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Efeito da conversão de campos nativos do Bioma Pampa em plantações de Eucalipto sobre a
funcionalidade do solo

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**Efeito da conversão de campos nativos do Bioma Pampa em plantações de Eucalipto
sobre a funcionalidade do solo**

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Dedicatória

À Evanir da Silva Jorge, minha querida mãe,
que me ensinou sobre resistência, resiliência e amor.

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“Vejo a vida passar num instante
Será tempo o bastante que tenho pra viver?
Não sei, não posso saber
Quem segura o dia de amanhã na mão?
Não há quem possa acrescentar um milímetro a cada estação
Então, será tudo em vão? Banal? Sem razão?
Seria, sim seria, se não fosse o amor.”

Resumo

O florestamento de campos nativos com espécies exóticas de rápido crescimento (silvicultura) é a categoria de mudanças do uso da terra que mais cresceu nos últimos anos no bioma Pampa. Estudos ao redor do mundo têm demonstrado efeitos negativos deste tipo de cultivo sobre a biodiversidade. Entretanto, informações sobre os efeitos nas comunidades do solo ainda são escassas. Os organismos que vivem no solo são extremamente diversos e participam de uma vasta gama de processos ecossistêmicos que dão origem a serviços ecossistêmicos essenciais, tais como estoque de carbono, regulação do ciclo da água e produção de alimentos. Portanto, solos diversos são saudáveis e apresentam elevada funcionalidade, promovendo o funcionamento dos ecossistemas e o bem-estar humano. Diante desse contexto, nesta dissertação objetivamos investigar os efeitos da conversão de campos nativos do bioma Pampa em plantações de Eucalipto sobre a microbiota e a fauna do solo (grupo modelo: Collembola) considerados indicadores da funcionalidade do solo. O estudo foi desenvolvido em 20 unidades amostrais pareadas no bioma Pampa (10 campos nativos e 10 plantações de Eucalipto) distribuídos em quatro municípios no estado do Rio Grande do Sul. Em cada unidade amostral foi estabelecida uma transecção de 250 m onde foi coletado solo na camada de 0-5 cm. Metade das amostras foram utilizadas para determinação do pH e umidade gravimétrica do solo e do tamanho e atividade da comunidade microbiana (respiração basal do solo e atividade enzimática). A temperatura do solo e a riqueza de plantas foram mensuradas *in situ*. A outra metade foi utilizado para extração (14 dias) de colêmbolos pelo método de funis de *Berlese-Tüllgren*, que foram identificados e descritos quanto á seus atributos funcionais. Os efeitos da mudança no uso da terra foram testados através de modelos lineares mistos generalizados. Nossos resultados demonstram que a conversão levou à redução da riqueza da comunidade de plantas, o que tende a diminuir a diversidade e qualidade da serapilheira que entra nas cadeias tróficas do solo. Este efeito, associado ao solo mais ácido e seco das plantações, pode explicar a drástica redução observada do tamanho e atividade da comunidade microbiana, o que pode comprometer as funções relacionadas a ciclagem do carbono e nitrogênio, como a decomposição, fertilidade do solo e estoque de carbono. A comunidade de colêmbolos apresentou menor riqueza total e sua composição taxonômica e funcional foram alteradas com a conversão, o que pode resultar em mudanças nas teias alimentares. Além disso, apesar de um aumento na diversidade funcional de colêmbolos nas plantações com o incremento de atributos adaptativos para o sombreamento, houve diminuição da redundância funcional, o que tende a moldar as plantações de Eucalipto a um estado menos estável perante mudanças ambientais, o que pode comprometer a funcionalidade do solo. Entretanto, os indicadores de funcionalidade do solo foram inferiores nas plantações de eucalipto. Os resultados obtidos neste estudo são um passo adiante para ajudar a preencher essa lacuna no conhecimento ecológico, apoiando a elaboração de políticas de conservação dos campos do Pampa a partir de informações de base científica.

Palavras chave: Mudanças no uso da terra; Biodiversidade; Collembola; Microbiota

Abstract

Grassland afforestation with fast-growing exotic species (forestry) is the category of land use change that has grown the most in recent years in the Pampa biome. Studies around the world have shown negative effects of this type of land-use change on biodiversity. However, information about the effects on soil communities is still scarce. The organisms that live in the soil are extremely diverse and contribute to a wide range of ecosystem processes that underlies essential ecosystem services, such as carbon stock, regulation of the water cycle and food production. Therefore, soils with high diversity are healthy and present major functionality, promoting ecosystem functioning of and human welfare. At this context, in this dissertation we aim to investigate the effects of converting native grasslands of Pampa biome into *Eucalyptus* plantations on soil microbiota and fauna (model group: Collembola) which are considered indicators of soil functionality. The study was carried out in 20-paired sampling units in Pampa biome (10 grasslands and 10 *Eucalyptus* plantations) distributed in four municipalities in the state of Rio Grande do Sul. In each sampling unit, a 250 m transect was established where 10 points were sampled to collect soil in the 0-5 cm layer. The soil from five samples was used to determine soil pH and gravimetric moisture and the size and activity of the microbial community (soil basal respiration of and enzyme activity). Soil temperature and plant richness were measured *in situ*. The soil from the other five points was used for extraction (14 days) of collembolans by the *Berlese-Tüllgren* funnel method, which were identified and described by their functional attributes. The effects of land use change were tested using generalized mixed linear models. Our results demonstrate that grassland conversion led to a reduction in plant richness, which tends to decrease litter quality and diversity that enters the. This effect on soil trophic chains, associated with the a more acidic and drier soil may explain the drastic reduction observed in the size and activity of the microbial community that further can impair the functions related to carbon and nitrogen cycling, such as decomposition, soil fertility and carbon stock. The community of collembolans presented reduction of richness and had their taxonomic and functional composition altered, which can result in changes in the food webs and, consequently, in their functions. Our most unexpected result was the increase of functional diversity at the plantations by the increase on collembolans with forestry-adaptive traits. In addition, there was a decrease in functional redundancy, which tends to shape *Eucalyptus* plantations in a less stable state what may harm soil functionality towards environmental changes. However, the indicators of soil functionality were lower in *Eucalyptus* plantations. The results obtained in this study are a step forward to help fill this gap in ecological knowledge, supporting the elaboration of conservation policies in the Pampa grasslands with scientific-based information.

Keywords: Land-use change; Biodiversity; Collembola; Microbial community

Introdução geral

Problemática central

A biodiversidade é essencial para o bem-estar humano, pois é o principal regulador dos processos relacionados com a provisão de bens (*i.e.*, matéria prima, alimento) e serviços (*i.e.*, polinização, ciclagem da matéria), dos quais dependem as atividades econômicas e a qualidade de vida da sociedade humana (Lohbeck et al., 2016). Esses benefícios e serviços ecossistêmicos ofertados pelo capital natural são produtos de processos ecológicos majoritariamente mediados pela biodiversidade (Fisher & Turner, 2008). Por exemplo, o serviço ecossistêmico de ciclagem da matéria, que leva à disponibilização de nutrientes para as plantas e regula estoques de carbono no solo, é originado através do processo de decomposição no solo mediado pelos decompositores primários e secundários (Yang et al., 2018). Portanto, quanto maior a diversidade de um determinado sistema, maior a variedade de funções providas, devido a complementariedade de nicho e maior estabilidade (Soliveres et al., 2016).

O solo é um importante compartimento dos ecossistemas terrestres, pois suporta uma alta diversidade de espécies, abrigando cerca de 25% de toda a biodiversidade do planeta (Decaëns et al., 2006). A maioria dos serviços ecossistêmicos são suportados e regulados pelo solo, como por exemplo, a provisão de alimentos, estoque de carbono, regulação do ciclo da água e o controle de pragas e doenças (Jónsson & Davíðsdóttir, 2016). A provisão destas funções (funcionalidade do solo) está diretamente relacionada a suas propriedades físicas (*e.g.*, umidade, agregação, compactação, porosidade), químicas (*e.g.*, pH, disponibilidade de nutrientes) e principalmente, pelo seu componente biológico (*e.g.*, quantidade, diversidade e atividade de organismos) (Coleman, 2008). A funcionalidade do solo é caracterizada pela sua capacidade em promover as propriedades do ecossistema que originam os serviços ecossistêmicos (Adhikari and Hartemink, 2016).

A biota edáfica é composta por microrganismos e invertebrados, tais como ácaros, colêmbolos, isópodes, diplópodes, minhocas, cupins e alguns besouros. Esses organismos fornecem a base para a funcionalidade do solo através de suas atividades e complexas interações que promovem a fertilidade do solo (Figura 1). A microbiota age sobre a matéria orgânica e a ciclagem de nutrientes, nos processos de raízes e rizosfera e na produtividade primária. Micropredadores regulam as populações microbianas e de outros organismos que interferem nas propriedades do solo. Através do seu deslocamento, muitos organismos do solo são capazes de criar microporos ou túneis por meio de bioturbação, de acordo com o tamanho do corpo. Os

decompositores atuam na degradação da matéria orgânica do solo e mineralização dos nutrientes, que ficam disponíveis para serem utilizados novamente pelas plantas (Briones, 2014). Desta forma, estes organismos, em especial a microbiota e os decompositores, favorecem o crescimento de plantas e a sua produtividade (Wagg et al., 2014; Yang et al., 2018).



Figura 1. Interações tróficas e de engenharia do ecossistema entre os organismos do solo baseada no tamanho de corpo (adaptado de Briones, 2014).

Em ecossistemas terrestres, a diversidade de um compartimento pode promover a diversidade em outros, que é o caso dos links entre os compartimentos dentro e acima do solo (biota-plantas) (Lange et al., 2015; Winck et al., 2020). Esta regulação ocorre nos dois sentidos, por isso, quanto maior a diversidade de organismos edáficos maior a eficiência da transformação da matéria orgânica e maior fertilidade do solo (Hättenschwiler et al., 2005). A maior disponibilidade de nutrientes, propicia uma maior diversidade de plantas, que por sua vez, afeta positivamente a biota do solo, devido a entrada de serapilheira mais diversa (Cornwell et al., 2008). Portanto, a diversidade do solo afeta o funcionamento do ecossistema como um todo devido a seu efeito na produtividade primária, que é a base das cadeias alimentares terrestres (Bardgett and Van Der Putten, 2014; Briones, 2018).

