INSTITUTO LATINO-AMERICANO DE CIÊNCIAS DA VIDA E DA NATUREZA

PROGRAMA DE PÓS-GRADUAÇÃO EM BIODIVERSIDADE NEOTROPICAL

A INVASORA *Tradescantia zebrina* ALTERA A DECOMPOSIÇÃO VEGETAL EM MATA ATLÂNTICA?

GISELLE CRISTINA DE OLIVEIRA VAZ

Foz do Iguaçu
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Dissertação de mestrado apresentada ao Programa de Pós-Graduação em Biodiversidade Neotropical, do Instituto Latino-Americano de Ciências da Vida e da Natureza, da Universidade Federal da Integração Latino-Americana, como requisito parcial à obtenção do título de Mestre em Ciências Biológicas.

Orientador: Prof. Dr. Wagner Antonio Chiba de Castro
Coorientador: Profa. Dra. Rafaella Costa Bonugli Santos

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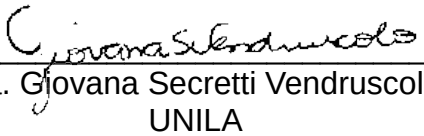

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RESUMO

Os impactos das invasões de plantas são complexos e têm o potencial de alterar permanentemente não só as comunidades vegetais mas também microbianas. As novas quantidade e qualidade de detritos imposta pela invasora são mecanismos sofisticados que tem capacidade de homogeneizar o ambiente invadido e propor mudanças no ciclo de nutrientes do solo. A decomposição de detritos via serapilheira, é a via mais importante de liberação de matéria orgânica e, consequentemente, de eventuais aleloquímicos em ambientes florestais. Esses últimos, podem afetar a germinação e o crescimento de plantas competidoras. Essas mudanças na dinâmica de detritos de ambientes invadidos influenciam a estrutura e composição das comunidades de fungos decompositores. No entanto, a inter-relação entre a qualidade do detrito invasor, a comunidade de fungos decompositores e as taxas de decomposição da serapilheira sob invasão ainda é controversa. Neste estudo, avaliamos 1) o potencial alelopático de folhas secas da invasora *Tradescantia zebrina* sob a germinação e crescimento inicial de *Solanum lycopersicum*, 2) se a invasora altera a taxa decomposição de detritos de plantas na Mata Atlântica e 3) a composição da comunidade de fungos lignocelulolíticos. Nossos resultados indicam que *T. zebrina* exerce efeito inibitório na germinação e crescimento inicial das sementes de tomate, apresentando potencial alelopático. Os detritos da invasora apresentaram decomposição mais rápida que detritos das espécies nativas. Entretanto, a invasão de *T. zebrina* não alterou as taxas de decomposição dos detritos das plantas, seja de plantas nativas ou da própria invasora. Embora as comunidades de fungos lignocelulolíticos sejam temporalmente estruturadas, a invasão e a natureza dos detritos não influenciaram essas comunidades. Acreditamos que a alta riqueza vegetal da Mata Atlântica permite uma biota decompositora altamente diversificada, capaz de atuar em detritos de diferentes naturezas e sob diferentes condições ambientais. Nossos resultados evidenciam a importância de futuros estudos dos efeitos aleloquímicos da invasão sobre vegetação nativa e comunidade de fungos decompositores.

PALAVRAS-CHAVE: Áreas protegidas, alelopatia, espécies nativas, litter bags, ciclagem de nutrientes, microbiota.

*VAZ, Giselle Cristina de Oliveira.**DOES THE INVASION OF Tradescantia zebrina CHANGE THE VEGETAL DECOMPOSITION IN ATLANTIC FOREST?** 2020. 68 pages. Master's thesis of the Graduate Program in Neotropical Biodiversity – Federal University of Latin American Integration, Foz do Iguaçu, 2020.*

ABSTRACT

The impacts of plant invasions are complex and can permanently alter not only plant communities but also microbial ones. The new quantity and quality of litters imposed by the invader are sophisticated mechanisms that can homogenize the invaded environment and propose changes in the soil nutrient cycle. The decomposition of detritus via litter is the most important way of releasing organic matter and, consequently, of allelochemicals in forest environments. The release of allelochemicals in the forest can affect the germination and growth of competing plants. These changes in the dynamics of litters from invaded environments influence decomposing fungi communities' structure and composition. However, the interrelationship between the quality of invasive litters, the community of decomposing fungi, and the decomposition rates of litter under invasion is still controversial. In this study, we evaluated 1) the allelopathic potential of dry leaves of the invasive Tradescantia zebrina under the germination and initial growth of Solanum lycopersicum, 2) whether the invader alters the decomposition rate of plant litters in the Atlantic Forest and 3) the composition of the lignocellulolytic fungi. Our results indicate that T. zebrina has an inhibitory effect on the germination and initial growth of tomato seeds, with allelopathic potential. Litters from the invader showed faster decomposition than litters from native species. However, the invasion of T. zebrina did not alter the decomposition rates of plant litters, either from native plants or from the invader itself. Although communities of lignocellulolytic fungi are temporally structured, the litters' invasion and nature did not influence these communities. We believe that the high plant richness of the Atlantic Forest allows for a highly diversified decomposing biota, capable of acting on different types of waste and under different environmental conditions. Our results demonstrate the importance of future studies on the allelochemical effects of invasion on native vegetation and the decomposing fungi community.

***Keywords**: Protected areas, allelopathy, native species, litter bags, nutrient cycling, microbiota.*

SUMÁRIO

1. INTRODUÇÃO GERAL

Espécies introduzidas fora de sua área natural de distribuição são consideradas exóticas, quando possuem capacidade de se reproduzir, migrar para além do local de introdução e se estabelecer, são denominadas invasoras (Simberloff & Rejmánek, 2011). O termo invasor é, frequentemente, usado para conotar o impacto que uma espécie introduzida causa no ambiente receptivo (Simberloff, 2011). Na economia, podem impactar negativamente a agricultura, a qualidade e quantidade da água, turismo e recreação (Charles & Dukes, 2008). Nos EUA, os danos das invasões biológicas custam entre 121 e 220 bilhões de dólares anualmente (Marbuah et al., 2014; Pimentel et al., 2005). Esforços no manejo destas espécies também representam ônus econômicos significativos. Anualmente, em números subestimados, a Austrália investe US$ 13,6 bilhões em controle e erradicação dessas espécies (Hoffamann & Broadhurst, 2016). Nos ecossistemas naturais, ameaçam a conservação da biodiversidade (Wittenberg & Cock, 2001) representando uma das principais causas de perda de espécies (Newbold et al., 2015) e de serviços ecossistêmicos (Walsh et al., 2016).

Os impactos das invasoras são fortemente dependentes do contexto e podem ter resultados diferentes, dependendo das características da invasora e do habitat invadido (Gaertner et al., 2014). Em áreas protegidas, estes impactos são complexos e podem alterar permanentemente a estrutura e a função das comunidades (Panetta e Gooden, 2017), além de causar extinções locais e homogeneizar o ambiente invadido (Sakai et al., 2000). Esses novos traços fisiológicos impostos ao ambiente invadido, são causa de grandes alterações nas funções do ecossistema receptor (Yelenik & Stock, 2007), alterando as propriedades do solo via mudanças na ciclagem de nutrientes (Simberloff, 2011). Por exemplo, o grande aumento da serapilheira por invasão de *Typha x glauca* Godr. (Typhaceae), reduz a disponibilidade de luz no solo (Angeloni et al., 2006), inibindo a regeneração de sementes e, consequentemente, diminuindo a abundância de espécies nativas (Tuchman et al., 2009). Essa maior disponibilidade de necromassa promovida pelas invasoras pode, inclusive, afetar o tempo de entrada das folhas no solo da floresta (Aragón et al., 2013), alterar a atividade metabólica de determinados microrganismos do solo e, consequentemente, o fluxo de carbono do solo para a atmosfera (Herrera et al., 2011).

A serapilheira é a principal fonte de matéria orgânica nos solos (Hobbie *et al*, 2015), via decomposição do detrito vegetal (Berg & McClaugherty 2014). É na serapilheira que

ocorre a ciclagem de diversos nutrientes que subsidiam a oferta de serviços ecossistêmicos fundamentais, como o crescimento das plantas e a estrutura das comunidades vegetais (Hattendchwiler et al., 2011). As potenciais alterações das comunidades do solo por invasões são motivos de muita atenção, pois a estrutura e composição dessas comunidades são associadas a processos funcionalmente significativos, como a decomposição da serapilheira. Se uma planta invasora promove alterações nas comunidades do solo, as relações de diversidade-função podem também ser alteradas (Wolfe & Klironomos, 2005). Já a perda de espécies microbianas de um ecossistema pode resultar em uma redução da eficácia e estabilidade do processo de decomposição (Bonanomi et al., 2015).

Os fungos são uma parte importante das comunidades microbianas do solo e participam ativamente da liberação de nutrientes e decomposição orgânica (Li et al, 2017). Para Lodge e Cantrell (1995), perturbações que mudam o ambiente podem afetar as populações e comunidades de decompositores fúngicos no solo da floresta tropical, essas mudanças podem alterar a disponibilidade e o destino de nutrientes minerais. As invasões vegetais podem aumentar a atividade metabólica total da microbiota do solo e o fluxo de carbono solo-atmosfera, devido ao incremento na quantidade de energia disponível para os microrganismos do solo (Herrera et al., 2011).

A riqueza de espécies de plantas, por si só, afeta naturalmente a decomposição da serrapilheira, uma vez que a qualidade e a quantidade de matéria orgânica vegetal influencia não somente a liberação de nutrientes (Pereira, 2010), mas também afeta a estrutura (Purahong et al., 2016), atividade e biomassa microbiana do solo (Stotzky, 1997 *apud* Herrera, 2011). Assim, invasões vegetais podem promover ciclagem de nutrientes mais lenta ou acelerada em decorrência das invasões (Godoy et al., 2010; Liao et al., 2008). Os arbustos invasores *Rhamnus cathartica* e *Lonicera maackii* na América do Norte exibem maior produtividade e decomposição mais rápida do que as espécies nativas que coocorrem, promovendo alterações no ciclo de nutrientes do solo que favorecem seu desenvolvimento perante a comunidade vegetal nativa (Arthur et al, 2012). No entanto, a decomposição dos detritos de *Fallopia japonica* (Houtt.) Ronse Decraene é 3 a 4 vezes mais lenta que a dos detritos nativos, promovendo alterações nos fungos associados (Mincheva et al., 2014). Portanto, a relação entre a qualidade do detrito invasor, composição da comunidade microbiana e as taxas de decomposição da serapilheira sob invasão é naturalmente controversa (Cleveland et al., 2014).

Quando essa grande quantidade de detritos é incorporada nas áreas invadidas, desempenham papel fundamental na dinâmica de variáveis físico-químicas e fitotoxicidade associada ao solo (Uddin et al., 2014). Algumas substâncias químicas liberadas da biomassa viva ou em decomposição de espécies exóticas e/ou invasoras podem inibir o crescimento de plantas nativas ou microrganismos do solo, o que pode aumentar a invasão dessas espécies (Simberloff & Rejmánek, 2011). É crescente o interesse no papel da alelopatia nas invasões vegetais. A hipótese “novel weapon” sugere que a alelopatia é um dos mecanismos chave que permite a uma planta invadir, se estabelecer em novos ecossistemas e, em última análise, determinar a estrutura e composição da comunidade vegetal invadida (Callaway & Ridenour, 2004). Além dos efeitos de inibição para plantas nativas, essa nova dinâmica do solo pode alterar sensivelmente a atividade decompositora da microbiota (Kaur et al., 2009). Portanto, as mudanças, mediadas por invasões vegetais, causadas na composição da comunidade vegetal e microbiana e condições do solo, podem levar a alterações na ciclagem de nutrientes (Godoy et al., 2010) fornecendo um *feedback* positivo para o sucesso das espécies invasoras (Farrer & Goldberg, 2009).

A herbácea *Tradescantia zebrina* Heynh. ex Bosse (Commelinaceae) citada em várias listas de espécies invasoras em unidades de conservação (Carpanezzi, 2011; IAP, 2015; Sampaio & Schmidt, 2013; Ziller & Dechoum, 2013) é tida como uma forte competidora, que afeta a diversidade de espécies de fragmentos florestais (Mantoani et al., 2013). Se multiplica facilmente a qualquer época do ano, estabelecendo grande biomassa em áreas invadidas (Lorenzi & Souza, 2008). Apresenta alta capacidade de adaptação à diferentes biomas brasileiros, com registros de invasão no Cerrado e Mata Atlântica (Carpanezzi, 2011; Mantoani et al., 2013; Pinto et al., 2007; Rodolfo et al., 2007; Zenni & Ziller 2011). É uma planta de porte herbáceo, rastejante, com até 25 cm, de folhas verde-arroxeadas, glabras, com duas faixas longitudinais prateadas na superfície adaxial e roxa na abaxial, com flores pequenas e pouco vistosas de tom róseo, multiplica-se facilmente por fragmentos de caule, sendo considerada uma planta infestante também na agricultura (Souza & Lorenzi, 2010). Essa espécie provavelmente originária do México e de países do norte da América Central, foi trazida ao Brasil para fins de ornamentação (Mantoani et al., 2013). Apresenta potencial alelopático em testes laboratoriais (Martins et al., 2014) e alguns trabalhos atribuem parte de sua dominância nas áreas invadidas à grande biomassa associada e alelopatia sobre competidoras (Mantoani et al., 2013; Silva & Voltolini, 2016).

