

UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
INSTITUTO DE BIOCÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

Dissertação de Mestrado

Variação nas taxas de decomposição ao longo de um gradiente altitudinal em florestas
Atlânticas do Sul do Brasil

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Porto Alegre, novembro de 2022.

Varição nas taxas de decomposição ao longo de um gradiente altitudinal em florestas
Atlânticas do Sul do Brasil

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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia, do Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como parte dos requisitos para obtenção do título de Mestre em Ecologia.

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Porto Alegre, novembro de 2022.

CIP - Catalogação na Publicação

Matos Marques, Maria Eduarda
Variação nas taxas de decomposição ao longo de um
gradiente altitudinal em florestas Atlânticas do Sul
do Brasil / Maria Eduarda Matos Marques. -- 2022.
64 f.
Orientadora: Sandra Cristina Muller.

Dissertação (Mestrado) -- Universidade Federal do
Rio Grande do Sul, Instituto de Biociências, Programa
de Pós-Graduação em Ecologia, Porto Alegre, BR-RS,
2022.

1. Decomposição. 2. Mata Atlântica. 3. Gradientes
climáticos. 4. Ecologia Vegetal. I. Muller, Sandra
Cristina, orient. II. Título.

Agradecimentos

Meu trabalho não teria sido possível sem a ajuda e apoio de diversas pessoas que estiveram ao meu lado ao longo do mestrado, as quais serei eternamente grata.

Primeiramente gostaria de agradecer a minha mãe e minha vó, Eliane e Maria, minhas maiores inspirações, por me incentivarem a ir mais longe do que elas conseguiram, por me darem oportunidades muito maiores do que toda nossa família já teve, por me deixarem sonhar em ser grandiosa mesmo com a nossa origem pouco privilegiada. Vocês me fizeram chegar até aqui. Vocês me permitiram ser a primeira pessoa em uma universidade federal (e agora com mestrado) em uma família tão grande como a nossa.

À Sandra Müller pela oportunidade, apoio, atenção e confiança no desenvolvimento do meu trabalho, que foi muito dificultado por ter sido feito inteiro durante uma pandemia e sob um governo fascista que pouco se importava com a ciência no Brasil. Obrigada pelos ensinamentos e pela dedicação.

À Rayana e Milena, que fazem parte deste trabalho e o tornaram possível, obrigada por toda ajuda nos campos e no planejamento do meu projeto, vocês têm minha admiração e carinho.

A todas as pessoas do Laboratório de Ecologia Vegetal da UFRGS, que muitas vezes esclareceram minhas dúvidas e me transmitiram conhecimentos novos. Obrigada por todas as trocas. Em especial às pessoas que me ajudaram nos campos e lavando intermináveis folhinhas, Andrei, Antonella, Davi, Gabi e Jean.

Aos meus amigos que estiveram presentes tanto durante as minhas vitórias e conquistas quanto durante as frustrações e medos ao longo desses dois anos tão importantes na minha vida – Ana, Amanda, Bella, Bibiana, Caio, Camana, Duda, Eduardo, Gabriel, Júnior, Kewen, Laura, Luiza, Marcelo, Sabrina, Sarah e Zimmer – vocês amenizaram o peso de todos os momentos difíceis, obrigada por permanecerem aqui. Sem vocês eu não seria capaz.

À Stella, minha namorada, por tornar meus dias mais leves e por me ajudar em muitas etapas do meu trabalho, até mesmo separando folhas de galhos por horas comigo no laboratório. Obrigada pelo carinho constante, afeto e segurança.

Ao Programa de Pós Graduação em Ecologia da UFRGS, aos professores que cruzaram meu percurso e às amigas que o mestrado me trouxe; levarei todas estas oportunidades para minha formação enquanto cientista e pessoa.

Agradeço ao CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico) pela bolsa de mestrado que possibilitou a dedicação quase integral ao programa de pós-graduação e à CAPES pelo apoio à Pós-Graduação via Programa de Excelência Acadêmica (PROEX).

E aos que acreditam na importância da ciência, resistimos. Que continuemos a fazer pesquisas relevantes para a sociedade e que possamos transmiti-las a todes que não se encontram no nosso meio.

Resumo

A decomposição de serapilheira é um processo biogeoquímico global de grande importância no ciclo do carbono e na ciclagem de nutrientes para as comunidades do solo e das plantas. Mudanças na taxa de decomposição podem ter impactos significativos nos ecossistemas, portanto, é crucial entender as variáveis que controlam esse processo em diferentes biomas. Poucos estudos integram fatores reguladores da decomposição em gradientes climáticos em florestas tropicais e subtropicais, embora sejam essenciais para prever respostas funcionais associadas ao carbono e nutrientes frente às mudanças climáticas. O objetivo deste trabalho é investigar o efeito da variação climática, da qualidade (composição funcional foliar), habitat de origem (espécies oriundas de florestas Atlânticas *stricto sensu* ou de florestas com Araucária) e diversidade (misturas de 1 a 4 espécies) de espécies na serapilheira sobre a taxa de decomposição de espécies nativas do sul da Mata Atlântica. Para tanto, realizamos um experimento de translocação de serapilheira utilizando o mesmo conjunto de espécies ao longo de um gradiente altitudinal (370 a 1003 m a.s.l.), que abrange florestas Atlânticas *s.s.* e florestas com Araucária. Os resultados evidenciaram que a temperatura e a qualidade da serapilheira foram preditoras das taxas de decomposição, enquanto o habitat de origem não afetou a perda de massa da serapilheira. Observamos efeitos não-aditivos nas misturas de serapilheira, porém não conseguimos confirmar uma relação entre a diversidade e as taxas de decomposição. Nossos resultados sugerem que a temperatura e as características funcionais das folhas, que determinam a qualidade da serapilheira, afetam as dinâmicas de carbono e nutrientes por meio da decomposição. Com mudanças associadas ao aquecimento global, poderemos observar aumento nas taxas de decomposição, tanto pelo efeito direto da temperatura, quanto indireto via mudanças nos padrões de composição e abundância de espécies, que podem resultar em maiores emissões de carbono da serapilheira para a atmosfera.

Palavras-chave: Gradientes climáticos; fatores condicionantes da decomposição; processos ecossistêmicos; aquecimento global; Mata Atlântica.