Índices de funcionalidade do solo

A funcionalidade do solo tem sido fortemente relacionada com o conceito de qualidade do solo proposto por Doran & Parkin (1994). Segundo estes autores, uma maior qualidade do solo está associada ao seu funcionamento dentro dos limites de um dado ecossistema. Esse funcionamento deve garantir que o solo desempenhem algumas funções básicas, que são: i) servir como um meio de crescimento para as plantas; ii) regular os fluxos de água; iii) atuar como um tampão ambiental na atenuação e degradação de compostos tóxicos; e, iv) promover a ciclagem de elementos na biosfera (Barrios, 2007). Como as propriedades do ecossistema que

originam a funcionalidade do solo dependem diretamente da diversidade e papel desempenhado pelos organismos do solo, uma forma de avaliar a funcionalidade do solo é descrever as comunidades edáficas a partir da identificação dos organismos nele presentes e seus níveis de atividades (de Vries et al., 2013). Devido à alta complexidade das cadeias tróficas do solo e sua enorme diversidade, é comum que trabalhos utilizem grupos alvos e processos chaves, considerados bioindicadores (*proxy*), para avaliar sua funcionalidade.

A identificação de espécies e a distribuição de suas abundâncias é a forma mais clássica de descrever uma comunidade biológica (Vellend, 2010). A riqueza de espécies consiste no número de diferentes grupos taxonômicos presente dentro da comunidade. Os índices de diversidade, tais como Simpson e Shannon são cálculos que levam em consideração a abundância de cada espécie dentro da comunidade (Izsák and Papp, 2000) e auxiliam na identificação de quais espécies são raras e quais são dominantes. Quanto maior o número de espécies e quanto melhor distribuída estiver a abundância de indivíduos dentro da comunidade, mais diversa esta será considerada (Magurran, 2004).

Apesar dos indicadores baseados em espécies (taxonômicos) serem os mais tradicionais nos estudos de comunidades, eles possuem duas premissas que podem torná-los insuficientes para descrever as comunidades (Moretti & Legg, 2009). Ao usar indicadores taxonômicos, parte-se do pressuposto de que espécies diferentes desempenham funções diferentes. Por essa razão, cada espécie é considerada única e sua extinção pode ser interpretada erroneamente como perda da função que por ela desempenhada (Mouchet et al., 2010). Isso porque, espécies diferentes podem desempenhar funções semelhantes dentro da comunidade por possuírem características morfológicas e fisiológicas similares que resultam em sobreposição de nicho. Além disso, uma mesma espécie pode desempenhar diferentes funções de acordo com a fase de desenvolvimento dos organismos ou pelo gradiente ambiental. Desta forma, a extinção de uma espécie pode não representar necessariamente a perda de uma determinada função no solo, assim como a riqueza de espécies pode não ser o principal *driver* da funcionalidade do solo. Portanto, é importante acrescentar nas avaliações de diversidade, métodos complementares aos descritores taxonômicos para abranger a complexidade das comunidades biológicas.

Um método complementar nas avaliações de comunidades é a descrição dos organismos em atributos funcionais, que são as características morfológicas e fisiológicas que respondem às mudanças no ambiente ou que afetam funções no ecossistema (Violle et al., 2007). Através da descrição destes atributos para cada espécie ou indivíduo (*e.g.*, nível de pigmentação,

tamanho do corpo, tipo de mandíbula, número de olhos, tamanho dos apêndices) é possível avaliar quais funções ela desempenha e como está respondendo às alterações do ambiente. A variação dos atributos funcionais dentro de uma dada comunidade pode ser medida pela diversidade funcional (Mason et al., 2003). Quanto mais distintas forem as espécies da comunidade em termos de atributos, maior será a diversidade funcional e potencialmente mais funções serão providas (hipótese da complementariedade de nicho). Por outro lado, a semelhança funcional de determinadas espécies, denominada redundância funcional, também é importante no funcionamento das comunidades biológicas. Um certo nível de redundância funcional confere maior estabilidade às comunidades (*insurance hypothesis*) (Pillar et al., 2013) pois caso uma espécie seja localmente extinta, outra semelhante a ela seguirá cumprindo a função. Outro fator que pode ser determinante para a funcionalidade do solo é os atributos médios dominantes da comunidade, pois os atributos funcionais dos organismos mais abundantes da comunidade tendem a determinar as funções providas (*mass-ratio hypothesis*) (Bíla et al., 2014) (hipótese da razão de massa).

Neste trabalho, focamos nos microartrópodes (mesofauna) do grupo Collembola (Hexapoda) como representantes da biota do solo. Estes organismos se destacam por serem abundantes e diversos no solo e por sua influência em processos ecossistêmicos (Eisenhauer et al., 2011; Wang et al., 2009). Os colêmbolos controlam as taxas da mineralização de nutrientes e a disponibilidade de nutrientes no solo, seja diretamente pela fragmentação da serapilheira (Potapov et al., 2018) ou indiretamente por controlar a comunidade microbiana no solo através do pastejo seletivo de fungos e bactérias (Kaneda & Kaneko, 2008). Neste último caso, a atividade microbiana é regulada, modificando as taxas de mineralização dos nutrientes no solo (Coulibaly et al., 2019). Além disso, eles podem modificar a distribuição dos nutrientes na região da rizosfera, favorecendo a aquisição de nutrientes pelas plantas e promovendo seu crescimento (Eisenhauer et al., 2011).

Colêmbolos apresentam tamanho variando de 0,2 a 3 mm e podem ser classificados em três grupos definidos com base em seu hábito alimentar e na camada em que vivem no solo, que conseqüentemente refletem suas funções no ecossistema (Figura 2; Castaño-Meneses et al., 2004). O grupo epiedáfico inclui as espécies que vivem na superfície do solo e se alimentam preferencialmente de fungos e material orgânico de alta qualidade. São organismos que possuem atributos funcionais que favorecem sua movimentação, como apêndices locomotores bem desenvolvidos (pernas e fúrcula) e órgãos sensoriais para detecção de movimentos (ocelos) e alterações no ar (antenas e tricobótrios). O grupo euedáfico é composto por espécies de

colêmbolos que vivem dentro do solo e alimentam-se de fungos, algas, bactérias, compostos orgânicos e também são predadores oportunistas. Tendem a ser menos seletivos, pois apresentam menor mobilidade. Este grupo é caracterizado por indivíduos com pernas menores, ausência de fúrcula, ausência de olhos e presença de órgão pós-antenal e pseudocelos que substituem a visão. Por fim, o grupo hemiedáfico é composto por colêmbolos que vivem na interface solo-serapilheira, apresentando características ecológicas intermediárias entre o grupo epiedáfico e euedáfico. Através da movimentação vertical e horizontal, este grupo atua fortemente na mistura da matéria orgânica nas primeiras camadas do solo, podendo ter um forte efeito nos processos de mineralização.

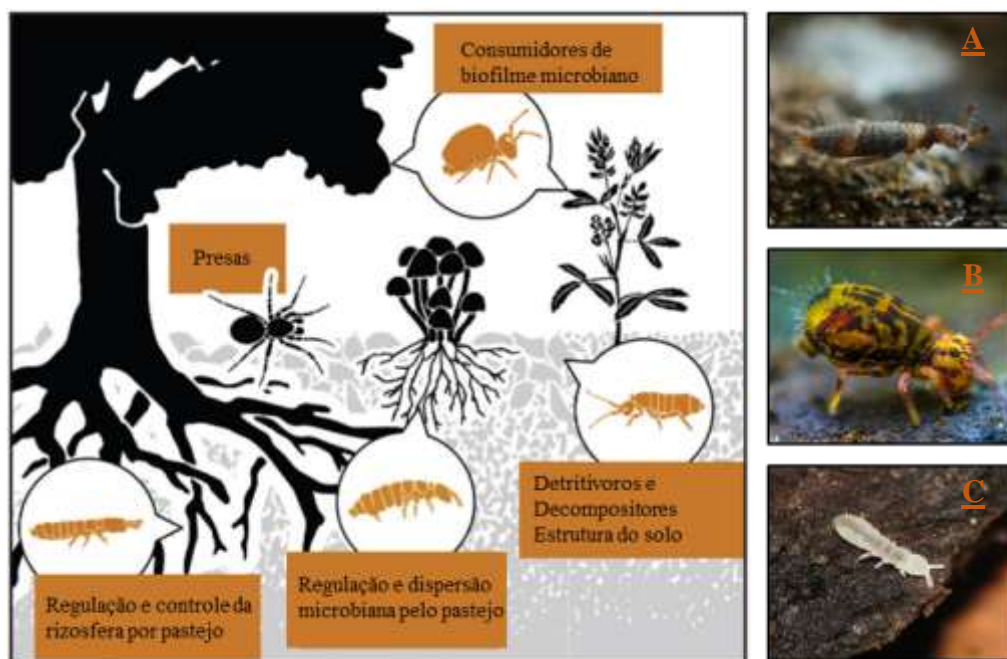


Figura 2. Processos ecossistêmicos que podem ser afetados por diferentes grupos funcionais de Collembola. O colêmbolos são divididos em 3 ordens: Entomobryomorpha (A), Symphleona (B) e Poduromorpha (C) são facilmente distinguíveis pelo seu formato de corpo, que está associado à profundidade em que vivem no solo. (Adaptado de (Potapov et al., 2020).

Plantações de Eucalipto no bioma Pampa

Devido à crescente demanda da população humana por alimentos, combustível e fibras, os ecossistemas naturais têm sido convertidos em áreas cultivadas ao redor de todo o mundo (Ellis, 2011). Juntamente com as mudanças climáticas, a mudança do uso da terra é considerada a principal causa de perda da biodiversidade, pois ecossistemas altamente diversos são substituídos por sistemas mais simplificados (*i.e.*, agricultura, pastagens e silvicultura) o que

leva à extinção de espécies nativas (Foley et al., 2005; Tsiafouli et al., 2015). Mudanças nos componentes da biodiversidade causam preocupações pois possuem potencial para alterar propriedades do ecossistema e a oferta de bens e serviços que eles provem (Hector & Bagchi, 2007). Como o solo é um importante componente do ecossistema, conhecer os efeitos dessas mudanças em seu componente biológico, sobretudo nos decompositores, é importante para o estabelecimento de políticas públicas de conservação e restauração que podem garantir os serviços ecossistêmicos e a qualidade de vida das gerações presentes e futuras.

Uma das principais atividades humanas que causam declínio da biodiversidade e qualidade do solo é o plantio em grande escala de árvores exóticas para produção de celulose (silvicultura) (Ellis, 2011). Um exemplo deste tipo de conversão são as monoculturas de Eucalipto na América Latina, que no Brasil ocupam aproximadamente 3 milhões de ha (Brockerhoff et al., 2008). Mudanças no uso do solo geralmente levam a mudanças nas propriedades do solo, como umidade, temperatura, teores de nutrientes e acidez (Leite et al., 2010; Zhang et al., 2012), afetando diretamente o habitat edáfico. Compreender os impactos de tais mudanças na biodiversidade do solo é especialmente importante em ecossistemas ameaçados e pouco conhecidos, como é o caso dos campos nativos do bioma Pampa (Guerra et al., 2020; Overbeck et al., 2007).