Devido a importância de estudos envolvendo mecanismos de dominância de plantas e impactos de invasão no funcionamento do ecossistema (Levine et al*.,* 2003), avaliamos se a invasora *Tradescantia zebrina* altera a ciclagem de nutrientes em comunidades vegetais de Mata Atlântica. As hipóteses do nosso trabalho são de que (1) detritos da invasora apresentem taxas de decomposição mais altas que detritos de nativas e (2) em áreas invadidas por *Tradescantia zebrina,* detritos da invasora apresentem taxa de decomposição mais alta que em áreas não invadidas, enquanto o oposto acontece para detritos de plantas nativas. Estes fatores, associados à diminuição da regeneração nativa pela invasora (Chiba de Castro et al*.,* 2019) e potencial alelopático da invasora, acarretariam a restrição de nichos disponiveís para os organismos decompositores de Mata Atlântica, alterando a diversidade de fungos lignocelulolíticos. A partir das hipóteses supracitadas, esperamos que 3) a diversidade de fungos decompositores em áreas invadidas seja menor que em áreas não invadidas e que 4) a diversidade de fungos decompositores em detritos de plantas nativas seja maior que em detritos da invasora.

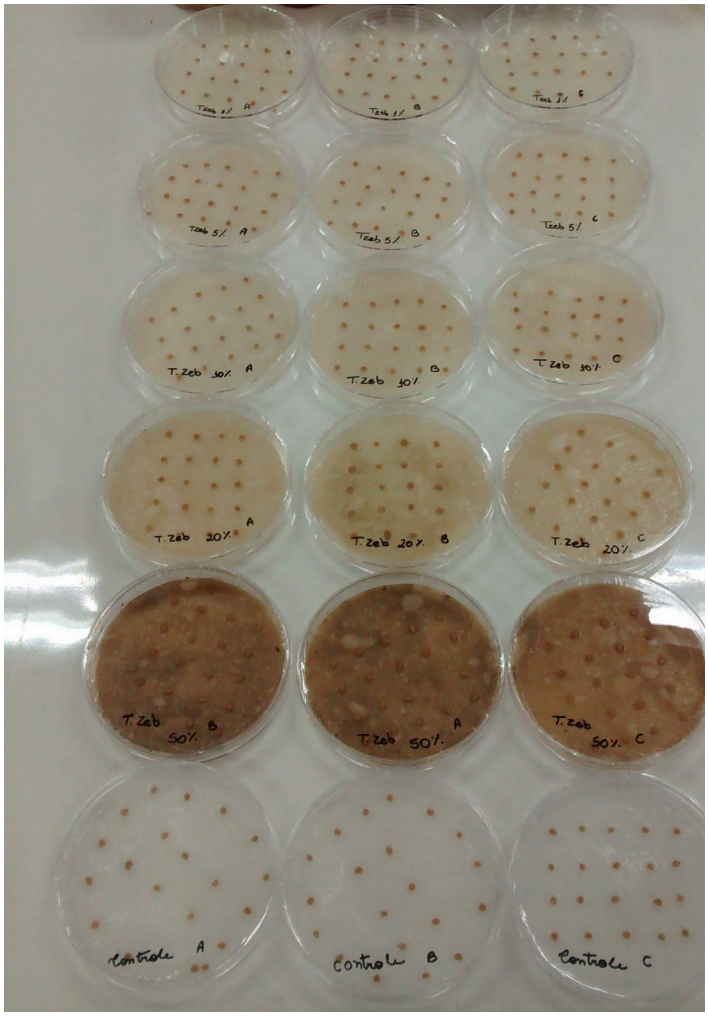
2. APRESENTAÇÃO DOS CAPÍTULOS

A presente dissertação de mestrado está dividida em dois capítulos. O primeiro corresponde a um resumo expandido apresentado no XIV Congresso de Ecologia do Brasil (http://seb-ecologia.org.br/ceb2019/sistema/presenca_trabalho.php?id=37), onde analisamos o potencial alelopático de folhas secas da invasora *Tradescantia zebrina* Heynh. ex Bosse (Commelinaceae) em teste laboratoriais. O segundo, a um manuscrito onde avaliamos se a mesma invasora altera (1) a decomposição de detritos vegetais e (2) a composição de fungos decompositores em Mata Atlântica.

3. FIGURAS

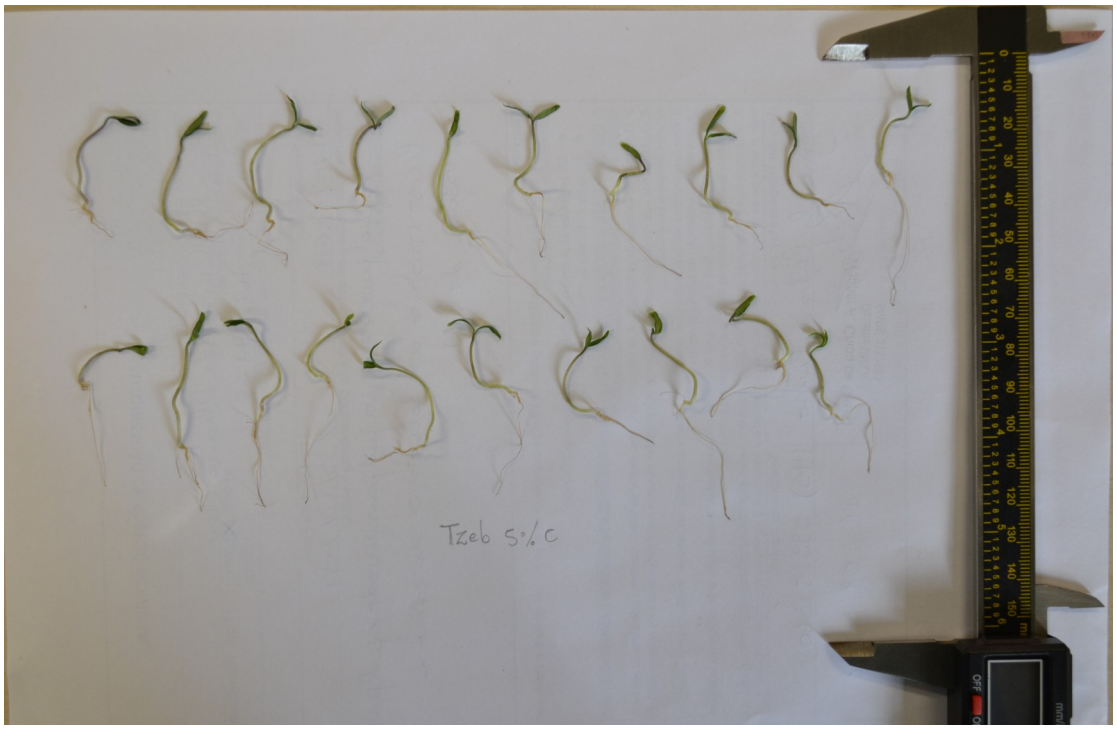
As figuras seguintes ilustram algumas etapas metodológicas dos capítulos I (figuras A, B, C, D) e II (figuras E, F, G, H, I, J, K, L referentes aos experimentos de decomposição e M, N e O ao experimento de composição de fungos lignocelulolíticos).

A: Extratos prontos para os testes de alelopatia elaborados a partir de fragmentos secos de *T. zebrina*, cada porcentagem representa o peso, em gramas, dos fragmentos secos misturados em 100ml de água destilada.



B: Placas prontas para o teste de potencial alelopático de *T. zebrina* sob a germinação de *Solanumm lycopersicum*, cada placa recebeu 20 sementes e 6ml de extrato, o teste constou de seis tratamentos, as cinco concentrações dos extratos mais a situação controle, com apenas água destilada.

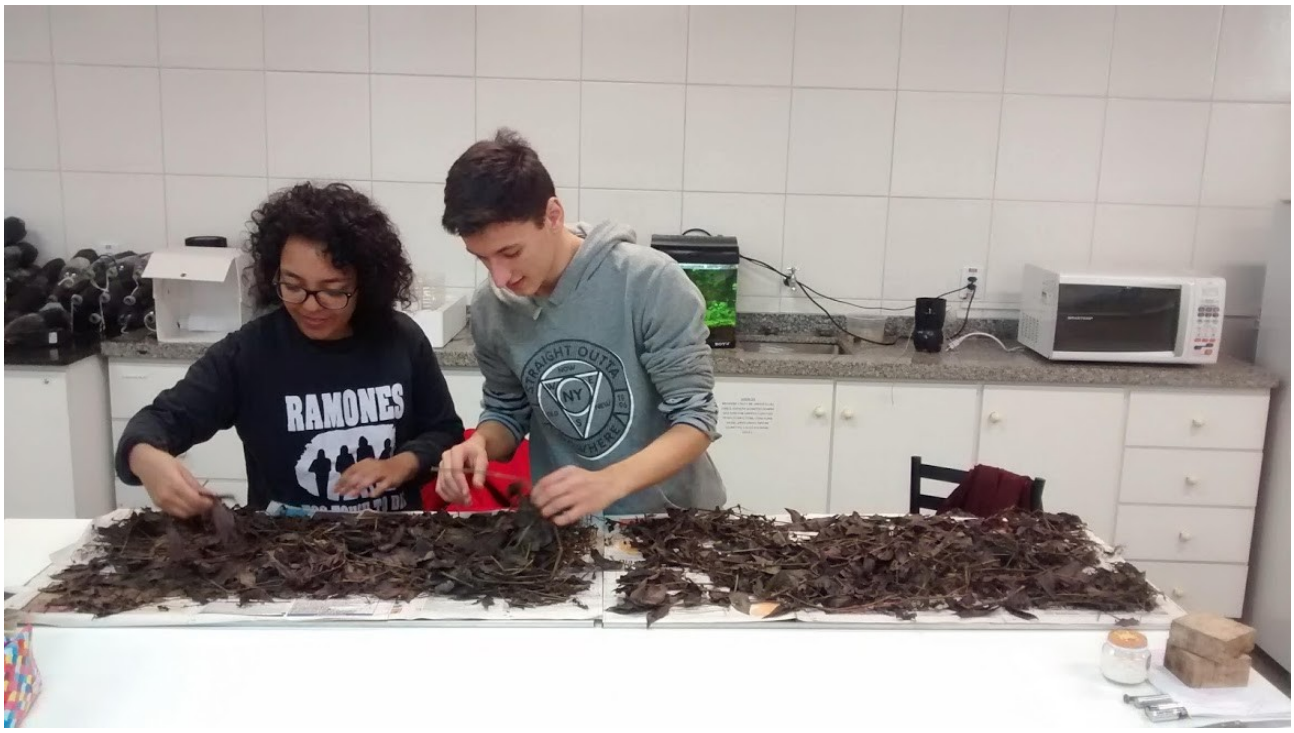
C: Placas do teste de germinação, mostrando a situação controle, com apenas água destilada, no quinto dia.



D: Para o teste de potencial alelopático de *T. zebrina* sob o crescimento inicial de *S. lycopersicum* foram medidos os comprimentos da radícula e do hipocótilo, no quinto dia de transplante das sementes pré-germinadas de *S. lycopersicum* para as placas com extratos de *T. zebrina* (1%, 5%, 10%, 20%, 50% e o tratamento controle).

E: A equipe (esquerda para direita: Luiz, Alvaro, Giselle, Chiba e Any) coletando fragmentos de *T. zebrina* e espécies nativas para os experimentos de decomposição.

F: Fragmentos de *T. zebrina* e espécies nativas coletados para os experimentos de decomposição.



G: Any e Luiz, triando fragmentos de *T. zebrina* posteriormente secos e utilizados nos experimentos de decomposição.

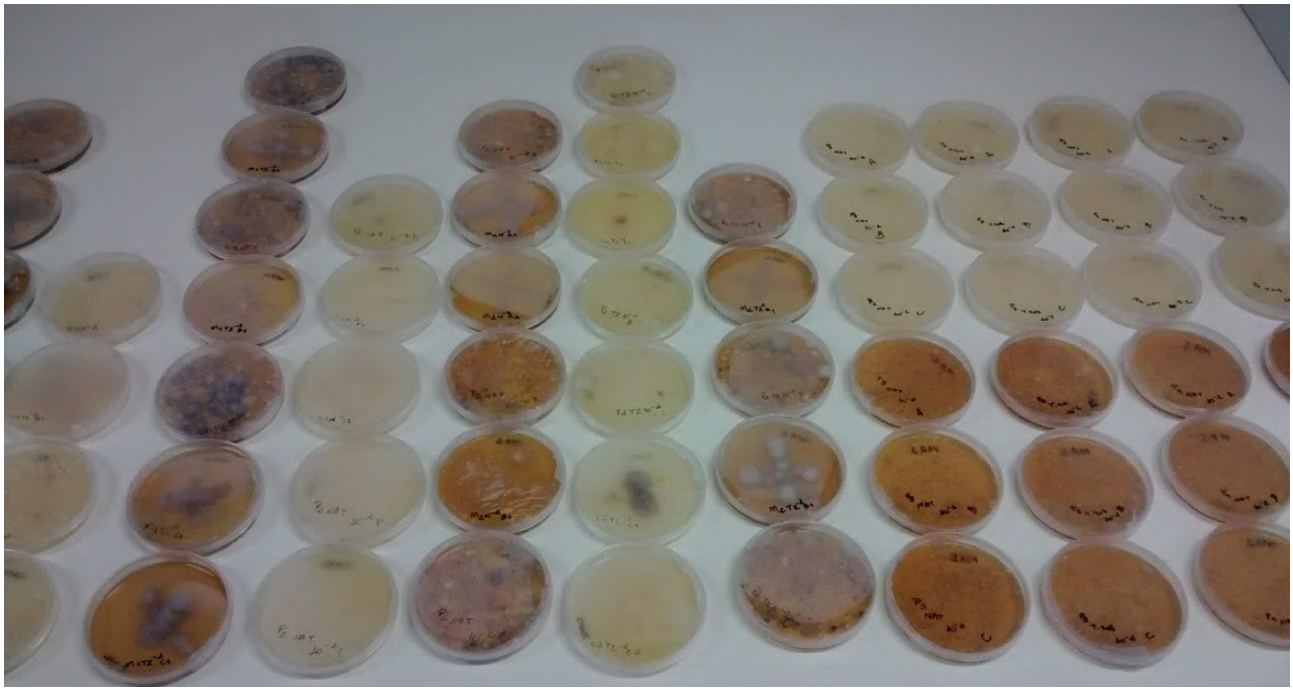
H: Pesagem dos detritos das espécies nativas e preenchimento dos *litter bags* com 5g de detritos para o experimento de decomposição *in situ*.