Abstract

Litter decomposition is a global biogeochemical process highly important in the cycle of carbon and in the recycling of nutrients to the communities of soil and plants. Decomposition rate shifts can have significant impacts on ecosystems and therefore, it is crucial to understand the factors controlling this process in all biomes. Few studies integrate different conditioning factors of decomposition in climate gradients in tropical and subtropical forests, although this is essential for predicting functional responses associated with carbon and nutrients in the face of climate change. In this study we aim to investigate the effect of climate variation, litter quality, habitat of origin and diversity of litter mixtures on decomposition rates of native species in the subtropical Atlantic Forest, southern Brazil. We conducted a litterbag experiment to study leaf litter mass decay of four native tree species incubated in monocultures and litter mixtures differing in quality, plant origin and diversity over a period of four months. Our sampling sites were distributed across a 633 m altitudinal gradient (370 to 1003 m a.s.l.), ranging from Atlantic forests *stricto sensu* (*s.s.*) to Araucaria forests. Our results confirmed that temperature and litter quality predicted litter mass loss whilst habitat of origin did not affect litter decomposition. We observed non-additive litter mixture effects but couldn't confirm a relationship between diversity and decomposition rates. Our results suggest that temperature and leaf functional traits, which determine litter quality, affect carbon and nutrient dynamics through decomposition. Changes related to global warming will potentially increase decomposition rates, directly as an effect of temperature, and indirectly via changes in species composition and abundance patterns, which may result in higher carbon release from leaf litter to the atmosphere.

Key words: Climate gradients; decomposition drivers; ecosystem processes; climate change; Atlantic Forest.

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Introdução geral

A decomposição de serapilheira é o processo pelo qual o material foliar é quebrado em partículas menores para liberar formas solúveis de nutrientes para absorção pelas plantas e fornecimento de matéria orgânica ao solo (Swift et al. 1979; Waring & Schlesinger 1985). A decomposição constitui um processo ecossistêmico chave onde o carbono fixado durante a fotossíntese é devolvido à atmosfera (Singh & Gupta 1977), tendo assim efeito importante nos fluxos de energia, nos ciclos biogeoquímicos globais e no fornecimento de serviços ecossistêmicos, como a manutenção da produtividade primária através da mineralização de nutrientes e a formação dos solos (Aerts 1997; Díaz, Hector & Wardle 2009; Swift et al. 1979; Zhou et al. 2015). Estima-se que a decomposição total da serapilheira contribua com mais de 70% do fluxo anual total de carbono, que é previsto em 87.9 Pg C/ano ($\text{Pg} = 10^{15} \text{ g}$) (Raich & Schlesinger 1992; Warner et al. 2019). Em virtude disso, a variação espacial e temporal das taxas de decomposição pode ter consequências significativas para o funcionamento dos ecossistemas e para o orçamento global de carbono (Aerts 2006; Esquivel et al. 2019; Salinas et al. 2011). Tais variações estão em geral associadas às condições de temperatura e precipitação, que por sua vez são afetadas por ações antrópicas através do aumento na emissão de CO_2 atmosférico (Esquivel et al. 2019). Logo, torna-se fundamental a melhor compreensão dos mecanismos condutores da decomposição de serapilheira para modelar e prever as respostas dos fluxos de nutrientes e carbono às mudanças climáticas futuras.

Os principais fatores que controlam o processo de decomposição da serapilheira são as condições climáticas, a qualidade do substrato e a atividade da fauna decompositora do solo (Aerts 1997; Cadish & Giller 1997; Wieder et al. 2009; Zhou et al. 2015). Existem outras variáveis que também influenciam esse processo, ainda pouco exploradas, e que atuam individualmente ou interagindo umas com as outras (de la Riva et al. 2019; Freschet et al. 2012). Entre essas variáveis destacam-se a origem do material foliar associado ao local de decomposição (denominada *home-field advantage hypothesis*) e a diversidade da serapilheira em misturas de material foliar (Freschet et al. 2012; Zhou et al. 2020). O tamanho do efeito dessas variáveis muda conforme a escala. O clima e a qualidade da serapilheira são mais relevantes em escalas amplas (Cornelissen 1996; Wall et al. 2008), enquanto fatores edáficos, a comunidade de decompositores, a origem do material que compõe a serapilheira e a interação entre as diferentes espécies da serapilheira influenciam mais em escalas mais restritas (Freschet et al. 2012; de la Riva et al. 2019).

Variações no **clima**, principalmente quanto à temperatura e à precipitação, exercem controle na decomposição da serapilheira através da alteração das taxas metabólicas dos organismos decompositores (Aerts 1997; Zhang et al. 2008; Zhou et al. 2020). Igualmente, mudanças de temperatura como o aquecimento global levam a um possível aumento nas taxas de decomposição e uma maior concentração de CO₂ na atmosfera, podendo interferir na ciclagem de nutrientes e fazendo com que o tempo de armazenamento de carbono no solo diminua (Aerts 2006; Esquivel et al. 2019). As consequências dessa modificação podem gerar um feedback positivo para a elevação das temperaturas globais já atuante no cenário mundial atual (Zhou et al. 2015), caso não ocorra um aumento de mesma magnitude na produtividade primária. Essa magnitude, considerando o balanço líquido das florestas tropicais em drenar carbono, parece estar diminuindo, pois apesar do maior crescimento, há maior mortalidade de árvores grandes (Brienen et al. 2015). A **qualidade da serapilheira** é também um fator importante determinando as taxas de decomposição. Ela é definida pelos atributos químicos e morfológicos das folhas verdes, que são comumente utilizados para categorizar as espécies como sendo mais aquisitivas ou mais conservativas (Aerts 2006; de la Riva et al. 2019), pois são indicadores do desempenho das plantas em termos de crescimento (Poorter & Bongers 2006). As características *químicas* foliares comumente utilizadas como preditoras das taxas de decomposição consistem no conteúdo de carbono, nitrogênio e fósforo foliar (Szefer et al. 2017); sendo que altas concentrações de nutrientes estão positivamente correlacionadas com taxas de decomposição, ou seja, quanto maior a concentração de nutrientes nas folhas, mais rápido a decomposição das mesmas (Wright et al. 2004). Entre as características *físicas*, destacam-se o conteúdo de matéria seca das folhas (LDMC), que reflete a proporção de mesófilo quanto aos compostos foliares estruturais e correlaciona-se negativamente com a taxa de decomposição (Szefer et al. 2017), e a área foliar específica (SLA), que representa a área de interceptação de luz por massa seca da folha e está positivamente correlacionada com a decomposição (Vaieretti et al. 2005; Szefer et al. 2017). Em estudos experimentais, a identidade das espécies da serapilheira quanto à sua **origem** também é uma variável que interfere nas taxas de decomposição. Trata-se da hipótese da vantagem doméstica (*home-field advantage hypothesis*, HFA, Gholz et al. 2000), que diz que substratos de serapilheira se decompõem a taxas maiores do que o esperado quando incubados em seu ambiente de origem (Freschet et al. 2012; Yuan et al. 2019). Este contexto é observado pois as comunidades locais de decompositores podem ser melhor adaptadas às espécies de plantas que encontram com mais frequência (Yuan et al. 2019). Ainda, as interações bióticas e abióticas que ocorrem em misturas de espécies na serapilheira originam maior **diversidade** e podem também alterar o

processo de decomposição, resultando em aceleração ou desaceleração na perda de massa da serapilheira (Gessner et al. 2010; Zhou et al. 2020). Os efeitos da mistura da serapilheira na decomposição são associados a: interações químicas entre as espécies componentes; por mudanças no microambiente onde o material está sendo decomposto; ou por alterações na comunidade de decompositores e detritívoros (Butenschoen et al. 2014; Chen et al. 2013; Hattenschwiler et al. 2005; Gartner e Cardon 2004). Não há generalizações sobre a relação entre diversidade e decomposição da serapilheira (Grossman et al. 2020), mas há evidências que a taxa de decomposição observada em misturas não corresponde à média aritmética das taxas individuais de cada espécie componente (Harguindeguy et al. 2007; Oliveira et al. 2018; Smith & Bradford 2003), o que indica a presença de efeitos não-aditivos nessas combinações (Liu et al. 2007).