O bioma Pampa está situado no extremo sul do Brasil, no estado do Rio Grande do Sul, estendendo-se também pela Argentina e Uruguai, onde é então denominado Pastizales del Rio de la Plata. Abriga ecossistemas campestres altamente diversos que prestam importantes serviços ecossistêmicos através da polinização, de estoques de carbono no solo (principalmente via raízes) e por ser fonte forrageira para a pecuária (Overbeck et al., 2007). Trata-se de ambientes campestres naturais que co-evoluíram com grandes mamíferos pastejadores, atualmente extintos, e hoje o manejo tem sido mantido por atividades humanas como fogo e pecuária (Behling and Pillar, 2007). Quando a oferta de forragem é bem manejada, o uso destes campos como fonte forrageira para a produção animal é considerada sustentável, pois mantém a fisionomia campestre e favorece a conservação da diversidade de plantas e animais associados (Leidinger et al., 2017). Entretanto, ao longo do último século a vegetação natural tem sido substituída por pastagem plantada ou plantações em monocultivo (*i.e.*, silvicultura, soja, trigo e milho), totalizando uma perda de mais de 44% de sua área original (Projeto MapBiomas, 2019; Souza et al., 2020). A conversão dos campos nativos em silvicultura é a classe de mudança do uso da terra que mais cresce atualmente no bioma, com crescimento de mais de

5% ao ano, sendo que 60% destas áreas são ocupadas por espécies de Eucalipto (Figura 3; Projeto MapBiomias, 2019).

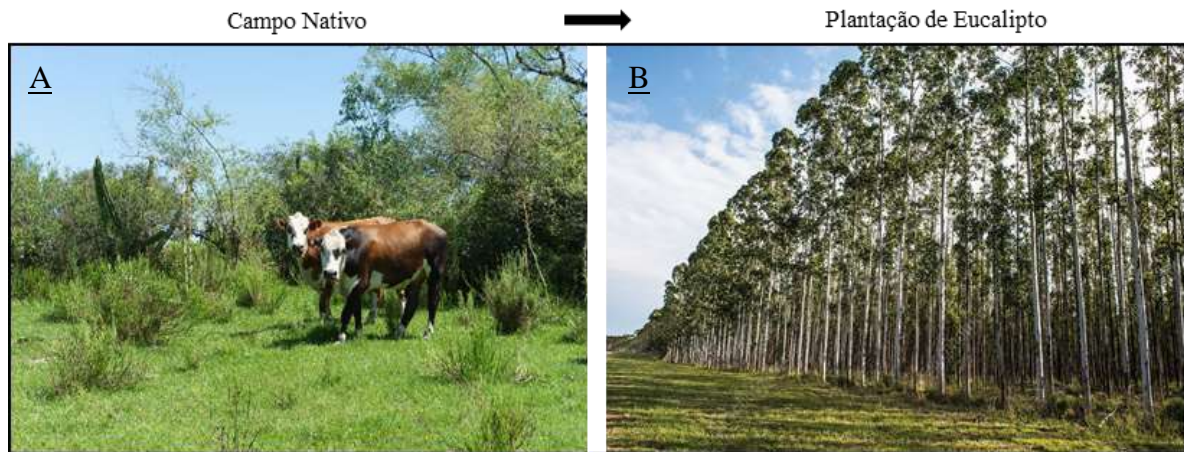


Figura 3. Área de campo nativo do bioma Pampa com alta diversidade de espécies vegetais mantida pelo pastejo (A) comumente convertida em áreas de monocultivo de Eucalipto (B), alterando drasticamente a estrutura da vegetação.

O Eucalipto é uma espécie de árvore nativa da Austrália, portanto é exótica no Brasil. Quando plantada em larga escala para a produção de madeira e celulose tende a diminuir drasticamente a diversidade da comunidade de plantas, tornar o solo mais seco e mais ácido (Becerra et al., 2018; Chen et al., 2013b; Zhu et al., 2019). As alterações são ainda mais drásticas quando a conversão ocorre em ecossistemas não-florestais, nos quais as espécies presentes não são adaptadas a ambientes sombreados, de dossel fechado. A mudança na estrutura da vegetação leva à diminuição da incidência de raios UV e, portanto, alterações no microclima. Portanto, essa transição de ambientes abertos para ambientes sombreados representa uma importante alteração nos filtros ambientais que moldam a comunidade edáfica e podem alterar sua composição taxonômica e funcional (Martins et al., 2016; Salmon et al., 2014; Winck et al., 2017).

Ao longo dos últimos anos alguns estudos que investigaram o efeito da conversão de campos nativos do bioma Pampa em plantações de Eucalipto sobre a diversidade de plantas e animais que vivem acima do solo (*e.g.*, Medan et al., 2011; Saccol et al., 2017; Souza et al., 2013) demonstraram o padrão majoritário de efeitos negativos sobre os indicadores de biodiversidade. Entretanto, estes padrões ainda são pouco explorados quanto aos efeitos em organismos e propriedades do solo. Rieff et al. (2016) em um trabalho em escala local demonstrou aumento da abundância da fauna edáfica em áreas de Eucalipto. O trabalho de

Winck et al. (2017) demonstrou efeito negativo (*i.e.*, diminuição dos indicadores taxonômicos e funcionais de diversidade) perante a intensificação do uso da terra, incluindo plantações de Eucalipto. Este trabalho contribuiu para o avanço do conhecimento sobre os efeitos da conversão dos campos nativos do bioma Pampa, através da inclusão de análises baseadas em atributos funcionais. Mais recentemente, Boeno et al. (2020) avaliou o efeito da idade do plantio na comunidade do solo e Sabbatté et al. (2021) verificou o efeito da conversão sobre as cadeias tróficas do solo, sendo este último um estudo realizado na porção argentina do bioma. Embora alguns pesquisadores tenham explorado separadamente alguns efeitos na comunidade microbiana e algumas propriedades do solo (*e.g.*, Lupatini et al., 2013; Sicardi et al., 2004) estes trabalhos não apresentam uma abordagem integrada que abranja a discussão dos efeitos do florestamento com Eucalipto sobre a funcionalidade do solo.

Estudos avaliando comunidades edáficas ainda são incipientes no bioma Pampa (Cameron et al., 2018) e esta realidade é replicada também para os campos subtropicais como um todo, onde permanecem lacunas sobre os efeitos desse tipo de mudança no uso da terra. Contudo, essa dissertação teve como objetivo investigar os efeitos da conversão de campos nativos do bioma Pampa em plantações de Eucalipto sobre a funcionalidade do solo. Precisamente, avaliamos mudanças na estrutura funcional e taxonômicas da comunidade de colêmbolos, assim como o efeito em processos ecológicos mediados pela comunidade microbiana.

Nós hipotetizamos que o florestamento de campos nativos com Eucalipto levará à redução da umidade, pH e temperatura do solo. Além de redução da biodiversidade de plantas e colêmbolos (de Filho et al., 2016; Sousa et al., 2000; Winck et al., 2017) e diminuição do tamanho e da atividade da comunidade microbiana (Chen et al., 2013; Zhu et al., 2019). Devido às alterações microclimáticas associadas à mudança de um ecossistema de dossel aberto para um ecossistema de dossel fechado, são esperadas alterações na composição funcional (CWM) e taxonômica de colêmbolos (Martins et al., 2016; Winck et al., 2017). Tais mudanças em compartimentos-chave do ecossistema representam diminuição da funcionalidade do solo, o que pode comprometer os serviços ecossistêmicos associados.

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Capítulo 1

Effects of grassland conversion to *Eucalyptus* plantations on soil functionality in Southern Brazil

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Highlights

- Microbial biomass and activity and taxonomical and functional diversity of Collembola were used as soil functionality indicators.
- Grassland afforestation led to soil acidification and decline of plant richness, soil microbial community size and general and specific activity.
- Grassland afforestation diminished Collembola richness and functional redundancy.
- Collembola taxonomical and functional composition were also altered.
- The Community Weighted Mean traits values changed from open-habitat traits to forestry-adaptive traits.

Abstract

Grassland afforestation has led to soil degradation worldwide. In subtropical grasslands, *Eucalyptus* plantations have largely increased during the last decade. Soil functionality monitoring can improve our ability to better formulate conservation strategies. Here we hypothesized that the conversion from natural grazed grasslands to commercial *Eucalyptus* plantations will alter soil biological properties and consequently soil functionality in South Brazilian grasslands. For this, we compared soil properties, plant richness, microbial parameters and diversity indicators of a key-group of soil fauna (Collembola) between the two land-use types in a paired sampling design. Plant richness, soil pH, moisture and temperature decreased significantly, what represents shifts on microhabitat conditions, a clear environmental filter, for microbial and Collembola communities. Microbial biomass, respiration and enzymes activities were negatively affected by land-use change, which can impair functions as decomposition, soil fertility and carbon stock. Collembola richness and functional redundancy was diminished which may shape *Eucalyptus* plantations in a less stable state, and harm soil functionality towards environmental changes and biodiversity loss. In addition, Collembola taxonomic and functional composition were altered, which can result in changes in the food webs. The Community Weighted Mean traits values changed from open-habitat traits to forestry-adapted traits, what leads to our most unexpected result was the increase of functional diversity. However, the indicators of soil functionality were lower in *Eucalyptus* plantations. Our results are in accordance with others around de the World that shows a major pattern of negative effects of *Eucalyptus* plantations on ecosystem diversity and functioning.

Keywords: Land-use; Collembola; Soil microbiota; Soil enzymes; Functional diversity

Introduction

Soils support and regulate a variety of environmental, social and economic functions (Blum, 2005; Wagg et al., 2014), being considered the main provider of ecosystem services that support life on the planet (Ponge, 2015). Soil ecosystem services include: provision of food and fuel, regulation of water, climate and pollution and disease control (Jónsson and Davíðsdóttir, 2016; Wall et al., 2015). The ability of soil to perform such functions depends on ecological processes that are mediated by its biological component (de Vries et al., 2013). The wide diversity of microorganisms and animals that live in soil underlies soil functionality through the decomposer food web (Briones, 2018; García-Palacios et al., 2013) by influencing soil formation (*i.e.*, bioturbation), nutrient cycling (*i.e.*, decomposition) and plant growth (Briones, 2014). Likewise, evidences also points that soil biodiversity plays a key role on the resistance and resilience of ecosystems in face of environmental perturbations (Adhikari and Hartemink, 2016; Bardgett and Van Der Putten, 2014). Therefore, soil biodiversity is a critical component of ecosystem functionality and its capacity to perform services considered essential to achieve global environmental sustainability (Bach et al., 2020; McBratney et al., 2014).