I: Deposição do *litter bags* acima da serapilheira nas áreas invadidas por *T. zebrina*, para o experimento de decomposição *in situ* no Parque Nacional do Iguaçu.

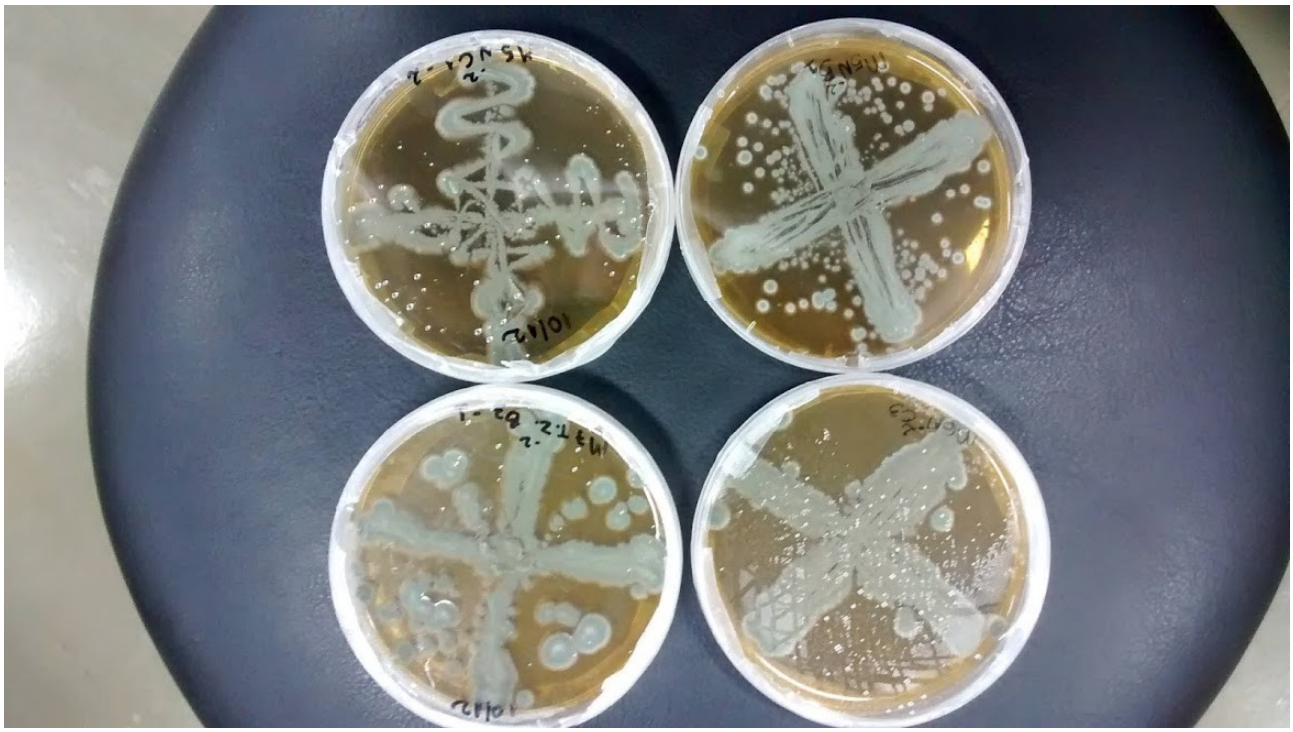
J: Registro do primeiro dia do experimento de decomposição *in situ* com os *litter bags* depositados nas áreas invadidas por *T. zebrina* no Parque Nacional do Iguaçu.

K: Primeiro dia do experimento de decomposição *in vitro*, duas bandejas simulando áreas invadidas e duas áreas não invadidas por *T. zebrina*, nas bandejas *litter bags* preenchidos com 2g de detritos de espécies nativas e da invasora.

L: Durante o experimento de decomposição *in vitro*, da esquerda para direita: duas bandejas simulando áreas invadidas e duas áreas não invadidas.



M: Registro referente ao experimento de composição de fungos lignocelulolíticos, etapa de isolamento para posterior determinação de morfotipos.



N: Isolados do experimento de composição de fungos lignocelulolíticos, agrupados de acordo com as características morfologicas para determinação dos morfotipos.

O: Etapa de preservação dos isolados do experimento de composição de fungos lignocelulolíticos, os isolados foram preservados em água e armazenados a -20°C e em glicerina a -80°C.

P: A equipe, esquerda para direita: Alvaro, Chiba, Luiz, Any e Giselle.

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CAPÍTULO I

INTERFERÊNCIA ALOPÁTICA DE *Tradescantia zebrina* Heynh. ex Bosse (Commelinaceae) NA GERMINAÇÃO E CRESCIMENTO INICIAL DE *Solanum lycopersicum* L.

INTERFERÊNCIA ALOPÁTICA DE *Tradescantia zebrina* Heynh. ex Bosse (Commelinaceae) NA GERMINAÇÃO E CRESCIMENTO INICIAL DE *Solanum lycopersicum* L.

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INTRODUÇÃO

Os aleloquímicos liberados por invasoras no ambiente podem afetar a germinação, o crescimento, a fisiologia e até mesmo se manifestar em fatores genéticos de plantas competidoras (Harun *et al*, 2014), sendo assim, um mecanismo sofisticado pelo qual as espécies invasoras sobrepõem espécies nativas (Bais *et al*, 2003). A fitotoxicidade aleloquímica pode ter origem em fontes distintas, como processos de lixiviação de partes vivas de plantas, exsudados radiculares, volatilização e atividade microbiana (Inderjit, 1996). No entanto, a decomposição de detritos é reconhecidamente a via mais eficiente de liberação de aleloquímicos (Reigosa e Sánchez, 1999; Inderjit e Duke, 2003). A herbácea *Tradescantia zebrina* apresenta potencial alelopático em testes laboratoriais (Martins *et al*, 2014) e alguns trabalhos atribuem parte de sua dominância nas áreas invadidas à grande biomassa associada e alelopatia sobre competidoras (Mantoani *et al*, 2013; Silva e Voltolini, 2017).

OBJETIVOS

Este trabalho teve como objetivo analisar o potencial alelopático de folhas secas de *Tradescantia zebrina* sob a germinação e crescimento inicial de *Solanum lycopersicum*, utilizando protocolos ecotoxicológicos estabelecidos.

MATERIAL E MÉTODOS

Preparo do extrato: Foram coletados fragmentos de *T. zebrina* em áreas invadidas no Parque Nacional do Iguaçu em Foz do Iguaçu, PR. Em laboratório, os fragmentos foram lavados e as folhas foram secas em estufa a 60°C ± 5 por 48 horas. A biomassa seca foi particionada em cinco proporções diferentes: 1, 5, 10, 20 e 50g. Cada uma das partições foi triturada com liquidificador industrial de alta velocidade por dois minutos e misturada em 100mL de água destilada, para o estabelecimento dos extratos de concentração 1, 5, 10, 20 e 50% (Martins et al., 2014). A mistura permaneceu em repouso durante 24 horas sob refrigeração ± 10 ºC e, posteriormente, foi filtrada com Kitassato sob vácuo.

Bioensaio de germinação: O experimento constou de seis tratamentos diferentes, considerando as cinco concentrações dos extratos mais a situação controle, com água destilada apenas. Cada tratamento foi composto por três replicações e para cada réplica foram implantadas 20 sementes de *Solanum lycopersicum (*tomate comercial), totalizando 360 sementes. Para cada tratamento, as sementes foram distribuídas em três placas de Petri esterilizadas, depositadas sob duas folhas de papel filtro umedecida com 6ml do extrato aquoso correspondente. As placas foram acondicionadas em laboratório com temperatura (25°C± 2), luminosidade (3000 lux) e fotoperíodos controlados (12/12h). Os registros de germinação ocorreram a cada 24h pelo prazo de cinco dias.

Crescimento inicial: Transplantamos sementes de tomate pré-germinadas em água destilada para placas de Petri e folha de papel filtro sob os mesmos procedimentos de replicações e tratamentos do bioensaio de germinação. No quinto dia de transplante, medimos o comprimento da raiz e do hipocótilo, utilizando paquímetro digital.

Análise dos dados: Para testar o efeito dos extratos na germinação de sementes de tomate foi utilizado um Modelo Linear Generalizado Misto (GLMM) com distribuição de Poison e pseudo-replicação temporal. O efeito fixo inclui o tempo experimental como fator categórico com 5 níveis, assim como sua interação com as diferentes concentrações do extrato. A estrutura de efeitos aleatórios inclui tanto intercepção aleatória para as réplicas experimentais quanto uma intercepção diferente para cada reamostragem aninhada dentro das réplicas e diferentes concentrações do extrato (Crawley, 2005). Para verificar se existem diferenças significativas entre as concentrações do extrato para radícula e hipocótilo de tomate, utilizaremos uma análise de variância (ANOVA) com teste a posteriori de Tukey. Todas as análises dos dados foram realizadas no ambiente estatístico R (R Development Core Team).

RESULTADOS E DISCUSSÃO

Germinação: Os tratamentos 5% e 10% apresentaram número de sementes germinadas (35 e 15 respectivamente) significativamente inferior (GLMM; $p<0,01$) ao controle (54 sementes). Nas concentrações 20% e 50%, não houve germinação (Figura 1). Testes com extratos da raiz de *T. zebrina* também indicaram efeito alelopático sobre a germinativo de alface (Moura *et al*, 2018).

Crescimento: Os tamanhos médios da radícula de tomate foram significativamente menores para todos os tratamentos, se comparados ao controle (ANOVA; $F=96$; $p<0,01$) (Figura 2). Quanto maior a concentração do extrato, menor o tamanho médio da radícula como encontrado por Martins *et al* (2014) em testes de crescimento com alface. Para o hipocótilo o maior tamanho médio foi encontrado no tratamento de 1% (32,26 mm) e menor no tratamento de 20% (4,51 mm). O tratamento de 50% não houve crescimento de ambas estruturas (Figura 3). Estes resultados podem indicar que durante a decomposição da espécie invasora, compostos aleloquímicos dificultem o estabelecimento de outras espécies vegetais (Santos *et al*, 2012), mesmo após a retirada desta invasora em áreas naturais (Silva e Voltolini, 2017).

CONCLUSÃO

Tradescantia zebrina apresenta efeito inibitório na germinação e crescimento inicial das sementes de tomate, apresentando potencial alelopático e evidenciando a importância do estudo dos efeitos aleloquímicos da invasão sobre vegetação nativa.

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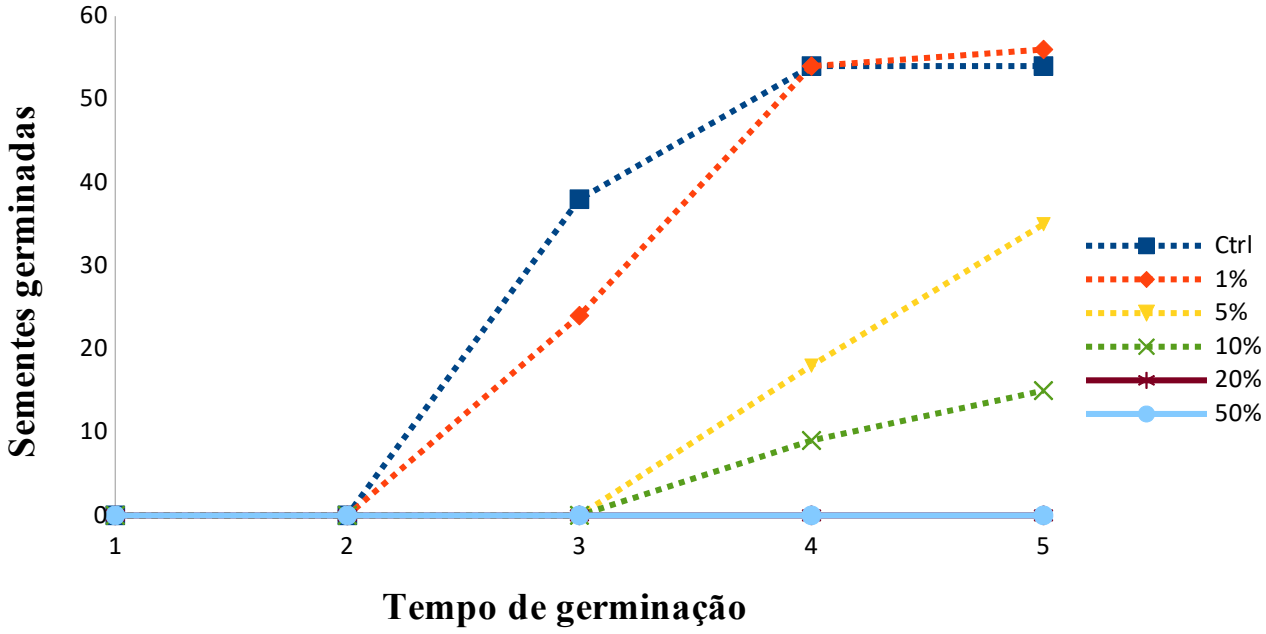

Figura 1. Número de sementes germinadas a cada 24 horas por 5 dias em cada tratamento (1%, 5%, 10%, 20%, 50% e controle, com apenas água).

