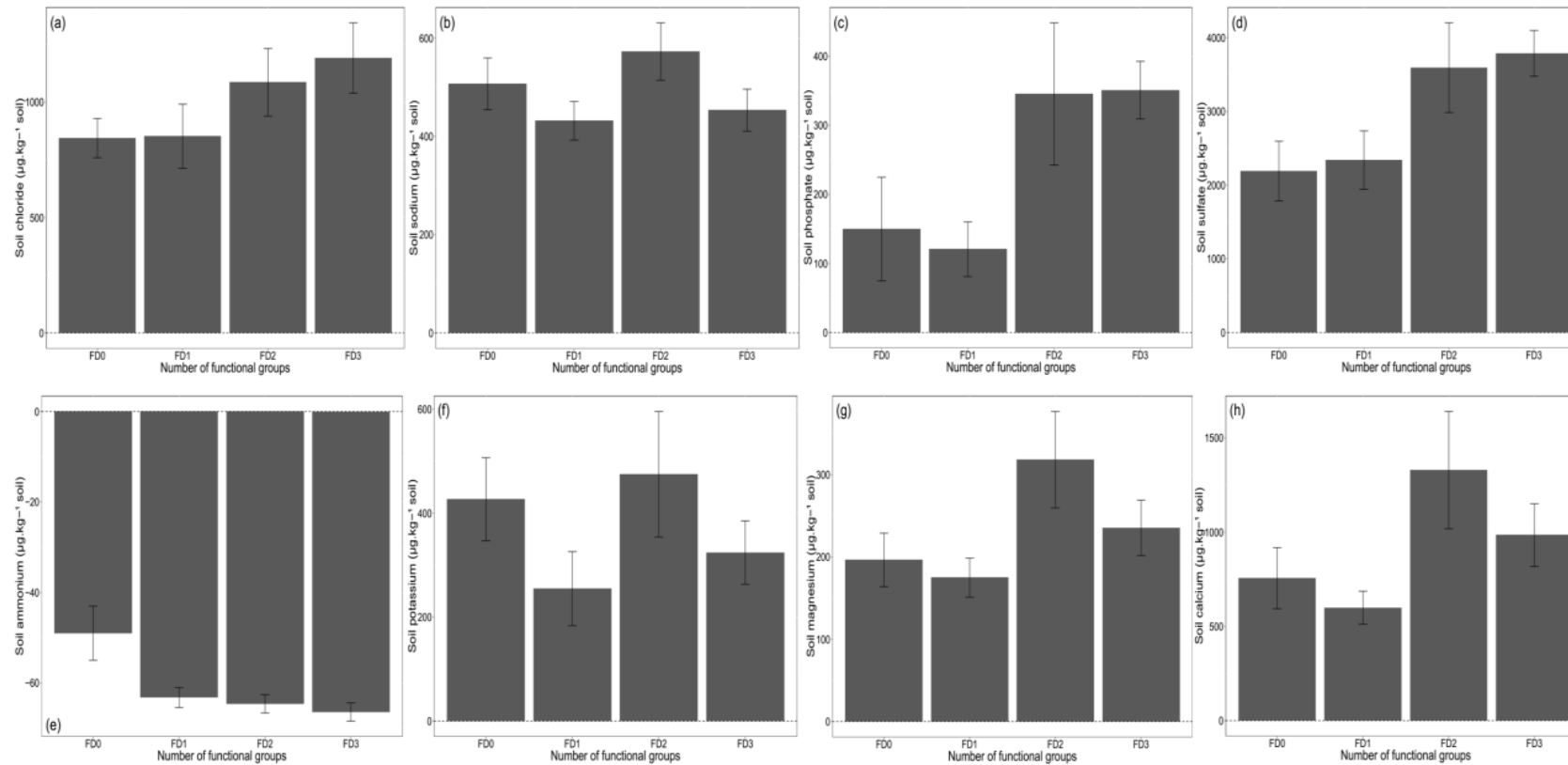| Post-hoc (Tukey HSD) - number of functional groups effects			
Soil water chloride	*diff*	*lwr*	*upr*	*p adj*
FD1-FD0	-0.88	-2.35	0.59	0.379
FD2-FD0	-1.17	-2.64	0.30	0.155
FD3-FD0	-0.80	-2.27	0.67	0.461
FD2-FD1	-0.29	-1.76	1.17	0.947
FD3-FD1	0.08	-1.39	1.55	0.999
FD3-FD2	0.37	-1.10	1.84	0.899
Soil water sodium			
FD1-FD0	-0.22	-0.42	-0.02	**0.023**
FD2-FD0	-0.24	-0.44	-0.04	**0.012**
FD3-FD0	-0.16	-0.36	0.03	0.128
FD2-FD1	-0.02	-0.22	0.18	0.994
FD3-FD1	0.06	-0.14	0.25	0.857
FD3-FD2	0.08	-0.12	0.27	0.720
Soil water phosphate			
FD1-FD0	-0.71	-1.32	-0.10	**0.017**
FD2-FD0	-0.65	-1.25	-0.04	**0.035**
FD3-FD0	-0.76	-1.37	-0.15	**0.010**
FD2-FD1	0.07	-0.54	0.67	0.991
FD3-FD1	-0.05	-0.66	0.56	0.996
FD3-FD2	-0.12	-0.73	0.49	0.952
Soil water sulfate			
FD1-FD0	-1.87	-5.35	1.61	0.471
FD2-FD0	-1.72	-5.20	1.76	0.542
FD3-FD0	-0.92	-4.40	2.56	0.888
FD2-FD1	0.15	-3.33	3.63	0.999