The structure of the soil biological communities relies not only on the natural soil forming factors but also on human activities (*i.e.*, agriculture, forestry, urbanization) (Blum, 2005; Tsiafouli et al., 2015). Land-use changes are globally affecting belowground communities, causing declines in soil biodiversity, that can reduce and impair its provision of benefits (Tsiafouli et al., 2015; Vandewalle et al., 2010). Therefore, soil biodiversity monitoring by using indicators of biological community changes is highly required. Among soil biota, springtails (Hexapoda: Collembola) are abundant and numerous in species (Hopkin, 1997) considered representatives of the soil fauna, being used as a model group in soil biodiversity assessments (*e.g.*, Martins et al., 2016; Parisi et al., 2005; Sousa et al., 2006; Winck et al., 2017).

Collembola directly enhance soil mineralization and nutrient availability by feeding on litter (Potapov et al., 2018) and microbial communities (Kaneda and Kaneko, 2008), mainly fungal hyphae. In turn, soil microbiota growth and activity are stimulated, increasing the release of enzymes that catalyze many biochemical reactions related to the breakdown of complex organic molecules, accelerating the mineralization processes (Li et al., 2009). Also, by excreting nutrient-rich fecal pellets, Collembola influence nutrient distribution in the rhizosphere (Eisenhauer et al., 2011; Hopkin, 1997). Therefore, the balance of negative and positive interactions between microbial and Collembola communities are often associated with improvements on soil fertility and plant performance (Forey et al., 2015; Verma and Paliwal, 2010), as well as with plant diseases control (Meyer-Wolfarth et al., 2017).

In order to evaluate responses of collembolan communities to environmental changes, studies have already shown that a combined approach of taxonomic and functional indicators are the most adequate (Reis et al., 2016; Salmon et al., 2014; Winck et al., 2017). Functional diversity is a dimension of biodiversity described by niche-based characteristics of species or individuals, called functional traits, which reflect their responses to the environment factors, as well their effects on the ecosystem functioning (Violle et al., 2007). Two main mechanisms have been hypothesized to regulate the influence of traits composition on ecosystem processes and therefore, soil functionality. The mass ratio hypothesis (Grime, 1998) states that the effect of a species on a given ecosystem process is proportional to its relative abundance in the community. Therefore, ecosystem processes should correlate with the community-weighted mean trait scores (CWM). While, the niche complementarity hypothesis argues that it is the degree of trait variation (*i.e.*, functional diversity) within a community that matters most, as higher complementarity in resource use between species may promote a more efficient acquisition of resources, and hence higher number of functions (Balvanera et al., 2006; Díaz, et al., 2006). The functional redundancy is the fraction of species diversity not expressed by functional diversity, which represents the species that are functionally similar but may differ in their responses to changes in environmental factors or disturbances. According to the insurance hypothesis (Yachi and Loreau, 1999), functional redundancy buffers the local extinction of individual species leading to ecosystem stability (Biggs et al., 2020; Pillar et al., 2013).

Several works have showed that changes in taxonomical and functional structure of soil organism directly affect microbial community and all ecological functional related to them. Among many microbial indicators to measure soil quality, Muscolo et al. (2015) suggests the eco-physiological indices such as community size (*i.e.*, microbial carbon) and activity (*i.e.*, soil basal respiration) which may measure soil functions status.

Large-scale afforestation, concerning the planting of trees in naturally canopy-open ecosystems (Chazdon et al., 2016), is considered one of several types of human activities leading to loss of soil quality (Ellis, 2011). Afforestation with *Eucalyptus*, for example, usually leads to changes in soil properties, such as humidity, temperature, nutrient contents and acidity (Leite et al., 2010; Zhang et al., 2012), reducing soil biodiversity. In Brazil context, about 5.92% of converted lands are covered by afforestation with exotic species, mainly *Eucalyptus* plantations (Brockerhoff et al., 2008, MapBiomass Project, 2019). Therefore, understanding the impacts of native vegetation conversion to *Eucalyptus* plantation on soil biodiversity and consequently on soil ecosystem functioning is essential for the development of effective biodiversity conservation strategies (Briones, 2018) since soil-based conservation comprise all

terrestrial diversity. This especially important in threatened and poorly know ecosystems, such as the subtropical grasslands (Zhao et al., 2020).

The subtropical grasslands of southern Brazil are biodiversity-rich and poorly studied ecosystems (Overbeck et al., 2007) that supports a wide range of ecosystem services, such as livestock and forage production (Nabinger, 2009). These grasslands coevolved with large herbivore mammals already extinct and nowadays the management has been maintained by human activities like fire and mostly, livestock grazing (Behling and Pillar, 2007). The livestock grazing can be beneficial to biodiversity conservation if adequately managed to keeps patches of intensive and alleviated levels of grazing which maintains a heterogeneous vegetation structure that supports biodiversity and ecosystem functioning (Ferreira et al., 2020). Less than 1% of the area of the southern Brazilian grasslands is currently protected in legal reserve areas, while most of its extension remains in private areas under livestock grazing (Metzger et al., 2019). In the last 33 years, activities like afforestation and temporary crops increased rapidly, summing up a loss of more than 44% of the area of grasslands on Pampa biome (Souza et al., 2020). Land-use change by afforestation is the category with major conversion rate, more than 5% per year and represents more than 4% of the Pampa biome area (Souza et al., 2020), with 60% of these being of *Eucalyptus* plantations (MapBiomas Project, 2019).

Soil ecology studies are particularly incipient in Brazilian grasslands (Cameron et al., 2018), thus there is a huge lack of knowledge regarding the impacts of afforestation of grassland on soil biodiversity and its related functions. Here we aimed to fill this gap by investigating the effects of converting native subtropical grasslands to *Eucalyptus* plantations on soil functionality, which can be defined as the capacity of the soil to promote and regulates ecosystem processes that sustains plants, animals and humans (Bünemann et al., 2018; Lehmann et al., 2020). We hypothesized that, despite considerably reducing plant diversity, *Eucalyptus* plantations will lead to changes in soil properties, such as decreasing soil moisture and acidification, which may modulate biota community and reduce microbial activity (Chen et al., 2013; Zhu et al., 2019). We expect to find a lower abundance, taxonomical and functional diversity in Collembola communities in *Eucalyptus* (de Filho et al., 2016; Sousa et al., 2000; Winck et al., 2017), and changes in taxonomical and functional trait composition, potentially selecting organisms with forest-adapted traits (Martins et al., 2016; Winck et al., 2017).

Material and methods

Site description

We carried out the study in the Pampa biome in South Brazil. The study region is located in a transitional zone between tropical and temperate climate, being classified as humid subtropical (Cfa, Köppen climatic classification) (Peel et al., 2007). Predominant type of soils are Acrisols and Leptsols. Vegetation is formed by mosaics of forest (semi-deciduous seasonal) and dominantly grasslands (Cordeiro et al., 2009) regionally known as *Campos*.

Sampling was based on 10 paired grassland-*Eucalyptus* plantations (20 sites) distributed in four different municipalities of Rio Grande do Sul state (Pinheiro Machado, Jaguarão, Lavras do Sul and São Gabriel). Within each site, we established a transection of 250 m, 100 meters away from the edge of another land-use type, allocated in similar soil conditions (*i.e.*, soil type and elevation level) of its respective pair. Along the transection, we established five sampling 1 m x 1 m plots (*i.e.*, one at every 50 meters) where we sampled abiotic and biotic variables. The 10 grassland sites were located in private farms with extensive grazing management. *Eucalyptus* plantation sites were adjacent or nearby the grasslands and presented a standardized age of approximately 10 years. All samplings occurred between November 2018 and April 2019.

Vegetation Sampling

The plant community was surveyed for species richness on ten 1 m x 1 m plots distributed along the transection (*i.e.*, one at every 25 meters) between the soil samples plots.

Soil sampling

In each plot, we took two soil cores with a steel cylinder (\varnothing 6 cm, 5 cm depth), being one for analyses of pH, gravimetric moisture (mg g^{-1}) and microbial community parameters related to microbial community size and activity (Monteiro and Frighetto, 2000), and another for fauna extraction (Figure 1). During soil sampling, we measured soil temperature ($^{\circ}\text{C}$) at 5 cm depth using digital thermometer.

Microbial biomass carbon (MBC) was determined by using the fumigation-extraction method (Vance et al., 1987). Soil samples were fumigated with alcohol-free CHCl_3 for 24 h at 25 $^{\circ}\text{C}$. Dissolved C in both fumigated and non-fumigated samples were extracted with 0.5 M K_2SO_4 and determined according the method proposed by Silva et al. (2007). MBC was estimated based on the differences between the organic C extracted from the fumigated soil and that from the unfumigated soil, and an extraction efficiency coefficient of 0.33 was used to convert soluble C into biomass C (Vance et al., 1987).

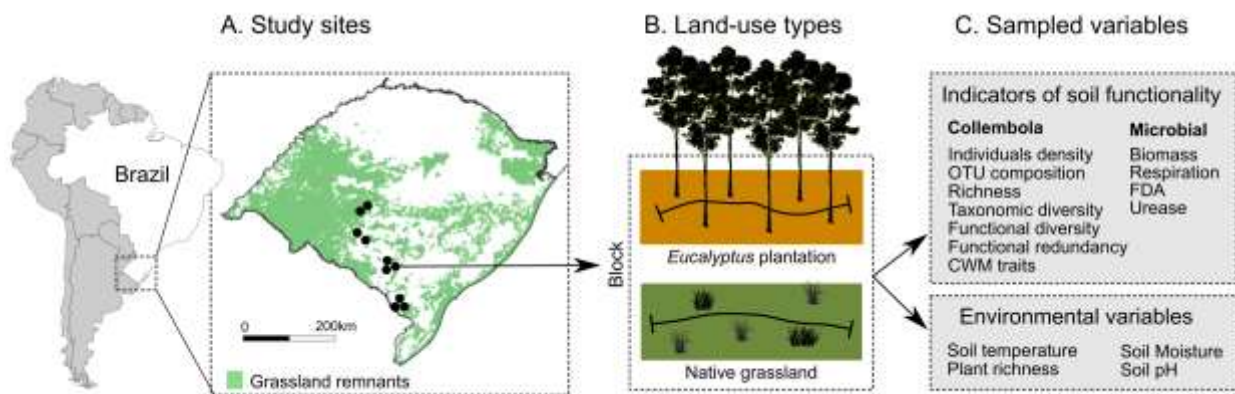


Figure 1. Grassland remnants in southern Brazil and location of the 10 paired grassland-*Eucalyptus* plantations (A). In each site, we established a transection of 250m, represented by the continuous line (B), from where indicators of soil functionality and environmental variables were sampled (C).

Microbial activities were measured by soil respiration and enzyme activity. We determined soil respiration by estimating CO₂ production after incubation of soil during 10 days at 23°C, with the moisture content adjusted to 60% of water-holding capacity, in glass jars (1000 mL) with 10 mL of 1 M NaOH (Silva et al., 2007). Enzyme activity was determined through the release of fluorescein diacetate (FDA) hydrolysis, that measure the degradation of proteins, esters and lipids by protease, esterase and lipase, and urease enzyme activity that is involved in the transformation of nitrogen from amine (NH₂) to ammonium (NH₄⁺) and carbon dioxide (CO₂).