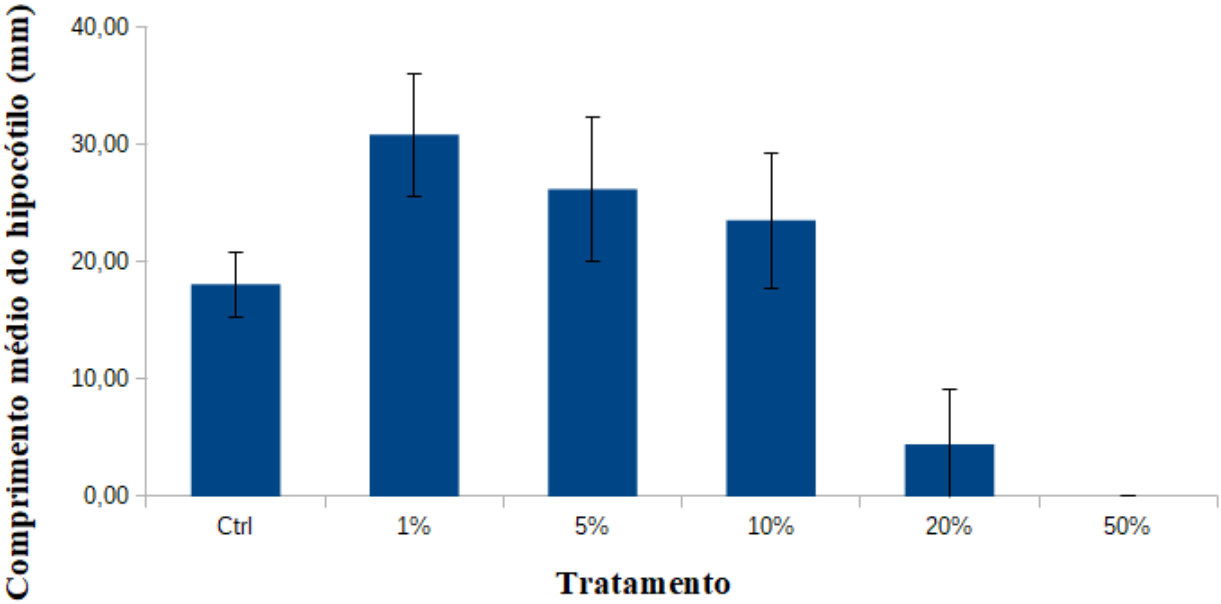

Figura 2. Comprimento médio da radícula após 5 dias de transplante em cada tratamento (1%, 5%, 10%, 20%, 50% e controle, com apenas água).

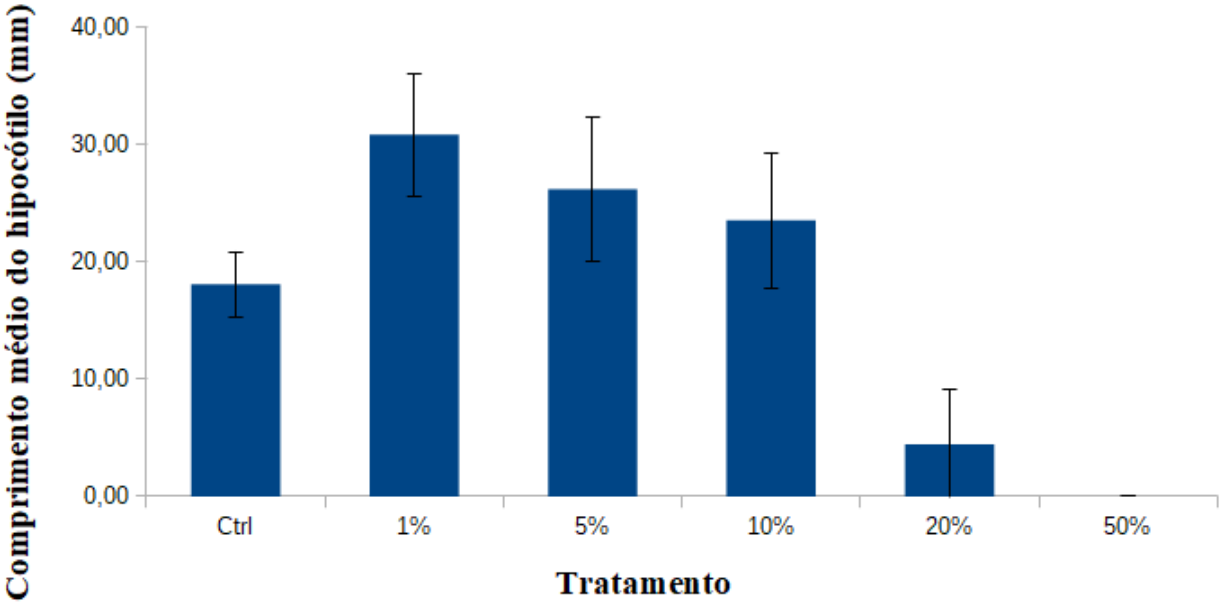

Figura 3. Comprimento médio do hipocótilo após 5 dias de transplante em cada tratamento (1%, 5%, 10%, 20%, 50% e controle, com apenas água).

CAPÍTULO II

DOES THE INVASION OF *TRADESCANTIA ZEBRINA* CHANGE THE VEGETAL DECOMPOSITION AND COMMUNITY OF LIGNOCELLULOLYTIC FUNGI IN ATLANTIC FOREST?

DOES INVASIVE *TRADESCANTIA ZEBRINA* ALTER LITTER DECOMPOSITION RATES AND LIGNOCELLULOLYTIC FUNGAL COMMUNITIES IN ATLANTIC FOREST?

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ABSTRACT

Aims: We evaluated whether the invasive herbaceous *Tradescantia zebrina* Heynh. ex Bosse (Commelinaceae) alters leaf litter decomposition in the Atlantic Forest and the lignocellulolytic fungal community composition.

Methods: Detritus decomposition: We deposited 30 litter bags with detritus from the invader and 30 with natives in each area, collected in rejoinder for eight months (10 days sample), dried and measured gravimetrically. Simultaneously, we carried out this experiment in the laboratory under controlled environmental conditions.

Lignocellulolytic fungi composition: In each area, we deposited six litter bags with invasive detritus and six with natives, collected in rejoinder during 4 months (2 sample days). We processed and inoculated the samples in 2% malt extract with guaiacol and 1% carboxymethylcellulose (CMC). To measure the composition, we selected one representative of each morphospecies for DNA extraction and molecular identification.

Results: Leaf litter from *T. zebrina* decomposed faster than leaf litter from native species. However, the invasion of *T. zebrina* did not alter decomposition rates of either leaf litter type. Although the lignocellulolytic fungal community composition changed over time, neither the invasion of *T. zebrina* nor leaf litter type influenced lignocellulolytic fungal communities.

Conclusion: We believe that the high plant richness in the Atlantic Forest enables a highly diversified decomposing biota, capable of affecting different leaf litter types under different environmental conditions.

KEYWORDS: Nutrient cycling, microbiota, litter bags, native plants, protected areas.

INTRODUCTION

Invasive species represent one of the greatest threats to biodiversity and ecosystem services (Burgiel and Muir, 2010). In natural ecosystems, the impacts of biological invasions are complex and can permanently alter the structure of communities, cause local extinctions, and homogenise the invaded environment (Dogra et al., 2010; Sakai et al., 2001). Invasive species alter ecosystems across various scales, from individuals (e.g. growth and reproduction rates) to population-community interactions and ecosystem nutrient cycling processes (i.e. litter production, nitrogen (N) retention, and nutrient cycling) (Currie et al., 2014).

Leaf litter decomposition is the primary source of organic matter in soils (Berg and McClaugherty, 2014; Hobbie, 2015). The decomposition of leaf litter interacts with the energy flow of ecosystems (Krishna and Mohan, 2017), and is largely mediated by microorganisms (Simpson et al., 2007). During decomposition, microorganisms modify the leaf litter chemical components, affecting the dynamics of carbon (C) and N in the soil (Simpson et al., 2007), which in turn affects plant growth and species composition of plant communities (Hättenschwiler et al., 2005; Krishna and Mohan, 2017). Furthermore, plant species richness affects leaf litter inputs (Pereira, 2010). Losses to plant diversity alter the quality of plant leaf litter and cause a reduction in the functional diversity of decomposing organisms, which reduces C and N cycling (Handa et al., 2014). However, the relationship between the structure of the microbial community and the decomposition of leaf litter during plant invasions is still poorly understood (Arthur et al., 2012; McTee et al., 2017).

Invasive plant species often have distinct nutrient requirements than native species (Liao et al., 2008). Therefore, invasive plants often produce leaf litter that differs from that produced by native species in terms of quality and quantity (Chiba et al., 2015; Ehrenfeld, 2010). The accumulation of plant leaf litter, resulting from a high amount of biomass of invasive plant species, also leads to changes in soil nutrients, primary productivity, and a consequent change in plant species (Berendse, 1999). The abundant leaf litter from

invasive plants can suppress the germination of native species (Gaertner et al., 2014), and further increase the biomass of invasive species (Bates et al., 2006). Furthermore, the quality of the invader's leaf litter often promotes changes to N dynamics, soil pH, and soil microbial enzyme activity patterns (Kourtev et al., 2002). In turn, these promote profound changes to leaf litter decomposition rates (Vitousek and Howarth, 1991).

Changes to leaf litter decomposition processes can influence interspecific competition and structure at the plant community level (Keller and Phillips, 2019; Swift et al., 1979). Often, plant invasions increase the concentrations and flow of C and N in invaded ecosystems (Liao et al., 2008), resulting in a positive feedback for the development of the invasive plant itself (Janusauskaite and Straigyte, 2011). In addition, many plant invaders produce leaf litter with a high nutritional quality (van Kleunen et al., 2010), capable of favouring specific communities of fungi over others (McTee et al., 2017; Zubek et al., 2016), further accelerating the nutrient cycling processes in invaded ecosystems (Allison and Vitousek, 2004; Arthur et al., 2012; Jo et al., 2017). However, the relationship between the quality of the invasive leaf litter, the microbial community's composition, and the decomposition rates of leaf litter under invasion are still controversial (Cleveland et al., 2014). Several studies corroborate changes in the microbiota and consequent changes in nutrient cycling in invaded areas (Kourtev et al., 2002, 2003; Mincheva et al., 2014; Stefanowicz et al., 2016). However, there is evidence that the microbial community can functionally adapt to different leaf litter qualities (Hoyos-Santillan et al., 2018; Kaiser et al., 2014). Therefore, the effect of the invasion on the microbial community would depend on the invasive species (Stefanowicz et al., 2016). Thus, plant invasions can profoundly impact the quality and quantity of leaf litter and the dependence between producers and decomposers (Naeem et al., 2000). These impacts result in changes not only in the plant community but also in the structure of the decomposing microbiota (Kourtev et al., 2002; Stefanowicz et al., 2016; Wolfe and Klironomos, 2005) and, ultimately, in the ecosystems functions (van der Putten et al., 2007).

Fungi are an essential part of soil microbial communities and actively participate in releasing nutrients and organic C via leaf litter decomposition (Li et al., 2017). Fungi produce lignocellulolytic enzymes, which are a type of carbohydrate-active enzyme (CAZyme). CAZymes include enzymes that decompose the polymers that make up plant biomass, such as cellulose, hemicellulose, and lignin (Lombard et al., 2014). The ability to produce these enzymes allows fungi to live in various natural conditions, being classically recognised as key organisms in leaf litter cycling in forests (Swift et al., 1979; Vogt et al.,

1986). Recently, there has been much interest in the changes promoted by leaf litter from plant invasions on fungal communities (Biasi et al., 2020; McCary and Wise, 2019; Woodworth et al., 2020). However, the effects are diverse, and the direction and magnitude of these effects are dependent on the invaded ecosystem (Zhang et al., 2019).

In this study, we evaluated whether the invasive *Tradescantia zebrina* Heynh. ex Bosse (Commelinaceae) alters the parameters of plant decomposition in the Atlantic Forest and the community of decomposing fungi. We hypothesised that (1) leaf litter from invasive plants has higher decomposition rates than that from native plants and (2) leaf litter in areas invaded by *T. zebrina* has a higher decomposition rate than in non-invaded areas, whereas the opposite pattern occurs for leaf litter from native plants. These factors, together with a decrease in native regeneration as a result of the invasive species (Chiba de Castro et al., 2019b), would result in the reduction of niches for the decomposing organisms of the Atlantic Forest, altering the diversity of lignocellulolytic fungi. Thus, we also hypothesised that (3) the diversity of decomposing fungi in invaded areas is lower than that in non-invaded areas and that 4) the diversity of decomposing fungi in leaf litter of native plants is higher than that in leaf litter of invasive plants.