FD3-FD1	0.95	-2.53	4.43	0.878
FD3-FD2	0.80	-2.68	4.28	0.923
Soil water ammonium			
FD1-FD0	0.00	-0.03	0.03	0.999
FD2-FD0	0.00	-0.03	0.03	0.999
FD3-FD0	-0.01	-0.04	0.03	0.969
FD2-FD1	0.00	-0.03	0.03	1.000
FD3-FD1	0.00	-0.04	0.03	0.988
FD3-FD2	0.00	-0.04	0.03	0.989
Soil water potassium			
FD1-FD0	-2.77	-4.36	-1.18	**0.000**
FD2-FD0	-2.82	-4.41	-1.23	**0.000**
FD3-FD0	-2.54	-4.13	-0.94	**0.001**
FD2-FD1	-0.05	-1.64	1.54	1.000
FD3-FD1	0.23	-1.36	1.83	0.978
FD3-FD2	0.28	-1.31	1.87	0.963
Soil water magnesium			
FD1-FD0	-0.19	-0.39	0.02	0.081
FD2-FD0	-0.28	-0.48	-0.07	**0.005**
FD3-FD0	-0.23	-0.44	-0.03	**0.021**
FD2-FD1	-0.09	-0.29	0.11	0.629
FD3-FD1	-0.05	-0.25	0.16	0.929
FD3-FD2	0.04	-0.16	0.25	0.932
Soil water calcium			
FD1-FD0	-1.37	-2.83	0.09	0.072
FD2-FD0	-1.44	-2.90	0.02	0.053
FD3-FD0	-1.03	-2.49	0.43	0.243
FD2-FD1	-0.08	-1.54	1.39	0.999
FD3-FD1	0.34	-1.12	1.80	0.918
FD3-FD2	0.42	-1.04	1.88	0.863