Para regiões de florestas tropicais e subtropicais, onde a absorção de nutrientes se dá predominantemente através da decomposição e mineralização da matéria orgânica vegetal (Hattenschwiler et al. 2011; Oliveira et al. 2018; Salinas et al. 2011), estudos sobre a decomposição de serapilheira são particularmente importantes. No entanto, estimativas empíricas que investigam a decomposição da serapilheira em florestas tropicais e subtropicais são pouco representadas na literatura. Assim, a região Sul do Brasil se configura como área potencial para tais estudos. Ademais, experimentos de translocação de serapilheira, utilizando múltiplas espécies em condições naturais de campo, são ferramentas eficazes para a compreensão dos fatores que afetam as taxas de decomposição (e.g., de la Riva et al. 2019; Esquivel et al. 2019; Grossman et al. 2020; Zhou et al. 2015; Zhou et al. 2020). Esses experimentos, quando dispostos ao longo de gradientes climáticos, são considerados chave para prever respostas funcionais associadas ao ciclo do carbono e de nutrientes frente às mudanças climáticas e de biodiversidade a que essas florestas estão sujeitas (Butenschoen et al. 2014; Esquivel et al. 2019; Oliveira et al. 2018).

Este trabalho visa avaliar o efeito da variação climática, associado à qualidade, origem e diversidade de folhas da serapilheira, sobre a taxa de decomposição de espécies nativas do sul da Mata Atlântica. Utilizando o mesmo conjunto de espécies ao longo de um gradiente altitudinal (370 a 1003 m a.s.l.) que abrange florestas Atlânticas *stricto sensu* (*s.s.*) e florestas com Araucária no sul da Mata Atlântica, investigamos a importância da variação climática; qualidade (em termos de atributos foliares: espécies aquisitivas *vs.* conservativas); origem da espécie (espécies em seu habitat de origem *vs.* fora dele); e diversidade da serapilheira (em termos de riqueza e combinações de espécies em misturas de serapilheira) como impulsores da taxa de decomposição nos locais de estudo. Hipotetizamos que (1) a

temperatura e a umidade terão efeito positivo sobre as taxas de decomposição, considerando todas as espécies e misturas; (2) espécies com características foliares mais aquisitivas terão taxas de decomposição maiores do que as conservativas; (3) o habitat de origem das espécies influenciará positivamente as taxas de decomposição, pois a fauna associada estará mais apta a decompor o material; e (4) a diversidade de espécies nas misturas terá um efeito positivo dado o efeito sinérgico (efeito não-aditivo positivo) relatado em diversos outros trabalhos. Entender as diferentes variáveis atuando na decomposição de serapilheira permite a conservação dos importantes serviços ecossistêmicos providos por este processo e a manutenção de comunidades vegetais através da ciclagem de nutrientes para reposição contínua destes no solo (Swift et al. 1979; Swift et al. 2004).

Referências bibliográficas

Aerts R. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos* 79, 439–449 (1997).

Aerts, R. The freezer defrosting: global warming and litter decomposition rates in cold biomes. *Journal of Ecology* 94(4), 713–724 (2006).

Brienen, R., Phillips, O., Feldpausch, T. et al. Long-term decline of the Amazon carbon sink. *Nature* 519, 344–348 (2015).

Butenschoen, O., Krashevskaya, V., Maraun, M., Marian, F., Sandmann, D., & Scheu, S. Litter mixture effects on decomposition in tropical montane rainforests vary strongly with time and turn negative at later stages of decay. *Soil Biology and Biochemistry* 77, 121–128 (2014).

Cadish, G. & Giller, K.E. *Driven by Nature: Plant Litter Quality and Decomposition*. CAB International, Wallingford XVI, 409p (1997).

Cornelissen, J.H.C. An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. *Journal of Ecology* 84, 573–582 (1996).

de la Riva, E.G., Prieto, I. & Villar, R. The leaf economic spectrum drives leaf litter decomposition in Mediterranean forests. *Plant Soil* 435, 353–366 (2019).

Díaz, S., Hector, A., & Wardle, D.A. Biodiversity in forest carbon sequestration initiatives: Not just a side benefit. *Current Opinion in Environmental Sustainability* 1, 55–60 (2009).

Esquivel, J. , Park, B.B., Casanoves, F., Delgado, D., Park, G.E., & Finegan, B. Altitude and species identity drive leaf litter decomposition rates of ten species on a 2950 m altitudinal gradient in Neotropical rain forests. *Biotropica* 52, 11-21 (2019).

Freschet, G.T., Aerts, R., & Cornelissen, J.H.C. Multiple mechanisms for trait effects on litter decomposition: moving beyond home-field advantage with a new hypothesis. *Journal of Ecology* 100(3), 619–630 (2012).

Gessner, M.O., Swan, C.M., Dang, C.K., McKie, B.G., Bardgett, R.D., Wall, D.H., & Hättenschwiler, S. Diversity meets decomposition. *Trends in Ecology & Evolution* 25(6), 372–380 (2010).

Gholz, H.L., Wedin, D.A., Smitherman, S.M., Harmon, M.E. & Parton, W.J. Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. *Global Change Biology* 6, 751–765 (2000).

Oliveira, R.A.C., Marques, R., & Marques, M.C.M. Plant diversity and local environmental conditions indirectly affect litter decomposition in a tropical forest. *Applied Soil Ecology* 134, 45–53 (2018).

Poorter, L. & Bongers, F. Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology* 87, 1733–1743 (2006).

Raich, J.W. & W.H. Schlesinger. The global carbon dioxide flux in soil respiration and its relationship to climate. *Tellus* 44B, 81–99 (1992).

Salinas, N., Malhi, Y., Meir, P., Silman, M., Roman Cuesta, R., Huaman, J., Salinas, D., Huaman, V., Gibaja, A., Mamani, M. & Farfan, F. The sensitivity of tropical leaf litter decomposition to temperature: results from a large-scale leaf translocation experiment along an elevation gradient in Peruvian forests. *New Phytologist* 189, 967–77 (2011).

Singh, J.S. & Gupta, S.R. Plant decomposition and soil respiration in terrestrial ecosystems. *The Botanical Review* 4, 449–528 (1977).

Swift, M. J., Heal, O. W., & Anderson, J. M. *Decomposition in Terrestrial Ecosystems* (Vol. 5). Univ of California Press (1979).