MATERIALS AND METHODS

Description of the study area

We conducted this study at the Iguassu National Park (PNI) in southern Brazil (25°05' and 25°41' S; 53°40' and 54°38' W). The PNI is the largest protected area in the Atlantic Forest in Brazil. It is 185,262.5 ha (Rodolfo et al., 2008), and is part of one of the most important biological areas in South-Central South America, which has more than 600 thousand hectares of protected areas and another 400 thousand hectares of primitive forests (WWF, 2014). The region has a subtropical climate with hot summers (Alvares et al., 2013), temperatures between 15 °C and 26 °C, and an average annual rainfall of 1,841 mm (IAP, 2015). The vegetation of the PNI is composed of an ecotone between (1) mixed ombrophilous forests and (2) semi-deciduous forests. The main tree species found in the forest areas in the PNI are *Euterpe edulis*, *Acacia bimucronata*, *Bastardiopsis densiflora*, *Cordia americana*, *Pilocarpus pennatifolius*, *Urera baccifera*, *Cecropia pachystachya*, *Eugenia subterminalis*, *Hennecartia omphalandra*, *Inga marginata*, and *Lonchocarpus nitidus* (Souza et al., 2017). We selected 10 areas for the experiment, five of which were invaded by *T. zebrina* (60 to 90% coverage of *T. zebrina*, with any other other dominant

species) and five non-invaded (without *T. zebrina*). The selected areas have been monitored for five years by our research group, with several studies happening simultaneously. The areas are located between 20 and 30 m from the edge of the forest, at least 500 m apart.

T. zebrina

The herbaceous *T. zebrina* is originally from Mexico and northern Central American countries, and was brought to Brazil for ornamental purposes (Mantoani et al., 2013). It has a high capacity for adaptation to different Brazilian biomes, with records of invasion in the Cerrado (Zenni and Ziller, 2011) and Atlantic Forest (Carpanezzi, 2011; Mantoani et al., 2013; Zenni and Ziller, 2011). It is an herbaceous plant, growing up to 25 cm with purple-green glabrous leaves, which have two silvery longitudinal bands on the adaxial surface and one purple band on the abaxial surface. It has small flowers, which are not showy and have a pinkish colour. It quickly multiplies by stem fragments, and is also considered a weed in agriculture (Lorenzi and Souza, 2008). It multiplies quickly at any time of the year, establishing a large biomass in invaded areas (Lorenzi and Souza, 2008). It is considered a strong competitor, affecting the diversity of species in forest fragments (Mantoani et al., 2013), mainly in the forest edge regions, inhibiting tree regeneration (Chiba de Castro et al., 2019a). It is cited in several lists of invasive species (Carpanazi, 2007; IAP, 2015; Sampaio and Schmidt, 2013; Ziller and Dechoum, 2013). Laboratory tests have revealed it is potentially allelopathic (Martins et al., 2014), and some studies attribute part of its dominance in areas invaded by its large biomass and allelopathy (Mantoani et al., 2013; Silva and Voltolini, 2017). In the PNI, the density of *T. zebrina* negatively affects the height of the regenerants, impairing the recruitment and development of the plant community (Chiba de Castro et al., 2019a). Additionally, invaded communities have higher predation rates, which increases the indirect effects of the invasion on the development of native species (Castro et al., 2016).

Litter bag preparation

We collected live fragments of (1) *T. zebrina* from the five invaded areas and (2) native trees/shrubs/herbs from the five non-invaded areas. We collected the native fragments opportunely, with manual removal of fragments of herbs and leaves of trees and shrubs and some senescent dry branches with clear signs of abscission. The invasive and native fragments were dried separately in an oven at 55 ± 5 °C until they attained a

constant weight. We prepared large litter bags for an *in situ* experiment and small litter bags for an *in vitro* experiment. The large bags were 225 cm² (15 × 15 cm) and contained 5 g leaf litter per bag. The small litter bags were 25 cm² (5 × 5 cm) and contained 2 g leaf litter per bag. Both litter bags were made using a plastic mesh of 5 mm pore diameter to allow access to macroinvertebrates. For each size bag, two types of litter bags were made, one with only dry fragments of the invader (invasive litter bags) and the other with dry fragments of native species (native litter bags). The composition of species and types of fragments in the native litter bags was random.

In situ experiment

We started the experiment in November. In each of the 10 areas of the experiment (five invaded areas and five non-invaded areas), we deposited 60 large litter bags, 30 invasive and 30 native litter bags. The litter bags were deposited alternately, with a distance of approximately 30 cm from each other. They were placed just above the leaf litter and tied to tree trunks with nylon thread to avoid displacement due to animals. Ten sampling days were established over an eight-month period (0, 10, 20, 30, 50, 70, 100, 140, 180 and 240 days from the beginning of the experiment). On each sampling day, we collected six litter bags in each area, three of each type (sub-replicates) (for an illustration of this method, please go to appendix A).

In vitro experiment

We collected soil from the A horizon in invaded and non-invaded areas, *T. zebrina* fragments from invaded areas, and leaf litter from non-invaded areas. In four 0.15 m² (0.5 × 0.3 m) trays, under controlled conditions of temperature (25 ± 3° C), light (3000 lux) and photoperiod (12/12 h), we simulated the environmental conditions of invaded and natural forest (presence and absence of *T. zebrina*, respectively). We made 120 small litter bags, 60 invasive and 60 native litter bags. In the trays, we deposited either: (1) the substrate and leaf litter of the invaded areas and 30 invasive litter bags, (2) the substrate and leaf litter of the invaded areas and 30 native litter bags, (3) the substrate and leaf litter of the non-invaded areas and 30 invasive litter bags, or (4) the substrate and leaf litter of the non-invaded areas and 30 native litter bags, totalling four trays. We collected three litter bags from each tray on the same sample days as the *in situ* experiment. All samples collected were dried at 55 ± 5 °C, and the remaining particulate plant material was measured gravimetrically.

Isolation and identification of decomposing fungi from plant litter

To analyse the composition of lignocellulolytic fungi, we deposited 12 large litter bags (15 ×15 cm) in each of the 10 areas, six invasive and six native litter bags. We sampled litter bags twice in four months, exploring two stages of decomposition: (1) decomposition of labile/soluble material (day 10) and (2) decomposition of recalcitrant material (day 100). At each sampling time, we collected six litter bags from each area, three of each type. We mixed the litter from the bags of the same type and area to compose a composite sample. Thus, we obtained 40 composite samples, 20 from day 10 and 20 from day 100. That is, at each sampling time, we obtained five samples of invasive leaf litter from invaded areas, five samples of native leaf litter from invaded areas, five samples of invasive leaf litter from non-invaded areas, and five samples of native leaf litter from non-invaded areas. In the laboratory, the 40 samples were disinfected by washing with distilled water to remove soil and other organisms present (Paulus, 2004). Then, the samples were processed using the particle filtration method (Bills and Polishook, 1994). This process consisted of homogenisation using a high-speed industrial blender for two minutes in 200 mL of distilled water, after which the particulate material was washed with distilled water jets (2 washes with 100 mL) in stainless steel sieves (600 µm, 300 µm, 150 µm, then 75 µm mesh size). The particles retained in the smallest mesh sieve were used to perform three serial dilutions (10:1, 10:2, and 10:3). Then, we plated 0.1 mL of the 10:3 dilution (Machado, 2004; Nicolau, 2014). For each plating, we performed triplicates with 2% malt extract supplemented with guaiacol (20 g/L of malt extract, 4 mM guaiacol, and 15 g/L of bacteriological agar) according to Kiiskinen et al. (2004) and CMC 1% (10 g/L of carboxymethylcellulose, 6.7 g/L of yeast extract, and 15 g/L of bacteriological agar) according to Makhuvele et al. (2017). All culture media were prepared with 10 mg/L of chloramphenicol to inhibit bacterial growth. We incubated the plates at 28 °C, and fungal growth followed for 30 days (Costa et al., 2015). The isolates were purified and preserved by the Castellani method (Castellani, 1939), and cryopreservation with 10% glycerol and kept at -80 °C. We stored the preserved material in the Culture Collection of Microorganisms of Biotechnological and Environmental Importance (UNILA CCMIBA).

Purification consisted of raising each isolate separately until confirmation that the isolate represented a single individual (until there was a single morphospecies). The use of

the concept of morphospecies has been useful in estimating the number of fungi since the species is conventionally the basic unit in biodiversity studies (Lacap et al., 2003).

We analysed the purified fungi for the determination of morphospecies. We identified the different morphospecies morphologically by microscopy of the mycelium. We used a stereoscopic magnifying glass and microscopically prepared slides and microcultures coloured with blue cotton lactophenol. We photo-documented the images for deposit at the CCMIBA and morphospecies archives.

We selected one representative of each morphospecies for DNA extraction and molecular identification. We extracted the genomic DNA of the isolates according to the protocol described by Raeder and Broda (1985). We amplified the ITS1-5, 8S-ITS2 region of the ribosomal DNA with the universal primers for fungi, ITS-1 (5`TCCGTAGGTGAACCTGCGG-3`) and ITS-4 (5`TCCTCCGCTTATTGATATGC-3`), which amplify a region of approximately 600 bp (White et al., 1990). We prepared the reactions in a final volume of 25 µL, containing genomic DNA (1.0 ng/µL), 2.5 µL of enzyme buffer, 0.5 µL of dNTPs, 0.6 µL of the ITS-1 primer, 0.6 µL of the ITS-4 primer, and 0.3 µL of Taq DNA polymerase. We programmed the thermal cycler for an initial denaturation at 94 °C for 2 minutes; followed by 30 cycles at 94 °C for 1 minute, 55 °C for 1 minute, and 72 °C for 1 minute; and a final extension at 72 °C for 10 minutes. We analysed the PCR product on agarose gel (1% w/v) with GelRed® Nucleic Acid Gel Stain (Biotium), with the addition of a molecular marker (1 Kb Plus DNA Ladder). Then, we purified the product using the enzyme ExoSap-IT. The samples were then sequenced using the SANGER method at ACTgene Analyzes Moleculares®.

The sequences obtained were blasted against the National Center for Biotechnology Information (Genbank-NCBI) database and the Biological Sequence Analysis Center (CBS) database (supplementary material). We performed the sequence alignment using the online program Clustal W and phylogenetic and molecular analyses were conducted using MEGA software version 7.0 (Kumar et al. 2016). We used the Kimura model (Kimura, 1980) to estimate the evolutionary distance and the Maximum Likelihood (ML) algorithm for phylogenetic reconstructions, with the bootstrap value calculated from 1,000 replicates. After analysing similarity using Blast N, we grouped the isolates classified with 97% similarity at the genus-level. We evaluated the isolates belonging to the same genus through phylogenetic analysis. To confirm the previously defined morphospecies, we then compared the fungi grouped in the same branch using

the global alignment of the Needleman-Wunsch Global sequence (for an illustration of this method, please go to appendix B).

Data analysis

We estimated the rate of decomposition using a first-order negative exponential decay model (Olson, 1963) widely used to adequately capture the decay dynamics in many systems (Keller and Phillips, 2019; Zhang et al., 2008):

$$X_t = X_0 e^{-kt}$$

where X_t and X_0 correspond to the initial and final mass of the waste, respectively, t is the time (days), and k is the mass loss constant.

We calculated the half-life ($t_{½}$) of leaf litter using the equation:

$$t_{½} = \frac{\ln(0.5)}{-k}$$

where k is a constant of mass loss in each litter bag of each experiment.

We used linear regression to compare the decomposition rates between *in situ* and *in vitro* experiments for both types of leaf litter (invasive and native). The line slope (regression parameter t) represents the rate between decomposition speeds of the two methodologies. To verify significant differences between the decay of leaf litter types in the different environmental treatments (invaded and non-invaded), for both decomposition experiments, we used a generalised linear mixed model with a binomial distribution and temporal pseudo-replication. The pseudo-replicates were sets of samples carried out over time. Thus, the fixed effect included sampling time as a categorical factor, with 10 levels (each re-sampling expressed in the estimation of the mass of the litter bag), as well as its interaction with the effects of (1) the type of litter bag and (2) environmental treatment. The structure of random effects includes interception for treatments and temporal sampling (Crawley, 2005).

Analysis of the community of fungal decomposers

We used morphospecies data to build distance matrices with Jaccard presence/absence data (0 < dJ <1, with 0 being identical and 1 being completely different; Jaccard, 1912). To verify significant differences in the composition of the morphospecies between the invaded and non-invaded areas at the different stages of decomposition (day 10 and day 100), we determined the beta diversity (Baselga, 2010) using the 'betadisper' function in the 'betapart' package (Baselga and Orme, 2012). To check if there were

significant differences regarding dissimilarity 1) between the areas (invaded and non-invaded) within the spatial replicates, and 2) between the different types of leaf litter within the sample replicates, in the different stages of decomposition (day 10 and day 100), we conducted a three-way PERMANOVA (Anderson, 2001) using the 'adonis' function of the 'vegan' package (Oksanen et al., 2019), where ‘time’, ‘area’, and ‘leaf litter’ were the three factors. We performed all statistical analyses in the R statistical environment (R Development Core Team, 2020)

RESULTS

Decomposition of detritus under different environmental conditions

The decay of different types of leaf litter (invasive and native) under different environmental treatments (invaded and non-invaded areas), as well as under different experimental conditions (*in situ* and *in vitro*), is illustrated in Figure 1. The negative exponential model was suitable to explain the temporal decay of different leaf litters (invasive and native) subjected to environmental treatments (invaded and non-invaded) both under *in situ* and *in vitro* experimentation (Table 1). The half-life of invasive leaf litter was shorter than that of native leaf litter in both experiments and environmental treatments. In the *in situ* experiment, the half-life of invasive leaf litter was 59 and 53 days and that of the native leaf litter was 126 and 134 days for invaded and non-invaded areas, respectively. In the *in vitro* experiment, the half-life of invasive leaf litter was 230 and 212 days and that of the native leaf litter was 315 and 317 for invaded and non-invaded areas, respectively.