Table S3: Results of the Tukey HSD *post-hoc* test evaluating the effects of the number of functional groups on nutrient stocks in the soil of the mesocosms.

Post-hoc (Tukey HSD) - number of functional groups effects				
Soil chloride	*diff*	*lwr*	*upr*	*p adj*
FD1-FD0	7.98	-450.03	465.99	1.00
FD2-FD0	241.72	-216.29	699.73	0.49
FD3-FD0	346.74	-111.27	804.75	0.19
FD2-FD1	233.74	-224.27	691.75	0.51
FD3-FD1	338.76	-119.25	796.77	0.21
FD3-FD2	105.02	-352.99	563.03	0.92
Soil sodium				
FD1-FD0	-75.00	-267.41	117.40	0.71
FD2-FD0	65.81	-126.60	258.21	0.79
FD3-FD0	-53.41	-245.81	139.00	0.87
FD2-FD1	140.81	-51.59	333.22	0.21
FD3-FD1	21.60	-170.81	214.00	0.99
FD3-FD2	-119.22	-311.62	73.19	0.35
Soil phosphate				
FD1-FD0	-29.14	-278.61	220.33	0.99
FD2-FD0	195.50	-53.97	444.97	0.17
FD3-FD0	201.08	-48.39	450.55	0.15
FD2-FD1	224.64	-24.83	474.11	0.09
FD3-FD1	230.22	-19.25	479.69	0.08
FD3-FD2	5.58	-243.89	255.05	1.00
Soil sulfate				
FD1-FD0	149.34	-1670.84	1969.52	1.00
FD2-FD0	1402.76	-417.42	3222.94	0.18
FD3-FD0	1597.44	-222.74	3417.62	0.10
FD2-FD1	1253.42	-566.76	3073.60	0.26
FD3-FD1	1448.10	-372.08	3268.28	0.16
FD3-FD2	194.68	-1625.50	2014.86	0.99
Soil ammonium				
FD1-FD0	-14.22	-26.15	-2.29	**0.01**
FD2-FD0	-15.62	-27.55	-3.69	**0.01**
FD3-FD0	-17.40	-29.34	-5.47	**0.00**
FD2-FD1	-1.40	-13.33	10.53	0.99
FD3-FD1	-3.18	-15.12	8.75	0.88
FD3-FD2	-1.79	-13.72	10.15	0.98
Soil potassium				
FD1-FD0	-172.24	-513.64	169.16	0.52
FD2-FD0	48.03	-293.37	389.44	0.98
FD3-FD0	-102.78	-444.18	238.63	0.84
FD2-FD1	220.27	-121.13	561.67	0.31
FD3-FD1	69.46	-271.94	410.87	0.94
FD3-FD2	-150.81	-492.21	190.59	0.63
Soil magnesium				
FD1-FD0	-0.06	-0.64	0.51	0.99
FD2-FD0	0.48	-0.09	1.05	0.13
FD3-FD0	0.25	-0.32	0.82	0.63
FD2-FD1	0.54	-0.03	1.11	0.07
FD3-FD1	0.31	-0.26	0.89	0.45
FD3-FD2	-0.23	-0.80	0.34	0.70
Soil calcium				
FD1-FD0	-0.08	-0.82	0.66	0.99
FD2-FD0	0.61	-0.13	1.35	0.13
FD3-FD0	0.43	-0.31	1.17	0.39
FD2-FD1	0.70	-0.04	1.44	0.07
FD3-FD1	0.52	-0.22	1.26	0.25
FD3-FD2	-0.18	-0.92	0.56	0.91