Swift, M.J., Izac, A.M., & Van Noordwijk, M. Biodiversity and ecosystem services in agricultural landscapes—are we asking the right questions? *Agriculture, Ecosystems & Environment* 104(1), 113-134 (2004).

Szefer, P., Carmona, C. P., Chmel, K., Konečná, M., Libra, M., Molem, K., *et al.* Determinants of litter decomposition rates in a tropical forest: functional traits, phylogeny and ecological succession. *Oikos* 126(8), 1101–1111 (2017).

Vaieretti, M. V., Harguindeguy, N. P., Gurvich, D. E., Cingolani, A. M., & Cabido, M.. Decomposition Dynamics and Physico-chemical Leaf Quality of Abundant Species in a Montane Woodland in Central Argentina. *Plant and Soil* 278(1-2), 223–234 (2005).

Wall, D.H., Bradford, M.A., St. John, M.G., Trofymow, J.A., Behan-Pelletier, V., Bignell, D.E., *et al.* Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. *Global Change Biology* 14, 2661–2677 (2008).

Waring, R.H., Schlesinger, W.H. *Forest ecosystems concepts and management*. New York: Academic Press. 340p (1985).

Warner, D.L., Bond-Lamberty, B., Jian, J., Stell, E., Vargas, R. Spatial predictions and associated uncertainty of annual soil respiration at the global scale. *Global Biogeochem Cy* 33, 1733–1745 (2019).

Wieder, W.R., Cleveland, C.C., & Townsend, A.R. Controls over leaf litter decomposition in wet tropical forests. *Ecology* 90(12), 3333–3341 (2009).

Wright, I.J., P.B., Reich, M., Westoby, D.D., Ackerly, Z., Baruch, F., Bongers, J., Cavender-Bares, T., Chapin, J.H.C., Cornelissen, M., *et al.* The worldwide leaf economics spectrum. *Nature* 498, 821-827 (2004).

Yuan, X., Niu, D., Wang, Y., Boydston, A., Guo, D., Li, X., Wen, H., Qin, Y., Fu, H. Litter decomposition in fenced and grazed grasslands: A test of the home-field advantage hypothesis. *Geoderma* 354, 113876 (2019).

Zhou, Y., Clark, M., Su, J., Xiao, C. Litter decomposition and soil microbial community composition in three Korean pine (*Pinus koraiensis*) forests along an altitudinal gradient. *Plant Soil* 386, 171–183 (2015).

Zhou, S., Butenschoen, O., Barantal, S., Handa, I. T., Makkonen, M., Vos, V., Aerts, R., Berg, M.P., McKie, B., Ruijven, J.V., Hättenschwiler, S., & Scheu, S. Decomposition of leaf litter mixtures across biomes: The role of litter identity, diversity and soil fauna. *Journal of Ecology* 00, 1-15 (2020).

CAPÍTULO 1

**Temperature and litter quality affect decomposition rates along a
temperature gradient in subtropical Atlantic Forests**

Introduction

Decomposition of leaf litter represents an important pathway for nutrient transfer from plants to soils, consisting of an important way to assess forest productivity (Ruess & Ferris 2002). Soils are the main organic carbon storage, surpassing vegetation carbon pools and the atmosphere together (Scharlemann et al., 2014). Decomposition of organic matter through heterotrophic respiration constitutes the majority of soil respiration, the latter being one of the main fluxes of carbon dioxide (CO₂) from soils to the atmosphere in the global carbon cycle (Bond-Lamberty and Thomson, 2010; Edwards et al. 1970; Hanson et al., 2000). Since soil respiration is proven to be responsive to environmental factors such as temperature (Raich and Schlesinger, 1992), it is important to assess how the decomposition process might be affected by global warming, considering its increase can result in higher atmospheric CO₂ release (Brienen et al. 2015; Kirschbaum et al. 1995).

The decomposition process is controlled by climate, substrate quality, decomposers activity (Aerts 1997; Cadish & Giller 1997; Wieder et al. 2009; Zhou et al. 2015), the origin of litter combined with the decomposition place (the *home-field advantage hypothesis*), and species diversity of leaf litter mixtures (Freschet et al. 2012; Zhou et al. 2020). These factors can act individually or interacting with one another but remain little explored in the literature in certain parts of the world (de la Riva et al. 2019; Freschet et al. 2012). Moreover, they affect the process in multiple scales, climate and substrate quality are more relevant at global scales (Cornelissen 1996; Wall et al. 2008) whilst edaphic factors, decomposers community, plant litter origin and leaf litter species composition interactions have a stronger influence at local scales (Freschet et al. 2012; de la Riva et al. 2019). Understanding the mechanisms behind the litter decomposition process is crucial to improve our capacity to estimate and predict the reactions of nutrient and carbon flows to future climatic changes.

Temperature and moisture are two of the most important environmental factors controlling the decomposition of organic matter (Davidson & Janssens 2006). Many studies have shown that warming temperatures result in higher decomposition rates (k) because they enhance metabolic responses from decomposer organisms (e.g. Cornelissen et al. 2007b; Zhang et al. 2008). Regarding moisture fluctuations, dry conditions generate water stress which can decrease decomposers' activities and reduce k (Manzoni et al. 2012). The effect of decomposer organisms on k may also vary with litter quality, which is determined by chemical and morphological leaf traits (Aerts 2006; de la Riva et al. 2019). According to the Leaf Economic

Spectrum (LES), the leaf traits determine plant resource use strategies and classify plants as being more acquisitive or more conservative (Wright et al. 2004). Conservative plants represent slow-growing species whilst acquisitive ones are usually fast-growing (Wright et al. 2004). Acquisitive life-strategies (i.e., higher concentration of nutrients such as nitrogen and higher SLA) are positively correlated with decomposition rates; on the contrary, conservative traits (leaves with higher concentration of lignin – a carbon compound and higher LDMC) are negatively correlated to decomposition (Reich et al. 1997; Reich 2014; Wright et al. 2004). Thus carbon and nitrogen leaf content, for example, are chemical features linking plant life strategy to litter decomposability (Kurokawa et al. 2008; Makkonen et al., 2012; Santiago 2007). Besides these chemical features, morphological traits such as LDMC (leaf dry matter content) – the ratio of leaf dry mass to saturated fresh mass, and SLA (specific leaf area) – light-capturing area deployed per dry mass allocated, also characterize the leaf economic spectrum and are often used to predict decomposition rates (Garnier et al. 2001*b*; Shipley & Vu 2002).

Litter identity in terms of its environment of origin can also affect decomposition due to the home-field advantage hypothesis (*HFA*, Gholz et al. 2000), that says that locally grown litter species will decompose faster than foreign species (Vivanco & Austin 2008; Yuan et al. 2019). This could be explained by the decomposer communities' specialization to the plant litter species they find the most – which are at their origin site (Gholz et al. 2000). That adeptness can be a consequence of decomposer organisms having specific structures such as enzymes that could only break down the litter substrate from their original habitat (Ayres et al. 2009). The above-mentioned context can be observed specially for the dominant species from ecosystems, which greatly contribute with leaf litter, because they shape the distribution of decomposer and detritivores communities in forests (Purahong et al. 2019).