The urease activity was measured by determining the ammonium released after incubating the soil with urea solution for 2h at 37°C (Kandeler, 1988). After 30 min of shaking and 5 min of centrifugation, released ammonium was extracted and determined by colorimetry using the salicylic acid method at 660 nm (EMBRAPA, 1997). Urease activity was expressed as ammonium (NH₄-N) released per unit soil weight and incubation time. FDA activity was measured through fluorescein diacetate hydrolysis, which hydrolyze colorless FDA to release a colored end product fluorescein (Schnurer and Rosswall, 1982). Absorbance of the supernatants were measured on a spectrophotometer at 490 nm.

Collembola sampling

Soil fauna were extracted from the collected soil by using modified *Berlese-Tullgren* funnels for 14 days and stored in 70% ethyl alcohol. Collembola specimens were sorted, clarified, and fixed on slides with Hoyer for further identification in family (Zepellini and

Bellini, 2004) and genus level (Cipola et al., 2018) when possible. Therefore, from now it will be referred as operational taxonomic units (OTUs).

To evaluate the functional responses of Collembola communities to the *Eucalyptus* afforestation we described the organisms in functional morphological traits (Winck et al., 2017). We measured traits that mirror their habitat preferences (*i.e.*, body pigmentation level, presence of scale, furca development, body size, number of ocelli, antenna and leg length), drought tolerance (body size) and sensorial ability (presence of post antennal organ, pseudocelli, antenna length and number of ocelli). The Image J software (Rueden et al., 2017) was used to measure the size of body, antenna and legs on the photos taken on microscope. All the nine traits were directly measured on every single individual using an optical microscope. For analysis, we used the mean value of the traits of each OTU. All traits, data type, relationship with the environment and how they were measured are listed in **Table 1**.

All dependent variables were averaged among the plots per site, except Collembola community variables that were pooled to provide site-level data.

Collembola community data were organized in two matrices: matrix **W**, containing the abundances of Collembola OTUs in each site, and matrix **B** which includes all OTUs described in functional traits. We used matrix **W** to calculate OTU richness, Simpson diversity and Shannon diversity per site using the “Vegan” package in R (Oksanen et al., 2019). We used the matrices **W** and **B** to calculate functional diversity (Rao's Q index), functional redundancy and community-weighted mean trait scores (CWM), which further characterizes the functional composition of the community (De Bello et al., 2010; Pillar et al., 2013; Pillar and Duarte, 2010; Vandewalle et al., 2010), with the “SYNCSA” package in R (Debastiani and Pillar, 2012).

Functional diversity (FD) is based on the quadratic entropy of Rao (1982), which summarizes the sum of dissimilarity of the traits d_{ij} , in the range of 0-1, between OTU i and j weighted by the relative abundance of OTUs ($p_i p_j$) in the community.

$$FD = \sum_{i=1}^s \sum_{j=1}^s d_{ij} p_i p_j$$

Functional redundancy (FR) (De Bello et al., 2007) is defined as the difference between species diversity (D) and functional diversity. FR values range from 0 to 1 and when the OTU's are completely different for the traits, then $FR = 0$ and $FD = D$. When all the OTU's are identical for all traits, then $FR = D$ and $FD = 0$.

$$FR = D - FD$$

CWM are the mean of a given functional trait weighed by the relative abundance p_i of the i Collembola taxa and x_i is the trait value for OTU i .

$$CWM = \sum_{i=1}^s p_i x_i$$

Statistical analyses

We tested for effects of *Eucalyptus* afforestation on local environment parameters (pH, gravimetric moisture, soil temperature at the sampling moment and plant richness), microbial community (microbial biomass and soil respiration), enzyme activity (FDA and urease) and Collembola community (density of individuals, richness, Shannon and Simpson diversity, functional diversity and functional redundancy) with generalized linear mixed models (GLMM). Land-use type (grassland or *Eucalyptus* plantation) was the predictor variable. Block identity (10 pairs) nested within municipalities (4) were considered random variables. All variables were fitted to a normal distribution. The Collembola density variable were log-transformed transformed in order to to meet assumptions of normality. We build models using function *lme* from the package nlme; Pinheiro et al. (2014). The models were tested against a null model by ANOVA and both marginal and conditional R^2 values (Nakagawa and Schielzeth, 2013) were calculated as a goodness of fit measure with the package MuMIn (Barton, 2019). All models were submitted to residual analysis to evaluate adequacy of the error distribution.

Table 1. Description of Collembola functional traits evaluated in this study with their ecological responses to land-use change.

Functional trait	Ecological Role	Data type
Body pigmentation level	Protection against UV radiation and camouflage	0 = absent
		1 = present
Scales	Protective features against luminosity and UV radiation	0 = absent
		1 = present
Furca development	Disperse and movement; Predator escaping	0 = absent
		1 = vestigial 2 = developed
Ocelli number	Habitat preference; Sensorial ability; Defense against predators	Count
Body size	Protective features against desiccation	Millimeters
Antennae length	Sensorial ability; detection and selection of available resources	Millimeters

Leg length	Disperse and movement; Predator escaping	Millimeters
		0 = absent
Post antennal organ	Sensory organ; Detection of food source	1 = present
		0 = absent
Pseudocelli	Sensory organ; Detection of microclimate changes and presence of food source	1 = present

Richness is a diversity measure that is largely affected by the number of sampled individuals in a community (Gotelli and Colwell, 2001). We controlled this dependence when comparing Collembola OTU richness of grassland and *Eucalyptus* plantations by using individual-based rarefaction (interpolation) and extrapolation curves value of abundance with 95% confidence intervals (Colwell et al., 2012). We extrapolate the total abundance of the less abundant land-use type, until the total abundance of the most abundant land-use type. We also compared richness between land-use types based on samples of equal coverage by using coverage-based rarefaction Chao and Jost (2012). We used the INEXT package (Hsieh et al., 2016). The sample coverage is a measure of sample completeness, giving the proportion of the total number of individuals in a community that belong to the OTU represented in the sample. The coverage-based rarefaction and extrapolation standardize samples by completeness rather than size like traditional size-based rarefaction, which is more efficiently to find the correct ranking of communities according to their true richnesses (Chao and Jost, 2012).

Variation of the taxonomical composition of Collembola between land-use types was explored with a non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity of matrix **W**. We further tested for differences between land-use types with PERMANOVA with 999 permutations (function Adonis from package vegan; Oksanen et al., 2020).

Since CWM computation for a local community is based on the trait values for the OTUs occurring in the community, the CWM values are influenced to some extent by the species distribution across the sites (Peres-Neto et al., 2017). Therefore, we use a novel approach of a permutation that involving site and taxa shuffle for evaluate the effects of land-use change on CWM. The test was based on permute the values among the sites and separately, among the OTUs, for control the association between CWM and the environmental gradient of interest. We used an adaptation of the function *CWM.sig* proposed by Duarte et al. (2018) that generates two probability values. Using site shuffle, if the null hypothesis is rejected, we conclude that the land-use type affects the distribution of species. The second value is the one we have interest, it refers to the influence of the land-use type on the variation of the CWM, not only as

an effect of the variation in the species composition (via taxa shuffle). These indices were calculated for each site, that is, all the sub-samples from the transection were averaged. The effect was evaluated by Gaussian models.

Moreover, we added an ordination biplot with the NMDS results of Collembola community and the CWM traits that significantly varied among the land-uses based on the linear model analysis. All analysis were performed using R software (R Core Team, 2020).

Results

Environmental and microbial parameters

Grassland conversion to *Eucalyptus* plantation negatively affected all environmental and microbial parameters (**Table 2**). Soils of *Eucalyptus* plantations were more acid ($p=0.001$; **Figure 2A**) and presented lower temperature ($p<0.001$; **Figure 2C**), as well as decreased herbaceous plant richness ($p<0.001$; **Figure 2D**) when compared to grasslands. Gravimetric moisture was not affected ($p=0.41$; **Figure 2B**).

Eucalyptus plantations also presented reduced microbial biomass ($p=0.02$; **Figure 3A**), soil respiration ($p<0.001$; **Figure 3B**), and activity of the soil enzymes FDA ($p<0.001$; **Figure 3C**) and urease ($p<0.001$; **Figure 3D**).

Table 2. Mean, standard deviation and results of linear mixed models of abiotic and biotic parameters of soil measured in native grasslands and *Eucalyptus* plantations in Southern Brazil.

Explanatory Variable	Land-use type		F	p	R ² m	R ² c
	Grassland	Eucalyptus plantation				
<i>Environmental parameters</i>						
pH	5.85 ± 0.23	5.44 ± 0.45	F _{1,9} = 9.65	0.01	0.24	0.51
Gravimetric moisture (g water/g ⁻¹ soil)	0.20 ± 0.12	0.175 ± 0.09	F _{1,9} = 0.74	0.41	0.01	0.52
Temperature (°C)	20.77 ± 2.06	18.28 ± 1.69	F _{1,9} = 12.08	<0.001	0.31	0.50
Mean plant richness (m ²)	12.02 ± 3.31	1.71 ± 0.65	F _{1,8} = 138.51	<0.001	0.83	0.89
<i>Microbial parameters</i>						
Microbial biomass (mg C g ⁻¹)	527.24 ± 210.78	336.31 ± 113.9	F _{1,9} = 7.32	0.02	0.25	0.35
Soil respiration (mg CO ₂ g ⁻¹)	707.76 ± 647.43	303.02 ± 276.68	F _{1,9} = 10.69	<0.001	0.12	0.77
FDA (mg/g soil)	39.65 ± 13.57	24.43 ± 10.55	F _{1,9} = 39.97	<0.001	0.29	0.86
Urease (mg/g soil)	5.43 ± 2.13	2.84 ± 1.42	F _{1,9} = 22.55	<0.001	0.34	0.70