Figure S6: Effects of the number of functional groups on nutrients in the soil water of mesocosms with synthetic grassland communities. The figures represent mean values (± SD) for two micronutrients (**a,** chloride; **b,** sodium) and six macronutrients (**c,** phosphate; **d,** sulfate; **e,** ammonium; **f,** potassium; **g,** magnesium; **h,** calcium). For the dependent variables, table S2 shows the differences among each one of the functional groups (*** $p \leq 0.001$; ** $p \leq 0.01$; * $p \leq 0.05$; (*) $p \leq 0.10$).
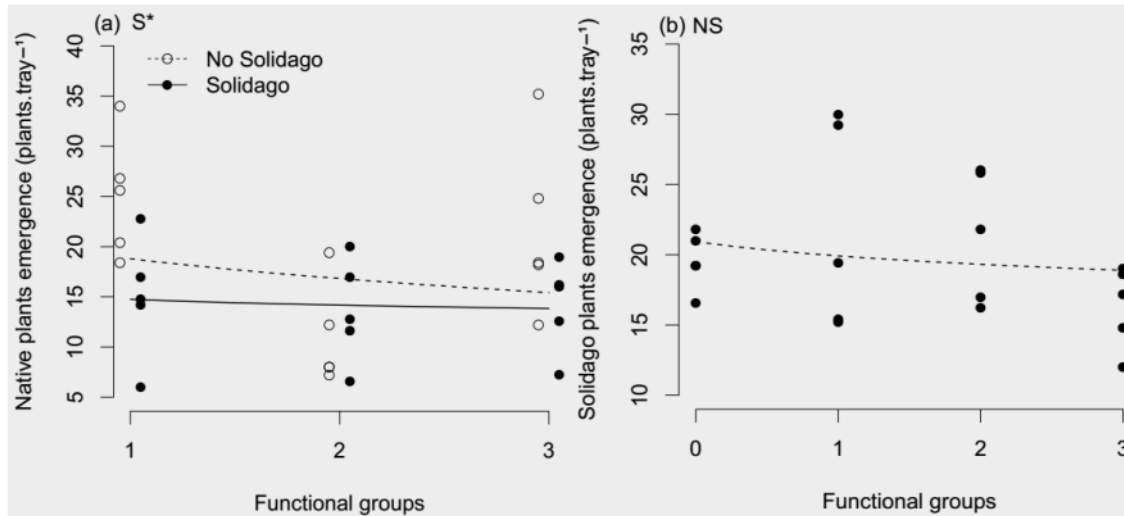
Figure S7: Effects of the number of functional groups on nutrients stocks in the soil of mesocosms with synthetic grassland communities. The figures represent mean values ($\pm$ SD) for two micronutrients (**a,** chloride; **b,** sodium) and six macronutrients (**c,** phosphate; **d,** sulfate; **e,** ammonium; **f,** potassium; **g,** magnesium; **h,** calcium). For the dependent variables, table S3 shows the differences among each one of the functional groups (*** $p \leq 0.001$; ** $p \leq 0.01$; * $p \leq 0.05$; (*) $p \leq 0.10$).

Appendix S4: Functional diversity and S. gigantea effects on plants emergence

Functional diversity effects on native plants emergence

Native plants emergence was not affected by the number of functional groups composing the plant communities (χ^2 = 1.7, df = 5, p> 0.05). Nevertheless, the number of emerged plants was slightly higher in the communities with three functional groups (Figure S8a). On the other hand, *S. gigantea* significantly decreased the number of native plants emergence, regardless the number of functional groups composing the plant communities (χ^2 = 6.8, df = 5, p ≤ 0.05).

S. gigantea plants measurements

Although no statistical differences were found (effects for functional diversity levels: F= 0.5, df = 14, p> 0.05), emergence of *S. gigantea* plants showed a slightly negative tendency when in higher functionally diverse communities (FG3). However, such effects were not stronger enough to affect invasive plants emergence rates by competition (Figure S8b).

Figure S8: Effects of functional diversity (represented by the number of functional groups - FG) and *Solidago gigantea* (S) on plant emergence at the beginning of the experiment. Figure **(a)** shows native plants emergence in six combinations of functional diversity (levels 1, 2, 3) and presence or absence of the invasive alien plant. Figure **(b)** represents results for *S. gigantea* emergence under four levels of functional diversity (0, 1, 2, 3); FD 0 was a monoculture of *S. gigantea*. Plants emergence were evaluated during the second week of the experimental period for each one of the communities, invaded or not. For native plants, we informed chi-squared values of dependent variables. For *S. gigantea* plants, F-values are presented (*** $p \leq 0.001$; ** $p \leq 0.01$; * $p \leq 0.05$; **.** $p \leq 0.10$). NS means non-significant effects.

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