Lastly, biotic and abiotic interactions that occur in litter mixtures are related to species richness and diversity and can also alter their decomposition rates (Gessner et al. 2010). Several studies have shown synergistic (e.g., enhanced rates of decay) or antagonistic (e.g., slowed rates of decay) non-additive effects on decomposition rates when leaf litter is mixed, frequently resulting in different rates from the monocultures of their component species (Gartner e Cardon 2004; Zhou et al. 2020). Such non-additive mixing effects have been attributed to a variety of explanations: nutrient transfer through leaching between litter species with distinct physical or chemical compositions, shifts in the interactions across trophic levels (e.g., microbial and detritivores communities), and alterations in microclimatic conditions (Chapman et al. 2013; Hattenschwiler et al. 2005; Makkonen et al., 2013).

Forests distributed across altitudinal gradients differ in environmental conditions, mainly temperature and humidity, and therefore may constitute relevant study regions to understand how these conditions affect ecosystem processes such as decomposition (Körner 2002; Salinas et al. 2011). Moreover, reciprocal transplant experiments – which involve introducing organisms from their environment of origin back to it instead of the laboratory – along elevation gradients allow us to separate site-specific effects (e.g., environmental variables) from litter substrate effects (e.g., species traits and composition) on decomposition (Cornwell et al. 2008; Makkonen et al. 2012; van de Weg et al. 2009). The study presented here investigates the effects of these factors (temperature and humidity, leaf quality, species origin and identity, and plant diversity) on litter decomposition in one of the most threatened biodiversity hotspots, remnants of South American Atlantic Forest (de Lima et al. 2020; Galindo-Leal & Câmara 2003). To our knowledge, no study has been done in subtropical forests across a temperature gradient in Brazil using litter reciprocal transplant. In a field-litterbag experiment we studied leaf litter mass decay of four native tree species incubated in monocultures and litter mixtures differing in quality, plant origin and diversity over a period of four months. Our sampling sites were distributed across a 633 m altitudinal gradient (370 to 1003 m a.s.l.), demonstrating how decomposition is influenced by a range of temperature and moisture and allowing a better understanding of how this process might be influenced by future climate change. We tested the hypothesis that (1) temperature and moisture will be positively related to decomposition rates; (2) species with acquisitive leaf traits will have higher decomposition rates than conservative ones; (3) the species original habitat will influence litter mass decay positively; and (4) litter species diversity will have a synergistic effect on decomposition.

Methods

Study sites

The study was carried out in mostly old-growth subtropical forests in the south region of the Atlantic Forest biome across an elevation gradient from sites in the Atlantic Forest *s.s.* (at 370 m a.s.l.) to sites in the Araucaria Forest (at 1003 m a.s.l.) in Brazil. Only one site is a mature secondary forest with at least 55 years old of natural regeneration (site Maquiné 2, Figure 1). The Araucaria Forest is a mixed moist forest due to the presence (and sometimes dominance) of the coniferous *Araucaria angustifolia* (Bertol) Kuntze, whereas the Atlantic

Forest *s.s.* is a moist forest characterized by tropical elements, most of them are species having their southernmost limit of distribution around the study region (Oliveira-Filho et al. 2013; Oliveira-Filho et al. 2015). Study sites correspond to permanent plots of the *Long-term Ecological Research in Subtropical Atlantic Forests* (LERSAF), which are maintained by our lab. More specifically, the present study was conducted in three plots at the Maquiné municipality, two in the Encantada Valley (M1 and M2) and one in the Forqueta Valley (M3), pertaining to the Atlantic Forest *s.s.*; three plots at a National Park called PARNA (“Parque Nacional de Aparados da Serra”; P1, P2, and P3), two plots at the Ecological Station of Aratinga (“Estação Ecológica Estadual de Aratinga”; Ar1, Ar3) and four plots at the Research Centre of Pró-Mata (“Centro de Pesquisas e Conservação da Natureza Pró-Mata”; PM1, PM2, PM3, PM4) (Table 1; Figure 1). These nine plots are included in the Araucaria Forest region, but the last one (PM4) is already located in a transition zone with the montane Atlantic Forest *s.s.*, and the conspicuous *A. angustifolia* is not present anymore.

Subtropical Atlantic Forests are characterized by highly heterogeneous environments (Oliveira-Filho et al. 2013), providing a wide range of contrasting climatic regimes within relatively small areas (Gonçalves & Souza 2013; Bergamin et al., 2012). In the study area, mean annual temperature ranges from 14.9 to 17.3° C and mean annual rainfall from 1700 to 2004 mm (Global Climate Data; Hijmans et al. 2011). We installed a 120-day-long litter decomposition transplant experiment in 12 subtropical old-growth/mature forest plots (three in Atlantic Forest *s.s.* and nine in Araucaria Forest) and collected temperature and humidity measurements using data loggers along the period.

Table 1. Study sites characteristics: latitude, longitude, altitude, mean temperature and mean moisture values. Study forest plots are denominated Aratinga (“Ar.”), Maquiné (“M.”), Pró-mata (“P.M.”), and PARNA (“P.”).

Sites	Lat.	Long.	Alt.	Mean temp.	Mean moist.
Ar. 1	-29.4433	-50.2367	934 m	15.52	96.26
Ar. 3	-29.3688	-50.2577	915 m	15.50	94.79
M. 1	-29.6171	-50.181	365 m	17.15	98.54
M. 2	-29.6117	-50.1883	310 m	17.57	96.96
M. 3	-29.5414	-50.1919	367 m	15.57	95.66
P.M. 1	-29.4855	-50.2116	928 m	15.57	95.66

P.M. 2	-29.4897	-50.1944	912 m	16.10	93.93
P.M. 3	-29.4833	-50.2227	924 m	16.48	93.28
P.M. 4	-29.47088496	-50.16488196	916 m	16.05	94.29
P. 1	-29.1758	-50.0994	950 m	15.39	98.57
P. 2	-29.1694	-50.1172	951 m	15.32	96.13
P. 3	-29.1577	-50.0919	1006 m	15.35	97.35