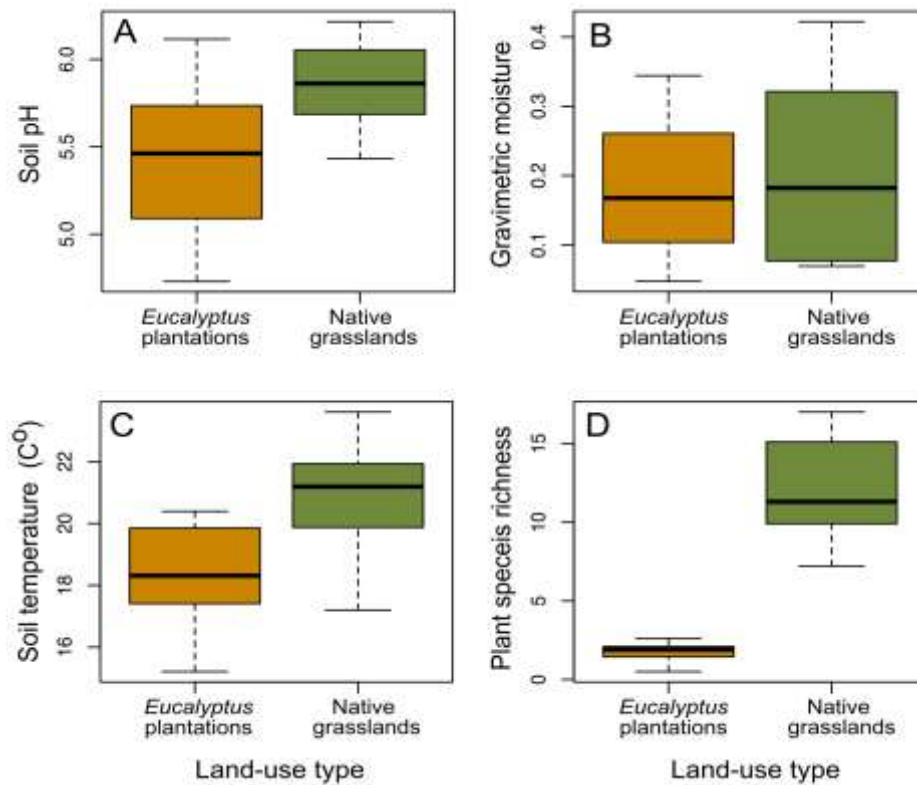


Figure 2. Boxplot of soil pH (A), gravimetric moisture (g water/g-1 soil) (B), soil temperature (C) and plant community richness (D) in *Eucalyptus* plantations and native grasslands in Southern Brazil. Each boxplot represents: smallest and largest observations (external bars), lower and upper quartiles (limits of the box) and median (within-box black line).

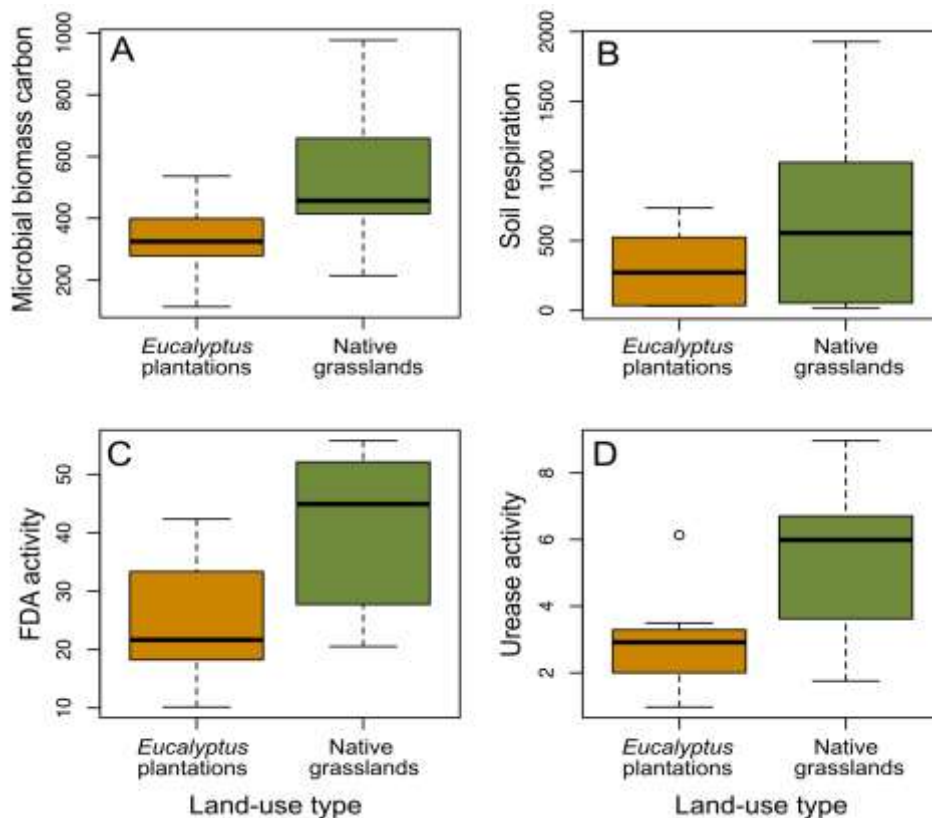


Figure 3. Boxplot of (A) microbial biomass carbon ($\mu\text{g C/g-1 soil}$), (B) soil respiration ($\text{mg CO}_2/\text{g-1soil}$), (C) FDA activity ($\text{mg fluorescein/g soil}$) and (D) Urease activity (mg/g soil) in *Eucalyptus* plantations and native grasslands in Southern Brazil. Each boxplot represents: smallest and largest observations (external bars), lower and upper quartiles (limits of the box)

Collembola community

We collected 209 individuals in our study, 114 of these on grasslands and 95 in *Eucalyptus*. In total, we identified 20 *Collembola* OTUs, being 17 sampled in grasslands and 12 in *Eucalyptus* plantations. Individual-based rarefaction and extrapolation curves showed no significant differences in this accumulated *Collembola* OTU richness in grasslands and *Eucalyptus* plantations, considering the overlap of 95% confidence intervals (**Figure 4A**). However, coverage-based rarefaction curves indicated significantly higher OTU richness in grasslands when standardizing the sample coverage of the land-use types, which was 96% in the tree plantations and 93% on grasslands (**Figure 4B**).

The 20 *Collembola* OTUs were classified among six families: Entomobryidae, Isotomidae, Brachystomellidae, Ondontellidae, Onychiuridae and Bourletiellidae. Ninety-five percent of the individuals were classified until genera, 3% only until family level, and 2% of the individuals only at the order level (**Supplementary Table 1**).

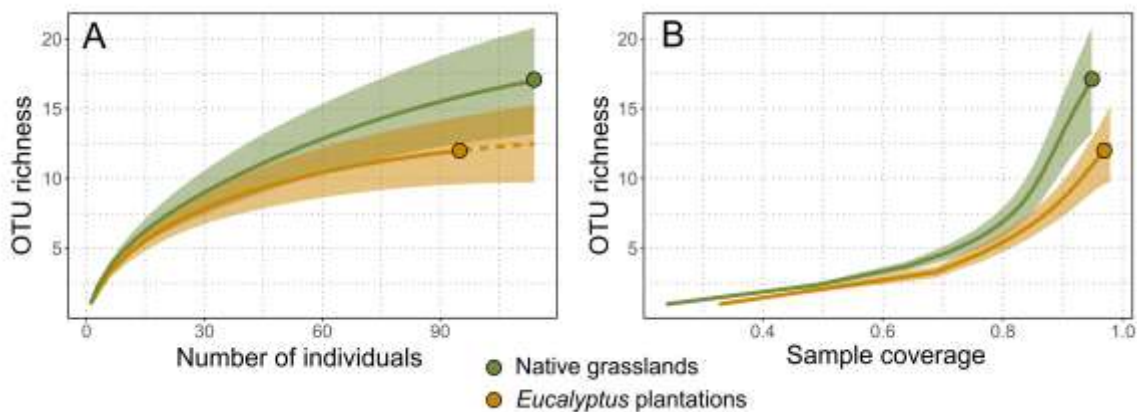


Figure 4. Rarefaction (interpolation) and extrapolation curves of *Collembola* OTU richness between native grasslands and *Eucalyptus* plantations based on abundance of individuals (A) and sample coverage (B). Full lines represent data interpolation and dashed lines represent data extrapolation. Lighter colored areas indicate a 95% confidence interval.

In grassland sites, we found eight exclusive OTUs (*Drepanura*, *Seira*, *Arlea*, *Folsomiella*, *Superodontella*, *Brachystomella*, *Sminthurinus* and Bourletiellidae). In *Eucalyptus* plantations, we recorded three exclusive OTUs (*Axelsonia*, *Psammisotoma* and *Agraphorura*). *Brachystomella* and *Thalassaphorura* were the most abundant OTUs in the study, being highly associated with the grasslands and *Eucalyptus* plantation respectively (**Supplementary Table 1**). The rarest OTUs (*i.e.*, singletons) were *Drepanura*, *Seira*, *Arlea*, *Folsomiella*, *Superodontella*, *Psammisotoma* and *Agraphorura*. Only the latter two were

present in *Eucalyptus* samples while all other were present only in grasslands (**Supplementary Table 1**).

We did not detect significant differences between land-use types regarding mean local Collembola density ($p=0.61$; **Figure 5A**), OTU richness ($p=0.34$; **Figure 5B**), Simpson diversity ($p=0.83$; **Figure 5C**) and Shannon diversity ($p=0.53$; **Figure 5D**) (**Table 3**). However, Collembola functional diversity (Rao's Q index) was significantly affected by conversion ($p=0.02$), presenting increased values on *Eucalyptus* plantations (**Figure 5E**) while functional redundancy was higher on grasslands ($p=0.01$; **Figure 5F**). The traits values of each OTU are described on **Supplementary Table 2**. PERMANOVA detected clear distinct community composition between the land-use types ($F_{1,7}=3.45$; $R^2=0.16$; $p<0.01$). This is reflected by the site discriminations in the biplot ordination (**Figure 6**).

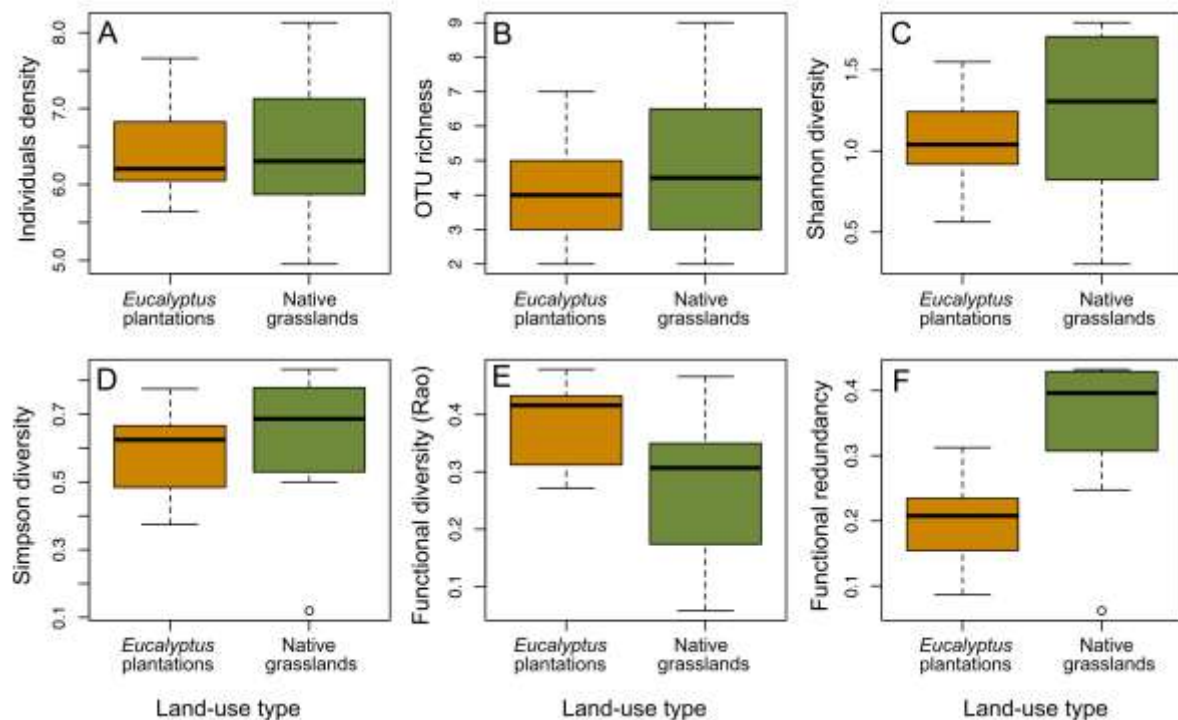


Figure 5. Boxplot of Collembola (A) density (individuals/m²), (B) OTU richness, (C) Shannon diversity index, (D) Simpson diversity index, (E) Functional diversity and (F) functional redundancy in native grasslands and *Eucalyptus* plantations in Southern Brazil. Each boxplot represents: smallest and largest observations (external bars), lower and upper quartiles (limits of the box) and median (within-box black line).