Decomposition occurred faster *in situ* than *in vitro* for both environmental treatments and leaf litter types (Figure 2). Under invasion, the rates of decomposition of invasive and native leaf litter *in situ* were 1.9 and 1.7 times faster than *in vitro*, respectively. In the absence of invasion, the rates of decomposition of invasive and native leaf litter *in situ* were 1.9 and 1.8 times faster than *in vitro*, respectively. There were no significant differences between the decomposition rates of the same leaf litter types under different environmental treatments, in the different experiments over time (Table 2).

Community of decomposing fungi

We isolated 191 fungi (117 from day 10 and 74 from day 100), classified into 81 morphospecies (42 from day 10 and 44 from day 100). After molecular identification, all isolates were confirmed to belong to distinct morphospecies and grouped into three phyla

and 25 genera (16 from day 10 and 18 from day 100). We could not identify the genera of seven isolates (two from day 10 and five from day 100). This could be due to the absence of specimens in the databases for the region studied (ITS). Thus, to confirm the unidentified morphospecies, the D1/D2 region of the ribosomal DNA 26S gene will be analysed in future experiments. The complete composition of the fungal community for each time, environment, and leaf litter type can be seen in Figure 3. We identified only one isolate of the phylum Basidiomycota (*Trametes* sp. 2AQ) in the invaded area on day 10. We identified two morphospecies from the phylum Mucoromycota, predominantly in day 10 when it was identified in eight of the 10 areas, five invaded and thre non-invaded areas (*Mucor* sp. 1D and *Mucor* sp. 2I). The remaining 78 morphospecies were from the phylum Ascomycota (96%). The most abundant genus was *Fusarium* (25%), followed by *Aspergillus* (12%), *Colletotrichum* (7.4%), *Penicillium* (6.2%), and *Trichoderma* (6.2%).

Fusarium sp. 2J and *Mucor* sp. 1D were highly prevalent on day 10, but were not observed on day 100. *Penicillium* sp. 2G was isolated from all 10 areas on day 10 and from most areas on day 100. On day 10, 52.2% of the morphospecies observed from the invaded areas were isolated from only one of the five areas. On the same day, 63.0% of the morphospecies observed from the non-invaded areas were isolated from only one of the five areas. On day 100, 56.7% of the morphospecies from the invaded areas were isolated from only one of the five areas. On the same day, 50% of the morphospecies observed in the invaded areas were isolated from only one of the five areas.

There were no significant differences in the composition of the lignocellulolytic fungi community between the invaded and non-invaded areas (Figure 4) both for day 10 ($F = 0.77$; $p = 0.39$) and day 100 ($F = 0.69$; $p = 0.42$). Neither the type of leaf litter, environment, nor interactions between leaf litter types and environment explained the lignocellulolytic fungal community structure.

DISCUSSION

Our results demonstrate that leaf litter from *T. zebrina* is decomposed quicker than leaf litter from native plants of the Atlantic Forest. However, the invasion of *T. zebrina* does not influence either the decomposition rates of leaf litter or the structure and composition of lignocellulolytic fungi.

In our experiment, both leaf litter types (invasive and native) were placed in both areas (invaded and non-invaded). In this way, both leaf litter types were subjected to the same microclimate variations in both areas. Therefore, the higher decomposition rate of *T.*

zebrina leaf litter than that of native leaf litter may be associated with the quality of the leaf litter. This higher rate may be related to a higher concentration of N commonly observed in invasive plants than in native species of invaded communities (Incerti et al., 2018; Liao et al., 2008). For example, the leaf litter of two invasive species, *Buddleja asiatica* and *Myrica faya*, was rich in N and decomposed faster than leaf litter from natives in invaded areas in Hawaii (Matson, 1990). The accumulation of N and other nutrients in the tissues of *T. fluminensis*, a species of the same genus and habit of *T. zebrina*, accelerates the decomposition of its leaf litter and, together with the large biomass of *T. fluminensis*, alters the availability of nutrients in invaded forest remnants of New Zealand (Maule et al., 1995; Standish et al., 2004).

The lability of *T. zebrina* leaf litter could also explain its faster decomposition rates. Similar to *T. fluminensis* (Standish et al., 2004), *T. zebrina* probably has lower levels of lignin and higher levels of labile compounds in its structure than native leaf litter in the Atlantic Forest. During the beginning of the decomposition process, a high N content can support large microbial populations that quickly consume labile compounds, which results in a faster loss of mass (Berg and McClaugherty, 2014), corroborating our decay results. The high concentration of N, both due to the quality and quantity of the leaf litter, can create positive feedbacks that promote the proliferation of the invasive species and/or other exotic species (Janusauskaite and Straigyte, 2011; Vinton and Goergen, 2006). Invasive species such as *T. zebrina*, with faster decomposition rates than native ones, can benefit from the high nutritional support provided by the invasion and, in certain situations, lead to the extinction of native species locally (Suding et al., 2005).

The lower rate of decomposition found for native leaf litter could be due to the habit of native species. In our experiment, the invasive leaf litter was of exclusively herbaceous origin, while the native leaf litter came from plants with different habits, and included fragments of branches. In general, the leaves of herbaceous species are more easily decomposed than the leaves of arboreal species (Zhang et al., 2008), since leaves are mainly composed of soluble carbohydrates, which decompose quickly (Songwe et al., 1995). Decomposition rates can also vary with plant tissue type (Gessner et al., 2010). For example, the leaves of *Lythrum salicaria*, invasive in wetlands in the northern United States, decompose faster than native species (*Typha* sp.) in invaded areas, while the invader's stems decompose more slowly (Emery and Perry, 1996). Even leaf litter composition, whether it is composed of one species or a mixture of species, can influence decomposition rates (Handa et al., 2014; Hättenschwiler et al., 2005; Lecerf et al., 2011).

Therefore, the composition of the native leaf litter, which included various plant sources with different habits and/or tissues, may have resulted in the lower decomposition rates. However, considering that the invasion results in a large monospecific biomass, we believe that the comparison between monospecific leaf litter (from the invader) and native leaf litter from a diversity of species and habits is a good approximation of the dynamics of leaf litter decomposition in the study area.

In general, *in situ* decomposition is faster than *in vitro* decomposition. The wear and tear in the natural environment by weathering; the action of more organisms, such as shredders; and loss by sedimentation of particles smaller than the mesh of the leaf litter bags, may favour higher decomposition rates in *in situ* experiments (Silva et al., 2011). Despite the absence of these factors and hence less realistic results in *in vitro* experiments (Vignati et al., 2007), investigations based on laboratory experiments are important tools for establishing causal links between selected variables and chemical or biological responses (Chiba de Castro et al., 2019b; Silva et al., 2011). In the *in vitro* experiment, the contribution of microbiota and chemical oxidation to the decomposition process can be measured (Santos et al., 2006). Chemical oxidation in aerobic incubations is responsible for 1 to 5% of all oxygen consumption from the decomposition of different plants (Nunes et al., 2007). Thus, by subtracting the effect of chemical oxidation (1 to 5%), we can estimate the microbial contribution to the general decomposition process. Our results suggest that the microbiota are responsible for 47-56% of all leaf litter degradation. This highlights the importance of studies of the role of microbiota in nutrient cycling processes in biological invasions (Chiba de Castro et al., 2019b).

In temperate forests, the leaf litter decomposition rate is often different in invaded areas compared with that in non-invaded areas (Keller and Phillips, 2019; Kourtev et al., 2002, 2003; Mincheva et al., 2014). However, our results do not corroborate the current literature. We believe that the lack of differences observed in our study can be attributed to the environmental characteristics of the Atlantic Forest, including the diversity of lignocellulolytic fungi. The climate (Bradford et al., 2016), the diversity of decomposing organisms, and the very nature of leaf litter (Makkonen et al., 2012), are determining factors in the rate of decomposition (Prescott, 2010; Smith and Bradford, 2003), and regulate the activity of decomposers of organic matter in the soil (Garcia-Palacios et al., 2013). Tropical forests generally have high average temperatures and high plant richness, which provide leaf litter with a more heterogeneous composition and result in a more constant nutrient cycle (Berg, 2014; Hooper et al., 2000). The leaf litter heterogeneity of

the Atlantic Forest provides a greater diversity of niches for the community of decomposers, keeping the fungal diversity more stable, even under forest gradients (Souza, 2010). These characteristics favour a highly diversified and active decomposing microbial community (Sanches et al., 2009). The natural range of different leaf litter from the Atlantic Forest provides an opportunity for this decomposing community, which also has high taxonomic and functional diversity, to optimise the cycling of nutrients (Gessner et al., 2010), including those from invasive leaf litter. The absence of a pattern in the composition of the lignocellulolytic fungi community corroborates this argument.

Our results indicate that, despite the changes in the quality of leaf litter due to the invasion, the diversity of lignocellulolytic fungi remained high, which likely contributed to sustaining the ecological processes related to plant decomposition. Even when leaf litter is difficult to decompose for part of the microbiota, interactions between decomposers can improve degradation efficiency (Boer et al., 2005). In the context of the high diversity of microbiota existing in the Atlantic Forest (Sanches et al., 2009), it is likely that these interactions enhance the efficiency of nutrient cycling of many types of leaf litter, even under different environments and coevolutionary histories between leaf litter and decomposing microbiota (Gessner et al., 2010). Thus, the use of different substrates by different fungal species promotes the maintenance of the diversity of soil fungi (Costa, 2015). For example, fungal hyphae can act as vectors for transporting bacteria, allowing them to colonize new substrates quicker (Kohlmeier et al., 2005). Furthermore, fungi exhibit a variety of morphological and adaptive traits under different forest microclimates (Marques et al., 2008). These factors can partially explain the absence of a difference in the decomposition rates of the same leaf litter type under invaded and non-invaded areas. That is, the decomposition conditions were likely optimal, even under the different environments.

Our study sought to isolate fungi with lignocellulolytic potential using the reagent guaiacol and the addition of CMC (carboxymethyl cellulose) as the only C source. Standard isolation makes it impossible to recover microorganisms that occur in low numbers but can provide critical ecosystem services (Pathak et al., 2020). We added the reagent guaiacol to the culture medium to select fungi that produce ligninolytic enzymes (Rahouti et al., 1999). For growth in the CMC culture medium, fungi must produce certain enzymes, especially endoglucanases, enzymes of the cellulolytic complex responsible for initiating the hydrolysis of cellulose (Zhang et al., 2009). These enzymes, known as CAZymes, are classified into several hundred different enzyme protein families. However,

a CAZyme family often houses proteins from a broad taxonomic range, covering different taxonomic classes and even different kingdoms (Barrett et al., 2020). In this way, we believe that the applied methodology was adequate to contemplate the three phyla identified in our study.

Most of the fungal morphospecies identified in our study belong to the phylum Ascomycota. Several previous studies have identified the global abundance and distribution of ascomycetes in soil systems worldwide (Tedersoo et al., 2014). This phylum, which is dominant in the soil, can use a higher number of resources than others and may be better equipped to withstand environmental disturbances (Egidi et al., 2019). This versatility may explain the significant occurrence of the phylum Ascomycota in the plant leaf litter of the Atlantic Forest, especially its dominant presence in leaf litter from the invaded area, since the leaf litter of *T. zebrina* has allelopathic properties (Moura et al., 2018; Navarro et al., 2018).

The most abundant genus was *Fusarium*. It was found at both day 10 and day 100. It is a genus widely represented among the filamentous fungi, associated with soil and plants worldwide. It has many symbiotic relationships as a phytopathogen, synthesising CAZymes to obtain energy via plant leaf litter (Abhijeet et al., 2020). Analysis of the gene expression profile of the fungus *Fusarium graminearum*, for example, revealed that most of the CAZyme genes related to cell wall degradation are up-regulated during plant infection (Zhao et al., 2013). Owing to its wide occurrence and enzymatic efficiency, *Fusarium* species may be primarily responsible for the degradation of plant leaf litter in our experiment.

Our results show that leaf litter decomposition time influences the composition of lignocellulolytic fungi. According to Figure 3, *Alternaria* sp., *Bipolaris* sp., *Epicoccum* sp., *Montagnula* sp. *Trametes* sp., *Volutella* sp., *Wiesneriomyces* sp., and the isolate from the taxonomic group Nectriaceae were exclusively found on day 10. In contrast, *Eutypella* sp., *Cladosporium* sp., *Lasiodiplodia* sp., *Myrothecium* sp., *Nigrospora* sp., *Pestalotiopsis* sp., *Sarocladium* sp., and the isolates belonging to the taxonomic levels Pleosporales and Bionectriaceae were exclusively found on day 100. This profile shows the rapid ecological succession of the fungal community that decomposes plant leaf litter (Voříšková and Bladrian, 2013), with highly active morphospecies in the initial (labile/soluble) and final (recalcitrant) phases of decomposition (Frankland, 1998). However, we found no influence of environmental treatment or leaf litter type on the fungal community. This could be because of the low number of individuals of each fungal morphospecies within the

environmental treatments. For both invaded and non-invaded areas, regardless of the sampling time, we found that maximum 50% of morphospecies were associated with more than a single sampling area. This reinforces the high diversity of lignocellulolytic fungi in the Atlantic Forest, where different microorganisms may be naturally available to decompose various leaf litter types (Keller and Phillips, 2019; Kohlmeier et al., 2005). The high diversity of the lignocellulolytic fungal community indicates that the performance of a specific fungus morphospecies under plant leaf litter is mediated by opportunity. Thus, the chances of the same fungus morphospecies occurring in plant leaf litter from several microhabitats is low. This can explain the absence of an effect of invasion and leaf litter quality on the composition of the lignocellulolytic fungi community.