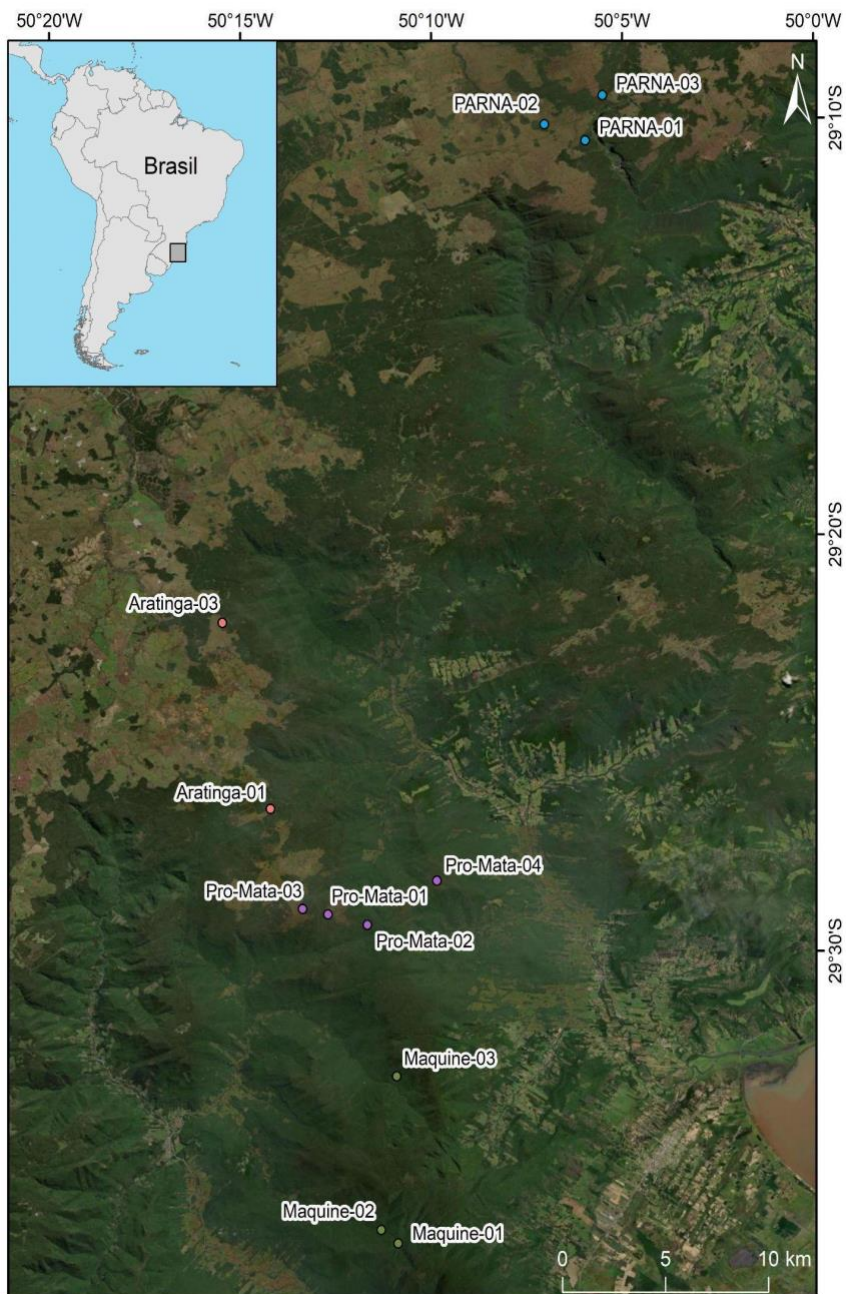


Figure 1. Map pointing study site localities at subtropical Atlantic Forest remnants in Southern Brazil where the decomposition experiment took place. Study forest plots are denominated Maquiné (three), located at the Atlantic Forest *s.s.*; Pró-mata (four), Aratinga (two) and PARNA (three), located at the Araucaria Forest. (Source: Adapted from *Google Earth Pro*)

Experimental design

Species used in the experiment were selected based on contrasting plant functional type composition (two having more acquisitive leaf traits and two with more conservative leaf traits) and species frequency in each forest type (two common species in the Atlantic Forest *s.s.* and two in the Araucaria Forest). The selected species were: *Cupania vernalis* (conservative) and *Mollinedia schottiana* (acquisitive), which are common species in the Atlantic Forest *s.s.*, *Campomanesia rhombea* (acquisitive) and *Myrcia retorta* (conservative), which are common species in the Araucaria Forest (Sobral et al. 2006). *Cupania vernalis* and *Campomanesia rhombea*, however, are broadly distributed and individuals may occur in both forest types. Information about the leaf traits of studied plant species were obtained from previous data collections from our lab in the study areas, following the methodology of Perez-Harguindeguy et al. (2013). Thus, to characterize the studied species, traits information are listed in Table 2, showing main differences between pre-defined groups (acquisitive, conservative), but also a gradual change in specific leaf area (SLA) and dry matter content (LDMC) from more acquisitive to more conservative (*M. schottiana* – *C. rhombea* – *C. vernalis* – *M. retorta*). The collections were based on at least five individuals per species and 10 leaves per plant (Perez-Harguindeguy et al. 2013), the table contains mean values of each trait.

Table 2. Single litter species used in the decomposition experiment – *Campomanesia rhombea*, *Cupania vernalis*, *Mollinedia schottiana* and *Myrcia retorta* – characteristics: SLA (cm²/g), LDMC (mg/g), N content (%), C content (%), P content (%) and functional type (acquisitive or conservative).

Species	Origin	SLA (cm ² /g)	LDMC (mg/g)	N content (%)	C content (%)	P content (%)	Functional type
<i>Campomanesia rhombea</i>	Araucaria	172.89	378.26	2.11	46.05	0.80	acquisitive
<i>Cupania vernalis</i>	Atlantic	110.80	418.10	2.09	47.68	1.26	conservative

<i>Mollinedia schottiana</i>	Atlantic	236.38	283.65	2.51	44.39	1.00	acquisitive
<i>Myrcia retorta</i>	Araucaria	48.66	476.48	1.19	46.07	0.61	conservative

Using the litter bag method, leaf decomposition was assessed. To fill the bags for the decomposition experiment, mature leaves of each species were collected from the tree branches in the sites where the study took place, because it was unfeasible to have the necessary amount by only collecting leaves that have naturally fallen. Many of the morphological and chemical characteristics of green leaves persist after abscission (Bakker et al. 2011; Santiago 2007). The leaves were taken to the laboratory, dried at ambient temperature (approximately 25° C) for two days and then at elevated temperature (50° C) for two days, to make sure about the dry weight each litter bag received (i.e., to have a standardizing initial weight). After drying, leaves were weighted, divided in the different treatments indicated in Table 3 and put into each 20 x 20 cm mesh nylon cloth litter bag (with 2 mm netting), each containing 6 g of dry mass. Treatments containing two species had 3 g each species, treatments with three species had 2 g each and the treatment with four species had 1.5 g each.

The combination of all factors (quality/functional, origin, diversity) resulted in 11 treatments: “Mix”, containing all species, considered in the analysis to respond the first hypothesis on temperature, and the fourth hypothesis on diversity; “Functional 1”, containing the acquisitive species and “Functional 2”, containing the conservative species, to evaluate the litter quality hypothesis; “Origin 1”, containing Atlantic Forest species, and “Origin 2”, containing Araucaria Forest species, to test the litter species origin hypothesis; “Diversity 1”, with three species, two from Araucaria Forest and one from Atlantic Forest, and “Diversity 2”, also with three species, one from Araucaria Forest and two from Atlantic Forest, considered in the analysis to test the diversity hypothesis (together with the monospecific treatments – one species, the functional treatments – two species, and the mix treatment – four species); and finally four “Monospecific” treatments, each containing one isolated species, used to evaluate the second and fourth hypotheses (Table 3).