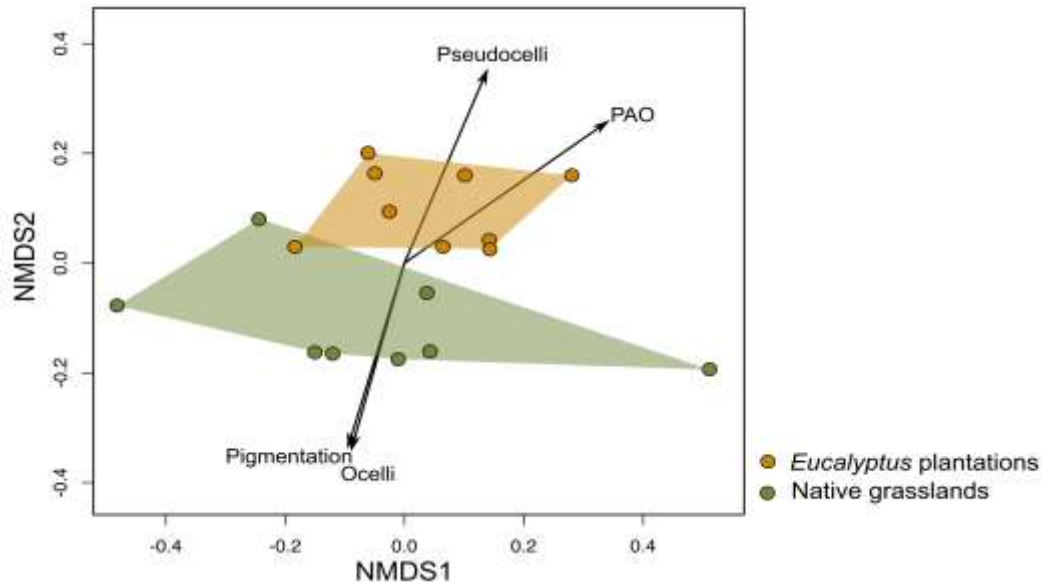


Figure 6. Biplot of a non-metric multi-dimensional scaling (NMDS) based on Bray-Curtis similarity matrix calculated using Collembola OTU abundance and CWM traits that vary significantly between two land-uses: *Eucalyptus* plantation (euc) and native grassland (gra) on Southern Brazil. Oce: number of ocelli; Pig: pigmentation level body; Pao: Post antennal organ; Psc: pseudocelli.

Table 3. Mean, standard deviation and results of linear mixed models of Collembola in native grasslands and *Eucalyptus* plantations in Southern Brazil.

Collembola diversity index	Land-use type		F	p	R ² m	R ² c
	Grassland	Eucalyptus plantation				
Density (individual per m ²)	999.64 ± 1084.20	747.03 ± 587.98	F _{1,7} = 0.16	0.69	0.01	0.01
Richness	4.87 ± 2.35	3.88 ± 1.61	F _{1,7} = 1.03	0.34	0.05	0.22
Simpson Diversity	0.61 ± 0.23	0.58 ± 0.14	F _{1,7} = 0.04	0.83	0.02	0.51
Shannon Diversity	1.22 ± 0.53	1.07 ± 0.34	F _{1,89} = 0.43	0.53	0.01	0.55
Functional Diversity	0.27 ± 0.13	0.38 ± 0.07	F _{1,7} = 8.16	0.02	0.22	0.56
Functional Redundancy	0.3 ± 0.12	0.2 ± 0.07	F _{1,7} = 10.67	0.01	0.27	0.58

Four of the nine functional traits varied significantly between the land-use types (**Table 4**). *Eucalyptus* plantations had a higher proportion of collembolan with pseudocelli (p= 0.02) and post-antennal organ (p= 0.02), while grasslands presented a higher proportion of pigmented Collembola (p= 0.01) with major ocelli number (p= 0.01).

Table 4. Mean Collembola CWM traits, standard deviation and p values of a linear model with 99 permutations of CWM values between sites (p site shuffle) and between OTUs (p taxa shuffle) in native grasslands and *Eucalyptus* plantations in Southern Brazil.

Functional trait	Land-use type		p (site shuffle)	p (taxa shuffle)
	Grassland	Eucalyptus plantation		
Pigmentation level body	0.90 ± 0.11	0.35 ± 0.11	0.01	0.01
Scales	0.14 ± 0.16	0.07 ± 0.09	0.30	0.56
Furca development	1.39 ± 0.59	0.77 ± 0.37	0.04	0.20
Ocelli number	7.22 ± 0.92	2.69 ± 0.89	0.01	0.01
Body size	1.02 ± 1	0.66 ± 0.04	0.28	0.56
Antennae length	0.30 ± 0.08	0.26 ± 0.04	0.31	0.73
Leg length	0.23 ± 0.05	0.21 ± 0.02	0.27	0.63
Post antennal organ	0.20 ± 0.31	0.69 ± 0.16	0.01	0.03
Pseudocelli	0.03 ± 0.06	0.47 ± 0.25	0.01	0.04

Discussion

In this study, we tested the effects of grasslands conversion into *Eucalyptus* plantations on several indicators of soil functionality. As expected, our results showed that this type of land-use besides largely reducing plant richness also reduced soil pH and temperature, as well as the microbial community size. These alterations represent shifts on the environmental filters shaping the soil detritivore community by altering microhabitat conditions and food quality, leading to the differences observed on Collembola taxonomic and functional structure between the two habitat types (**Figure 6**). Additionally, these changes on carbon and nutrient inputs caused by soil acidification and plant richness reduction may also have caused the global reduction of microbial activity observed at *Eucalyptus* plantations. However, our hypotheses were only partially confirmed, since the functional diversity was improved by the conversion, and some Collembola diversity indicators were not affected.

Although we did not detect variations on mean Collembola individuals' density, mean OTUs richness and indicators of taxonomical diversity per site between the land-use types, we indeed detect differences in the accumulated OTU richness. *Eucalyptus* plantations supported less Collembola OTUs than native grasslands, which was clearly identified when comparing land-use types based on samples of equal completeness, instead of equal number of individuals, as suggested by (Chao and Jost, 2012). Afforestation with *Eucalyptus* led to reductions of plants richness and consequently, diversity of resources for Collembola by decreasing the diversity of food resources, like microbial biomass (Rzeszowski et al., 2017) and plant residuals (Bahrndorff et al., 2018; Coulibaly et al., 2019). Moreover, the higher acidity in *Eucalyptus* plantations are liable to harm Collembola individual development due to effects on their physiology (Malik et al., 2018; Rossetti et al., 2015).

Collembola taxonomical composition showed a marked increase in the abundance of euedaphic and hemiedaphic OTUs in responses to the shadowing caused by *Eucalyptus* trees, resulting in a clear turnover from open-adapted to close canopy-adapted Collembola traits. The low vegetation height of grasslands leads to high UV incidence, inducing convergence of UV and dissection tolerance traits (Salmon et al., 2014). Therefore, *Brachystomella*, an epedaphic open habitat adapted group (*i.e.*, pigmented body and high ocelli number) was the most abundant OTU on grasslands. Mostly unpigmented and eyeless individuals adapted to a shaded habitat whether by thick litter layer and closed canopy composed Collembola communities on *Eucalyptus* plantations. For example, *Thalassaphorura spp.*, a canopy-adapted group, contributed with more than 50% of the total collembolan abundance in *Eucalyptus* plantations. In addition, Collembola in *Eucalyptus* had also more developed sensorial organs (pseudocelli

and post antennal organ). Pseudocelli is related to the chemicals excretion that repel predators, in turn to compensate for the difficulty to escape through active movement in deep soil (Negri, 2004). In the same way, the presence of post antennal organ compensate for the absence of ocelli (Salmon and Ponge, 2012). These selection of euedaphic traits caused by the strong modifications of vegetation structure (*i.e.*, plant height and canopy openness), diversity, and composition (Souza et al., 2013) are in line with previous studies that detected similar patterns on Europe (Martins et al., 2016; Salmon et al., 2014) and on Southern Brazil native grasslands (Winck et al., 2017).

Functional redundancy is associated with major ecological resilience and stability since communities with more redundant traits should be buffered against the local extinction of OTUs (Biggs et al., 2020; Yachi and Loreau, 1999). Our results show that this property was negatively affected by grassland afforestation (**Figure 5F**) what indicates that the grasslands communities tended to be more stable towards changes (*e.g.*, climatic, management, land-use), fulfilling soil functionality. The native grasslands presented a very specifically set of environmental conditions (*e.g.*, herbivore trampling and grazing disturbance, temperature variation, high UV incidence) that constrains traits composition, leading to major redundancy. However, these environmental filters were drastically changed by afforestation, diminishing the natural dominance of epedaphic OTUs by increasing the abundance of euedaphic and hemiedaphic ones. The hemiedaphic group presented a higher trait variation since its organisms presents intermediary characteristics between the other two groups. Therefore, it leads to reduction of functional redundancy and increase of functional diversity at the plantations, which is a different pattern from the natural grassland ecosystems.