Our study provides useful estimates of invasive and native leaf litter decomposition using in situ and in vitro methods under different environmental conditions. The fastest decomposition of *T. zebrina* was probably due to the leaf litter quality. In contrast with previously published reports, plant decomposition did not change in invaded compared with non-invaded environments. Similarly, *T. zebrina* did not promote a specialised fungal decomposing community. The high plant diversity in the Atlantic Forest probably supports a fungal community fully capable of decomposing a wide variety of leaf litters, including leaf litter from invasive species.

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Table 1: Results of the first-order negative exponential decay model (Olson, 1963) and half-life ($t_{½}$) for different experiments (*in situ* and *in vitro*), detritus type (*T. zebrina* and native species), and environmental treatments (invaded and not invaded).

Experiment	***Litter bags***	**Treatment**	**r^2**	**k (days^{-}**	**k (SD)**	**$t_{½}$ (days)**
In situ	*T. zebrina*	invaded	0.81	0.01165	0.0025	59
		non-invaded	0.89	0.01316	0.0022	53
	Natives	invaded	0.83	0.00550	0.0009	126
		non-invaded	0.76	0.00519	0.00110	134
In vitro	*T. zebrina*	invaded	0.79	0.00302	0.0005	230
		non-invaded	0.89	0.00327	0.0004	212
	Natives	invaded	0.73	0.00220	0.0004	315
		non-invaded	0.81	0.00219	0.0003	317

r^2 = adjustment factor of the decay model; k = decay coefficient.

Table 2: Results of the mixed linear model adjusted for differences between environmental treatments (invaded and not invaded) in both *in situ* and *in vitro* experiments. We used the decay values of *T. zebrina* and native detritus over time.

Response variable	**Factor**	**Estimate**	**SE**	**DF**	**T value**	**P value**
T. zebrina leaf litter	*In situ*	-0.01647	0.00986	80	-1.670	0.099
	In vitro	-0.001068	0.019613	44	-0.054	0.957
Native leaf litter	*In situ*	-0.009728	0.009725	80	-1.00	0.320
	In vitro	0.004726	0.015915	44	0.297	0.768

Table 3. Multivariate permutation analysis on the effect of decomposition time (10 and 100 days), type of leaf litter (native and invasive), and environmental treatment (invaded and not invaded by *T. zebrina*) and of the interactions between effects on the structuring of the Atlantic Forest lignocellulolytic fungi community, based on Jaccard distance matrices (presence/absence data).

Factor	df	Sum of Squares	Mean squares	F value	P value
Time	1	1.756	1.756	4.313	***
Environment	1	0.417	0.417	0.024	0.388
Detritus	1	0.382	0.382	0.022	0.563
Time x Environment	1	0.3871	0.38707	0.9509	0.53095
Time x Leaf litter	1	0.4101	0.41009	1.0075	0.41256
Environment x Leaf litter	1	0.5309	0.53094	1.3044	0.08549
Time x Environment x Leaf litter	1	0.4363	0.43630	1.0719	0.30807
Residuals	32	13.0254	0.40704		

*** < 0.0001, ** < 0.001, *< 0.05

Analysis conducted using PERMANOVA

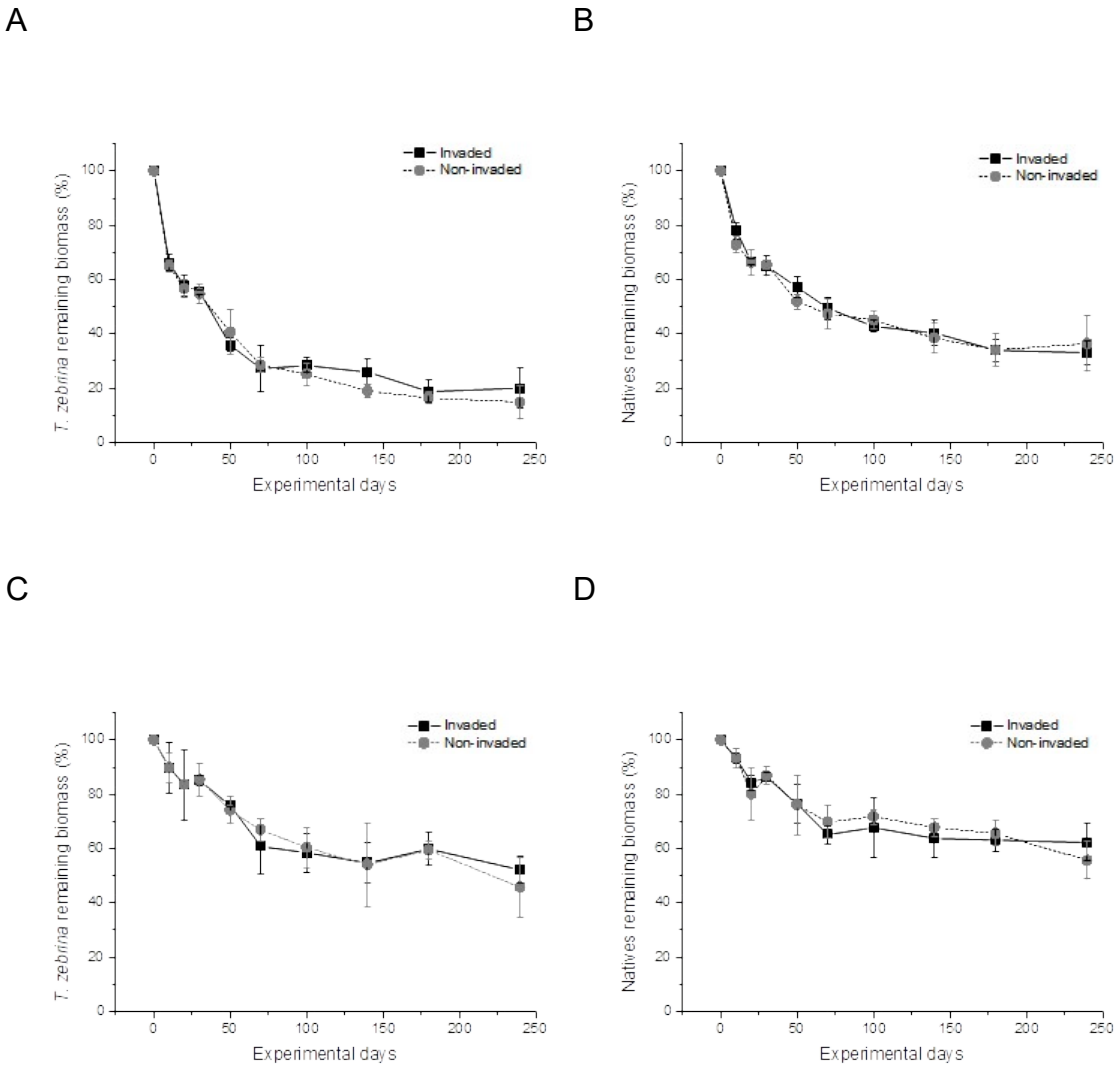


Figure 1. Temporal variation of the decomposition of *T. zebrina* and native species *in situ* (A and B) and *in vitro* (C and D) in Atlantic Forest areas invaded and not invaded by *T. zebrina* throughout the experiment.

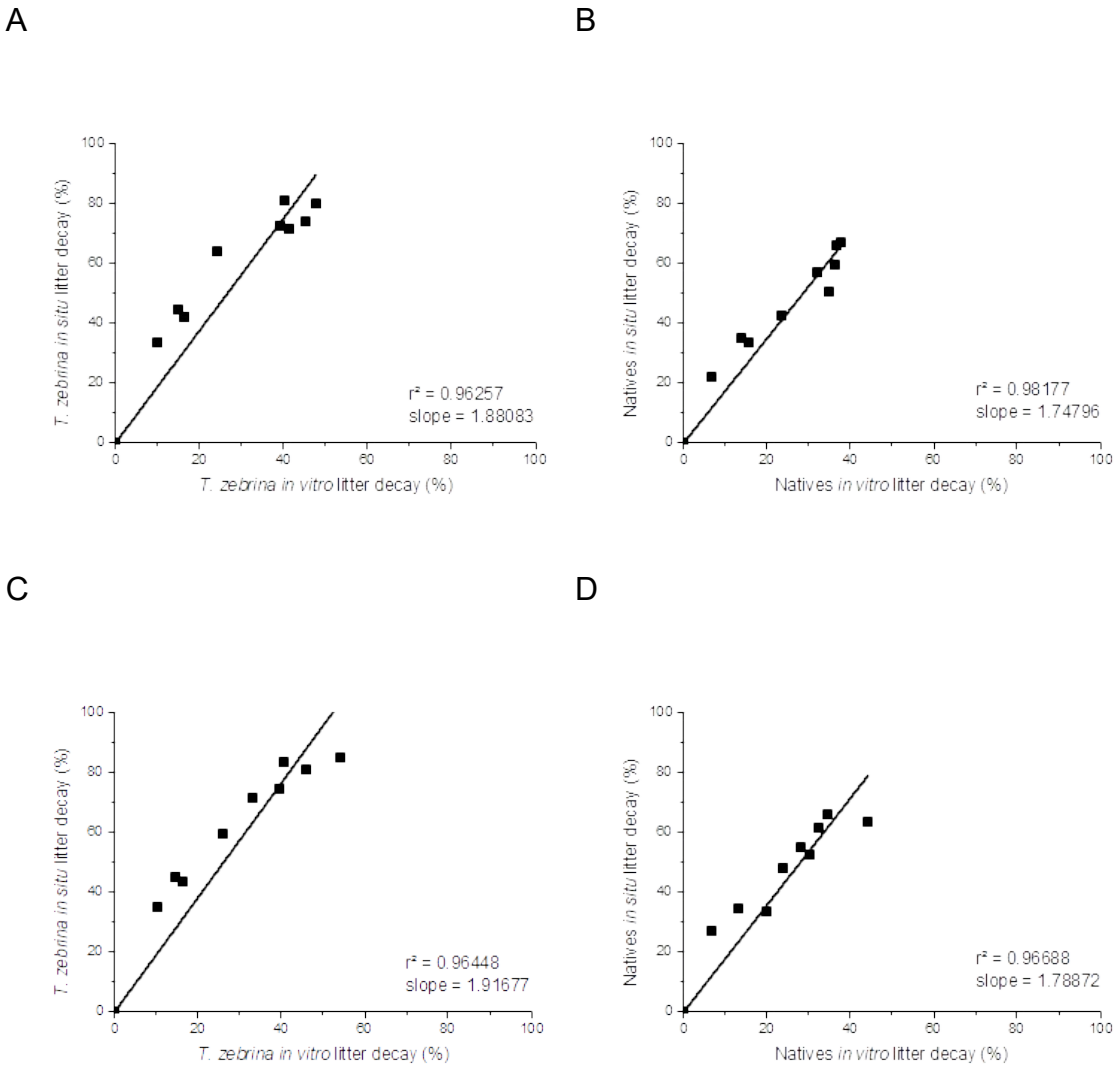


Figure 2: Linear regression between the decomposition values of detritus in *in situ* and *in vitro* experiments of *T. zebrina* and native species. A and B represent invaded areas, and C and D represent non-invaded areas. The model adjustment values (r^2) and slopes of the lines are shown.