Table 3. Detailed composition of litter treatments as: the origin of the leaves (from the Atlantic Forest *s.s.* – At or from the Araucaria Forest – Ar), the litter quality – determined by functional leaf traits (acquisitive – aq or conservative – co) and species diversity (different mixture types). We also indicated the hypotheses of the study contemplated in each treatment.

Treatments	Description	Treatment / litter bags composition	Hypotheses
1	Mix (4 spp)	mixture with all the four species	1, 4
2	Functional 1 (2 spp)	2 acquisitive species: 1 At-aq + 1 Ar-aq	2
3	Functional 2 (2 spp)	2 conservative species: 1 At-co + 1 Ar-co	2
4	Origin 1 (2 spp)	2 Atlantic Forest species: 1 aq + 1 co	3
5	Origin 2 (2 spp)	2 Araucaria Forest species: 1 aq + 1 co	3
6	Diversity 1 (3 spp)	3 species: 1 Ar-co, 1 Ar-aq e 1 At-aq	4
7	Diversity 2 (3 spp)	3 species: 1 At-co, 1 At-aq e 1 Ar-aq	4
8 to 11	Monospecific (1 sp)	each isolated species: sp1, sp2, sp3, sp4	2, 4

The bags were placed on the february 1st of 2022 on decomposition beds (a square on the forest surface, cleaned from vegetation and litter, with one litterbag per treatment side by side but distant ca. 10 cm) of circa 2 x 2 m across the 12 forest plots. Litter bags were covered with the leaf litter previously removed to install the beds, which were randomly placed into each forest site (we are considering an area of 50 x 50 m), to uniformize physical conditions, lessen the impact of the erratic surface environment, and prevent damage from birds and mammals (Cornelissen, 1996). Three litter beds (replicates) were accommodated 10 m distant from one another in each of the 12 forest plots (sampling units). Data loggers were also placed in the plots to measure the air temperature and moisture (for every 30 minutes throughout the experimental period). Hence, in total, 396 litter bags (3 replicates x 11 treatments x 12 plots) were installed in the experiment at the end of January 2022 (starting on the 25th and finishing on the 31st). The experiment happened during the end of summer and the beginning of fall. In the beginning of June 2022, after 116-125 days (hereafter named as ~120 days for simplicity) of exposure to temperature and rainfall conditions of the areas, bags were retrieved in separate envelopes and taken to the laboratory. Remaining litter material was carefully rinsed with water to remove extrinsic material, oven-dried to a constant mass at 50°C and weighted to determine the remaining dry mass.

Statistical analyses

The decomposition rate after the experiment period was set as our response variable, but the arrangement of this variable varied according to each analysis (see below). This rate corresponds to the percentage of litter mass decay (ML, *mass loss*), calculated as $ML(\%) = ((m_0 - m_1)/m_0) \times 100$, with m_0 being the initial dry weight of each litter bag content and m_1 the dry weight after retrieval. First at all, we compared the decomposition rate across all plots considering the monospecific treatments, i.e., the four studied species.

We performed linear models (LM) that included the litter mass loss as the response variable predicted by climatic variables, either by mean temperature or mean humidity (in response to the first hypothesis), considering the mix treatment (i.e., four species together in the bag) along our 12 forest plots. We also carried out linear mixed effects models (LMM) to infer about the effects of litter quality (in response to the second hypothesis) and species richness (in response to the fourth hypothesis), considering plot identity as a random factor (i.e., with three experiment beds in each forest plot). Still on litter quality and knowing each species represent a strategy – acquisitive or conservative, we executed a LMM to test whether the species identity was correlated to the decomposition rates (using the monospecific values) and a Tukey’s test for linear mixed models to compare species in the monospecific analysis.* Concerning species origin (in response to the third hypothesis) we performed a LMM to test if the species being in their environment of origin could predict decomposition rates (i.e. if the species decomposed faster being in their local of origin than outside of it), followed by a Tukey’s test for linear mixed models to test the differences among the four groups (Atlantic species at home and away; Araucaria species at home and away). Regarding diversity analyses we did a t-test to compare expected values in mixtures to our observed values (expected values were the above cited means of the component individual species of each mixture). Additionally, to detect any non-additive effects in the mixtures in the litter mass loss (hypothesis 4), we calculated the relative mixture effect (RME) as $RME(\%) = ((m_{obs} - m_{esp})/m_{esp}) \times 100$ to each mixture, with m_{obs} being the mass loss observed in each of the litter mixtures and m_{esp} the mass loss expected in the same mixture, calculated as the mean of the component individual species of the respective mixture (Wardle et al., 1997). Deviations from zero in the RME values indicate non-additive mixture effects: positive values indicate synergistic effects and negative values indicate antagonistic effects (Butenschoen et al., 2014).

Data analyses were conducted using R packages ‘*lme4*’ (Bates et al. 2015), ‘*vegan*’ (Oksanen et al. 2022), ‘*lmerTest*’ (Kuznetsova et al. 2017), ‘*emmeans*’ (Lenth 2022) and ‘*ggplot2*’ (Wickham 2016); from R version 4.2.1 (R Core Team 2022).

Results

Single litter species mass loss varied from a mean of 33.52% for *Myrcia retorta* (varying from 25.03% to 43.01%), 42.74% for *Cupania vernalis* (30.03 % to 62.13%), 52.52% for *Campomanesia rhombea* (35.36% to 77.86%) to 57.58% for *Mollinedia schottiana* (48.90% to 68.13%), considering ~120 days of experiment. *M. retorta* is the more conservative species, having the smallest SLA value, Nitrogen content and Phosphorus content values, and the highest LDMC. Whilst *M. schottiana* is the more acquisitive one, with the highest SLA and Nitrogen content, and the smallest LDMC and Carbon content (Table 2). Species identity differed significantly according to decomposition values ($p < 0.001$) and posterior Tukey analysis showed that they are all different from one another ($p < 0.001$) (Figure 2).