The improvement of functional diversity by the land-use change was a quite unexpected result, since many studies have demonstrated that land-use intensification decrease the functional diversity of soil fauna (Tsiafouli et al., 2015; Vandewalle et al., 2010; Winck et al., 2017). Although functional diversity has been associated with the delivery of more ecological functions (Díaz and Cabido, 2001), our results demonstrate a worsening of most indicators of soil functionality towards grassland afforestation. Therefore, it seems that soil functionality is being underpinned by the dominant traits (mass-ratio hypothesis). At grasslands, Collembola communities are dominated by epedaphic species that participate of decomposition process by litter fragmentation. Supported by a highly diverse plant community and a most abundant microbial community, they tends to improve the carbon and nutrients inputs, optimizing soil functionality.

Regarding microbial community, grassland afforestation negatively affected microbial abundance and its global metabolic processes (*i.e.*, soil respiration) and specific enzyme activities (*i.e.*, FDA and Urease). The reduction of soil microbial parameters in *Eucalyptus* plantations seems to also driven by the changes in soil properties and the reduction on plant community richness (Becerra et al., 2018; Souza et al., 2013). It can leads to a decrease on organic matter quality due to reduction of C:N ratio (Chen et al., 2019), associated to high recalcitrance and presence of antimicrobial compounds in *Eucalyptus* leaves (Martins et al., 2013; Sabo and Knezevic, 2019). Therefore, the biomass of microbial community was limited by resource quality on these areas (Hättenschwiler et al., 2005; Ndaw et al., 2009). Such changes seems to have impacted the broad and specific functions of soil respiration since fungal and bacterial abundance play an important role in controlling it (Delgado-Baquerizo et al., 2020). Reduction on microbial biomass and soil respiration are related to decrease on the decomposition activity, which can leads to losses on functions like C sequestration and soil fertility (Li et al., 2009; Zhang et al., 2012).

Soil enzyme activities are a directly measure of specific pathways of microbial metabolism involved on matter cycling (Bini et al., 2013; Muscolo et al., 2015). FDA hydrolysis and urease activities, which are directly involved in the transformation of soil organic matter, were all reduced by land conversion from grassland to *Eucalyptus*. FDA activity is related to degradation of proteins, esters and lipids, these being more abundant in soils where the fungal community is more diversified (Baćmaga et al., 2014; Lebauer, 2010). Urease activity is involved in the transformation from nitrogen in the amine (NH₂) form to ammonia (NH₃) and carbon dioxide (CO₂) by specialized bacteria (Kuypers et al., 2018; Staley et al., 2018). Therefore, these functions of soil were compromised by grassland afforestation, probably due to changes on the microbial composition (Chen et al., 2013a; Qu et al., 2020). Environments with relatively low resource conditions, like the *Eucalyptus* plantations, may require a very specialized microbial community to thrive under starving conditions by degrading recalcitrant organic matter (Delgado-Baquerizo et al., 2016; Sicardi et al., 2004). Therefore, the native organisms that can only survive within a narrow range of conditions seems not to be able to cope with the changes promoted by *Eucalyptus* on soil conditions what can impair soil functions, leading to a change on composition and reduction of biomass. Future research is needed to evaluate more precisely the effects of afforestation on microbial composition and diversity by metagenomic analysis of the 16S rRNA.

Recent studies have demonstrate that *Eucalyptus* plantations on Pampa biome tended to recovery the biological quality of the soil, with an increase in the abundance of edaphic

organisms, including Collembola (Boeno et al., 2020; Sabatté et al., 2021). Ours results are in accordance with Sabatté et al. (2021) which demonstrates that soil fauna communities in the younger *Eucalyptus* plantations ($\cong 10$ years) are transitional with greater variability and lesser stability (functional redundancy) than grasslands communities. The areas sampled in this study were around this age and shortly after it they were harvested, which is the most common practice. Zhao et al. (2020) detected the same pattern on a landscape scale, detected that the plantations were approaching an ecologically functional state by the time of harvest. Therefore, a latter harvest may be one solution to achieve a reasonably sustainable land-use, however the inevitable harvest will let a bare soil, with no vegetation cover, and many negative effects on the fauna.

Conclusion

Several studies have reported negative effects of *Eucalyptus* plantations on soil biota, which may harm soil functionality (e.g., Martello et al., 2018; Sicardi et al., 2004; Winck et al., 2017). However, despite the large-scale Pampa grasslands conversion to *Eucalyptus* plantations in recent years (MapBiomass Project, 2019), information on the effects on Collembola and microbial community is scarce. Our findings support the idea that grassland afforestation leads to a decrease on soil functionality. It reduced vegetation richness, diminishing the litter quality that enters on soil trophic chain (Becerra et al., 2018; Souza et al., 2013). In addition, intrinsic characteristics of *Eucalyptus* trees leads to soil acidification which could impair soil fertility and productivity (Berthrong et al., 2009). The combination of those factors seems to be constraining microbial biomass, which is a resource for Collembola community, such as the other affected parameters. Therefore, it leads to a variation of Collembola taxonomical and functional structure between land-uses by changes on the environmental filters (Winck et al., 2017) which can results on changes on the food webs and consequently on the functions provided by Collembola and other taxa that interacts with them (Masese et al., 2015). Such changes induced a decrease on microbial community size and activities that indicates a loss of soil functions related to C and N cycle like decomposition, soil fertility and C storage (Delgado-Baquerizo et al., 2016; Fisher et al., 2017). Unexpectedly, the functional diversity of Collembola community was improved by afforestation. However, all other indicators of soil functionality measured were lower in *Eucalyptus* plantations, suggesting that the most dominant traits may be a major factor that drives it (mass-ratio hypothesis). Moreover, there was a loss of functional redundancy towards grassland conversion, which tends to shapes

Eucalyptus plantations into a less stable state (Sabatté et al., 2021; Zhao et al., 2020; Zhu et al., 2019). These findings are important to support the development of conservation policies on Southern South America grasslands for sustainable land-use by managing the trade-offs between economic viability and soil functionality.

Supplementary Material

Table S1

Soil Collembola community and their abundance in native grasslands and *Eucalyptus* plantations in Southern Brazil.

Order	Family	Genera	OTU	Total abundance		
				Grassland	<i>Eucalyptus</i> plantation	Total
Entomobryomorpha	Entomobryidae	<i>Drepanura</i>	<i>Drepanura</i>	1	0	1
		<i>Entomobrya</i>	<i>Entomobrya</i>	21	13	34
		<i>Lepidocyrtus</i>	<i>Lepidocyrtus</i>	13	5	18
		<i>Seira</i>	<i>Seira</i>	1	0	1
	Isotomidae	<i>Arlea</i>	<i>Arlea</i>	1	0	1
		<i>Axelsonia</i>	<i>Axelsonia</i>	0	2	2
		<i>Folsomides</i>	<i>Folsomides</i>	2	1	3
		<i>Isotomodes</i>	<i>Isotomodes</i>	3	9	12
		<i>Proisotoma</i>	<i>Proisotoma</i>	2	4	6
		<i>Psammisotoma</i>	<i>Psammisotoma</i>	0	1	1
		<i>Yosiella</i>	<i>Yosiella</i>	1	3	4
Poduromorpha	Brachystomellidae	<i>Brachystomella</i>	<i>Brachystomella</i>	50	0	50
		<i>Folsomiella</i>	<i>Folsomiella</i>	1	0	1
	Ondontellidae	<i>Superodontella</i>	<i>Superodontella</i>	1	0	1
	Onychiuridae	<i>Agraphorura</i>	<i>Agraphorura</i>	0	1	1
		<i>Thalassaphorura</i>	<i>Thalassaphorura</i>	2	52	54
Symphleona	Bourletiellidae		Bourletiellidae	2	0	2
	Katiannidae	<i>Sminthurinus</i>	<i>Sminthurinus</i>	9	0	9
	Sminthurididae		Sminthurididae	2	2	4
			Symphleona	3	2	5

Table S2. Collembola OTUs described in functional traits, which are detailed on Table 1 in native grasslands and *Eucalyptus* plantations in Southern Brazil (**Matrix B**).

OTU	Functional Trait								
	Pigmentation	Scale	Furca development	Ocelli number	Average body size	Average Antenna length	Average leg length	PAO	Pseudocelli
<i>Agraphorura</i>	0	0	0	0	0.533325	0.154111	0.139437	1	1
<i>Arlea</i>	0	0	1	0	0.567539	0.242166	0.212451	1	1
<i>Axelsonia</i>	1	0	1	4	0.70219	0.088144	0.172354	0	0
Bourletiellidae	1	0	2	8	0.231332	0.442164	0.28775	0	0
<i>Brachystomella</i>	1	0	1	8	0.783606	0.199543	0.20912	0	0
<i>Drepanura</i>	1	1	2	8	0.965812	0.445285	0.272417	0	0
<i>Entomobrya</i>	1	0	2	8	0.796356	0.298724	0.265008	0	0
<i>Folsomides</i>	1	0	2	8	0.594827	0.235901	0.243233	1	0
<i>Folsomiella</i>	1	0	0	8	3.722243	0.174363	0.117638	0	0
<i>Isotomodes</i>	0	0	1	0	0.694071	0.20565	0.156443	1	0
<i>Lepidocyrtus</i>	1	1	2	8	0.955155	0.458025	0.299331	0	0
<i>Proisotoma</i>	1	0	1	8	0.710349	0.243457	0.238883	1	0
<i>Psammisotoma</i>	1	0	1	8	0.41527	0.342357	0.256218	1	0
<i>Seira</i>	1	1	2	8	1.179756	0.353404	0.339952	0	0
Sminthurididae	1	0	2	8	0.276999	0.678906	0.512892	0	0
<i>Sminthurinus</i>	1	0	2	8	0.293587	0.509033	0.308238	0	0
<i>Superodontella</i>	0	0	0	0	0.697821	0.042633	0.051489	0	0
<i>Thalassaphorura</i>	0	0	0	0	0.634339	0.220617	0.192127	1	1
<i>Yosiella</i>	0	0	0	0	0.568744	0.144275	0.156727	1	0
Symphyleona	1	0	2	8	0.209604	0.531654	0.346408	0	0

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Conclusões Gerais

- A conversão de campos nativos do bioma Pampa para plantações de Eucalipto levou ao declínio da riqueza de plantas, acidificação do solo e redução do tamanho da comunidade microbiana.
- Diminui a riqueza de organismos bioindicadores do grupo Collembola e alterou sua composição taxonômica e funcional.
- A composição funcional foi alterada através das mudanças de atributos funcionais adaptativos para ambientes abertos (campo) para atributos adaptativos de ambientes sombreados (plantações de Eucalipto).
- Todos os índices de atividade microbiana apresentaram valores menores nas áreas de plantio, indicando um possível comprometimento das funções relacionadas à ciclagem de C e N.
- Nossos resultados indicam que a conversão de campos nativos em plantios de Eucaliptos apresenta efeitos negativos sobre a funcionalidade solo.
- O próximo passo deste trabalho será a realização de análises para determinar os drivers das mudanças observadas na comunidade de colêmbolos.