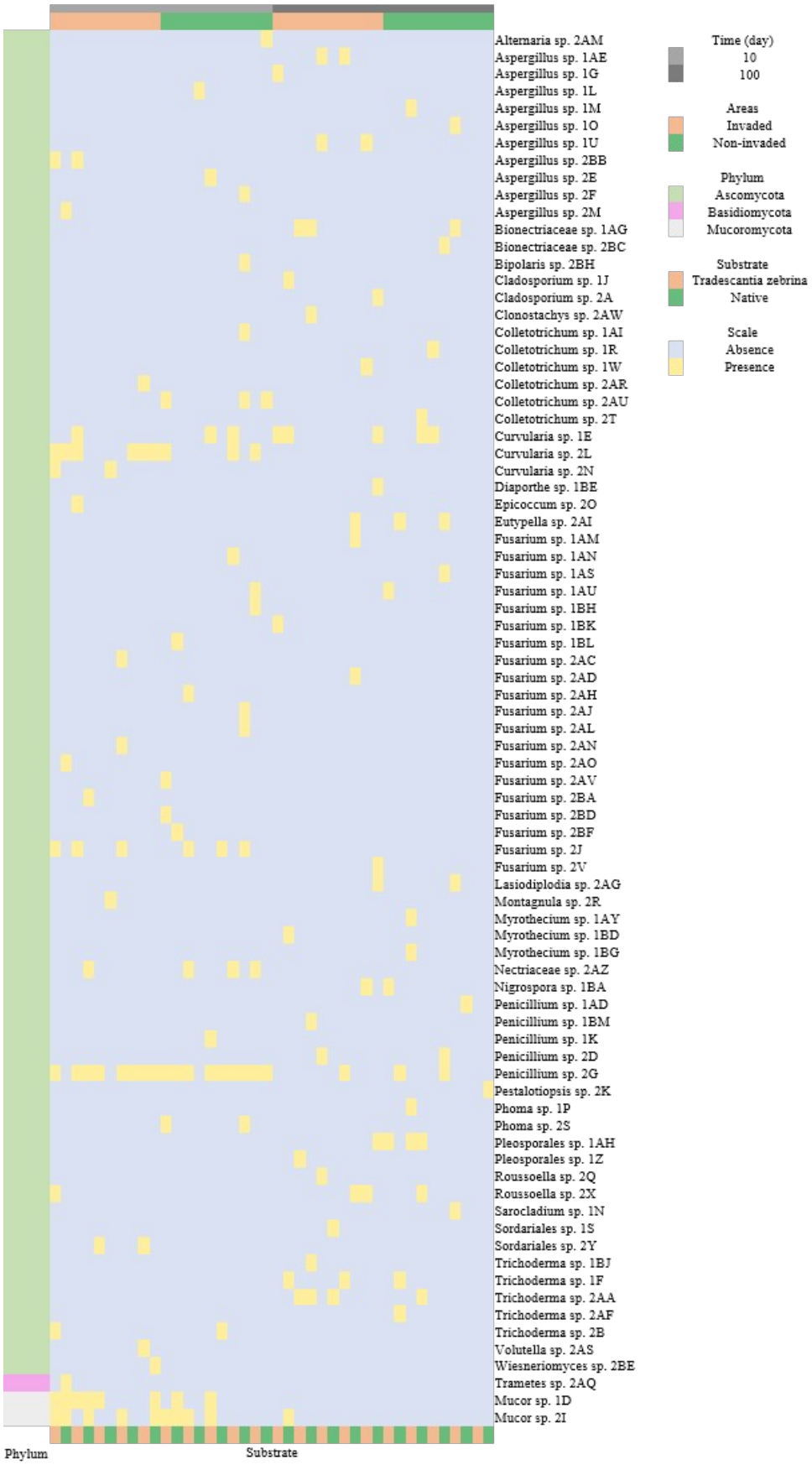

Alternaria sp. 2AM
Aspergillus sp. 1AE
Aspergillus sp. 1G
Aspergillus sp. 1L
Aspergillus sp. 1M
Aspergillus sp. 1O
Aspergillus sp. 1U
Aspergillus sp. 2BB
Aspergillus sp. 2E
Aspergillus sp. 2F
Aspergillus sp. 2M
Bionectriaceae sp. 1AG
Bionectriaceae sp. 2BC
Bipolaris sp. 2BH
Cladosporium sp. 1J
Cladosporium sp. 2A
Clonostachys sp. 2AW
Colletotrichum sp. 1AI
Colletotrichum sp. 1R
Colletotrichum sp. 1W
Colletotrichum sp. 2AR
Colletotrichum sp. 2AU
Colletotrichum sp. 2T
Curvularia sp. 1E
Curvularia sp. 2L
Curvularia sp. 2N
Diaporthe sp. 1BE
Epicoccum sp. 2O
Eutypella sp. 2AI
Fusarium sp. 1AM
Fusarium sp. 1AN
Fusarium sp. 1AS
Fusarium sp. 1AU
Fusarium sp. 1BH
Fusarium sp. 1BK
Fusarium sp. 1BL
Fusarium sp. 2AC
Fusarium sp. 2AD
Fusarium sp. 2AH
Fusarium sp. 2AJ
Fusarium sp. 2AL
Fusarium sp. 2AN
Fusarium sp. 2AO
Fusarium sp. 2AV
Fusarium sp. 2BA
Fusarium sp. 2BD
Fusarium sp. 2BF
Fusarium sp. 2J
Fusarium sp. 2V
Lasiodiplodia sp. 2AG
Montagnula sp. 2R
Myrothecium sp. 1AY
Myrothecium sp. 1BD
Myrothecium sp. 1BG
Nectriaceae sp. 2AZ
Nigrospora sp. 1BA
Penicillium sp. 1AD
Penicillium sp. 1BM
Penicillium sp. 1K
Penicillium sp. 2D
Penicillium sp. 2G
Pestalotiopsis sp. 2K
Phoma sp. 1P
Phoma sp. 2S
Pleosporales sp. 1AH
Pleosporales sp. 1Z
Roussoella sp. 2Q
Roussoella sp. 2X
Sarocladium sp. 1N
Sordariales sp. 1S
Sordariales sp. 2Y
Trichoderma sp. 1BJ
Trichoderma sp. 1F
Trichoderma sp. 2AA
Trichoderma sp. 2AF
Trichoderma sp. 2B
Volutella sp. 2AS
Wiesneriomyces sp. 2BE
Trametes sp. 2AQ
Mucor sp. 1D
Mucor sp. 2I
Time (day)
10
100
Areas
Invaded
Non-invaded
Phylum
Ascomycota
Basidiomycota
Mucoromycota
Substrate
Tradescantia zebrina
Native
Scale
Absence
Presence
Phylum
Substrate

Figure 3. The entire composition of the fungal community at experimental timepoints (10 and 100 days), under different treatments (invaded and non-invaded areas), and on each substrate (*T. zebrina* and native species).

A) B)

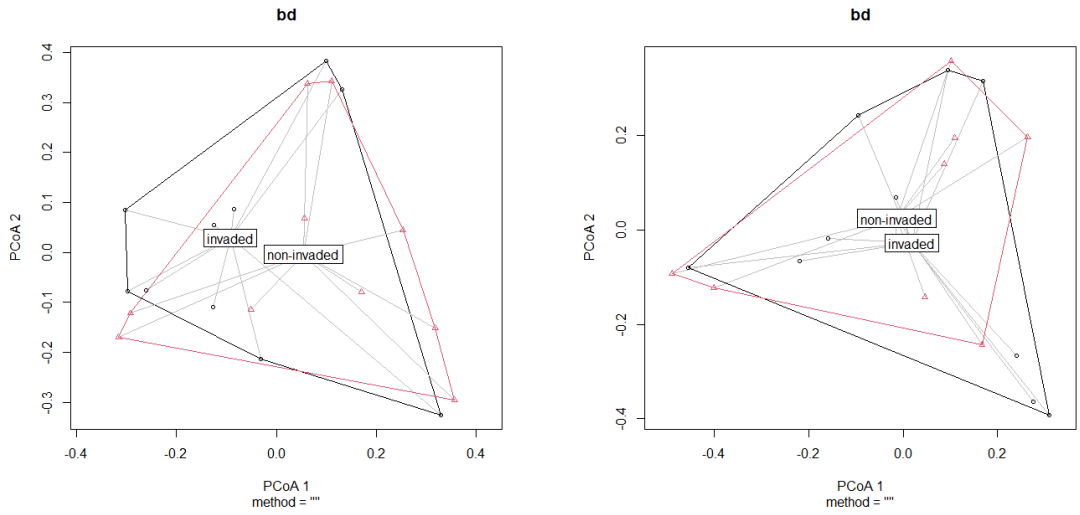


Figure 4. PCoA graphs showing the distribution of lignocellulolytic fungal communities in the invaded and non-invaded areas at (A) 10 and (B) 100 days of plant detritus decomposition experiment.

5. CONCLUSÕES GERAIS

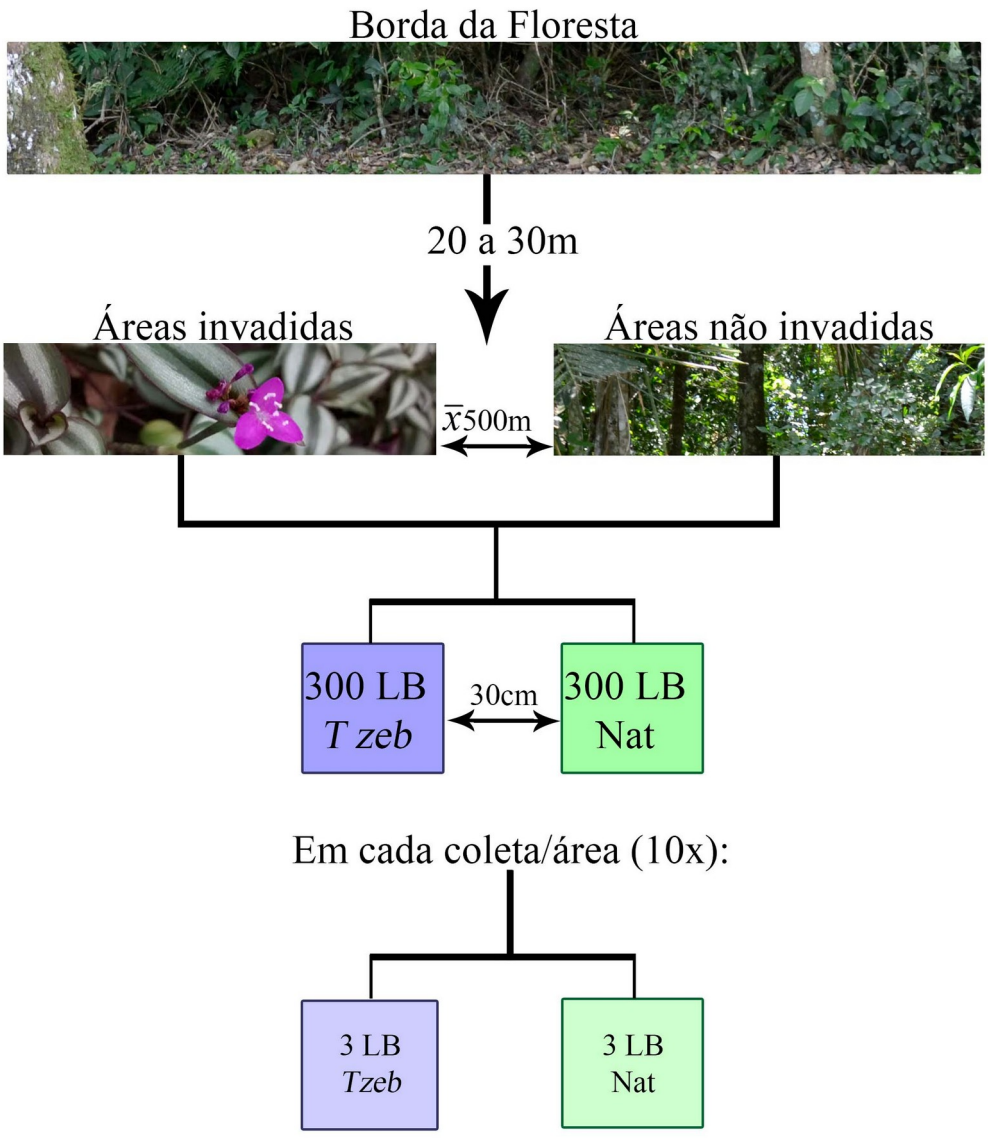
Nossos resultados indicam que *T. zebrina* exerce efeito inibitório na germinação e crescimento inicial das sementes de tomate, apresentando potencial alelopático. Isso indica a necessidade de trabalhos que testem em campo e com sementes nativas os efeitos dos aleloquímicos da invasora. Nosso modelo permitiu uma estimativa efetiva da dinâmica de decomposição de detritos de *T. zebrina* e espécies nativas *in situ* e *in vitro*. A decomposição de *T. zebrina*, mais rápida que a das espécies nativas, se deu pelas diferentes qualidades dos detritos. Nossos resultados divergem da literatura vigente por não apresentar diferenças significativas nos processos de decomposição vegetal entre áreas invadidas e não invadidas, tanto para detritos da invasora quanto para nativas, indicando que generalizações não se aplicam a todas espécies invasoras. Nossos resultados sugerem que a *T. zebrina* não incentiva o desenvolvimento de uma comunidade microbiana especializada na decomposição rápida de seus detritos e que a grande diversidade existente em ambiente de Mata Atlântica, proporcionaria uma comunidade decompositora capaz de degradar, com eficiência, ampla gama de substratos, inclusive da exótica.

Sendo assim, *T. zebrina* não altera a decomposição em relação ao tempo de decaimento e a comunidade de fungos lignocelulóliticos. Isso poderia ser visto como um impacto menor da invasora sobre a Mata Atlântica, mas não é. A grande biomassa que a invasora pressupõe nas áreas invadidas, associada a uma rápida decomposição dos seus detritos (tanto pela qualidade do detrito quanto pela atividade eficiente de fungos lignocelulolíticos) altera significativamente o aporte de nutrientes no solo. Acreditamos que esse enriquecimento nutricional promovido, favorece positivamente o estabelecimento desta invasora, além de potencialmente aumentar a invasibilidade do ambiente para outras invasões. Ademais, é preciso considerar os efeitos aleloquímicos e como pode impactar o ambiente invadido.

O estudo das invasões biológicas ainda possui muitas lacunas. A invasividade e as possíveis estratégias de invasão devem ser exaustivamente exploradas em estudos teóricos e práticos, buscando a prevenção de novas invasões. Nossos resultados demonstram que compreender os processos de ciclagem de nutrientes no contexto de invasões de espécies exóticas, pode subsidiar a identificação dos reais impactos da invasora e melhores estratégias de manejo e controle.

6. APÊNDICES

Apêndice A: Experimento de decomposição dos detritos vegetais.



Apêndice B: Isolamento e identificação fungos decompositores de detritos vegetais.