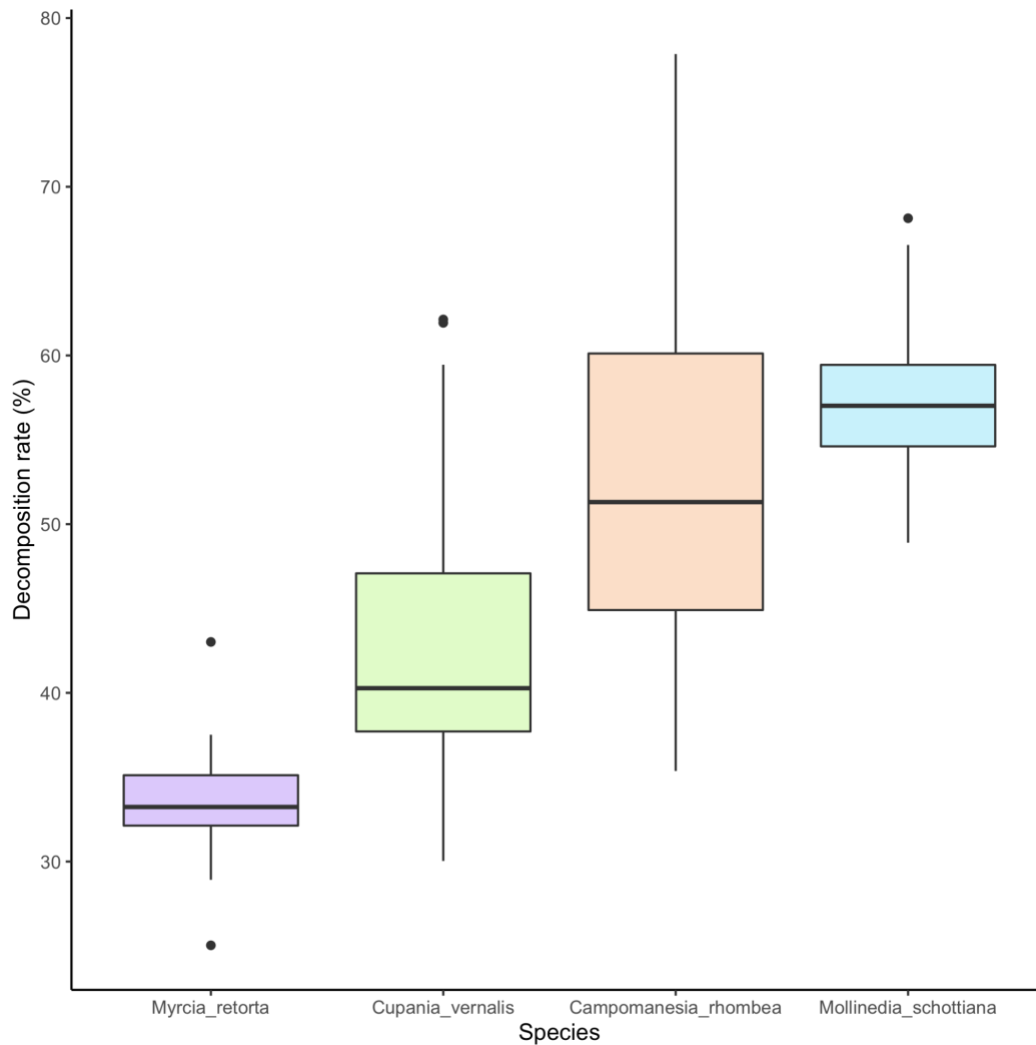


Figure 2. Boxplots of mean values of decomposition rates (%) along 120 days of four native trees from subtropical Atlantic Forests, *Myrcia retorta*, *Cupania vernalis*, *Campomanesia rhombea*, and *Mollinedia schottiana* incubated as single litter species.

Climate

The average temperature from late January to late May 2022 ranged from 15.3° C in one plot of Araucaria Forest (in PARNA) to 17.5° C (Atlantic Forest *s.s.* in Maquiné), and air moisture ranged from 93.2 to 98.57% (both plots in PARNA). Leaf decomposition rates were positively associated with temperature ($r^2 = 0.5645$; $p < 0.005$) (Figure 3), but not with air moisture ($p = 0.719$) and neither with the interaction between air moisture and temperature ($p = 0.3584$). We considered the “Mix” treatment to evaluate those relationships.

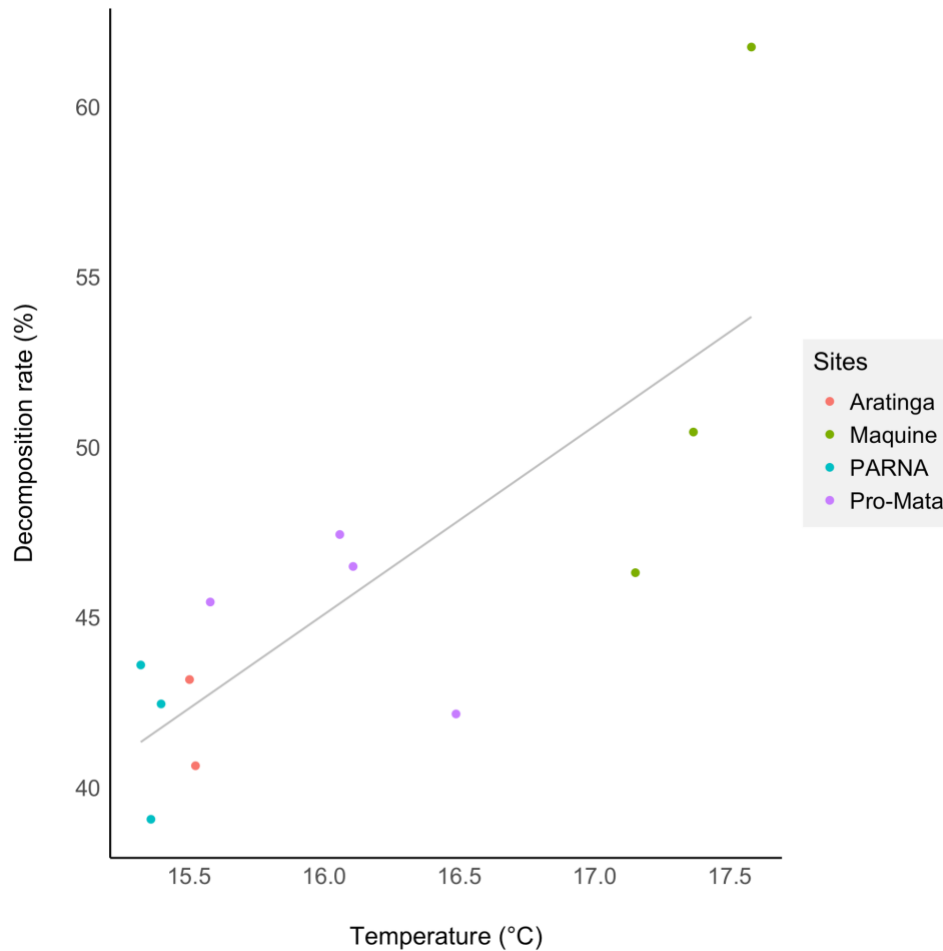


Figure 3. Decomposition rate (%) along 120 days of the “Mix” treatment (containing all the 4 species) predicted by plot temperature (° C) ($r^2= 0.5645$; $p<0.005$), measured during the decomposition experiments with local dataloggers. Each dot represents a study forest plot; colors identify the four main localities (Aratinga, Maquiné, PARNA and Pró-Mata).

Litter quality

Litter quality, here evaluated by contrasting two categories of litter functional type (bags containing either acquisitive or conservative leaf traits of species), predicted decomposition rates significantly ($p<0.0001$). Species with leaves considered more conservative decomposed more slowly (mean = 39.953%) than did the acquisitive ones (mean = 50.852%) (Figure 4).

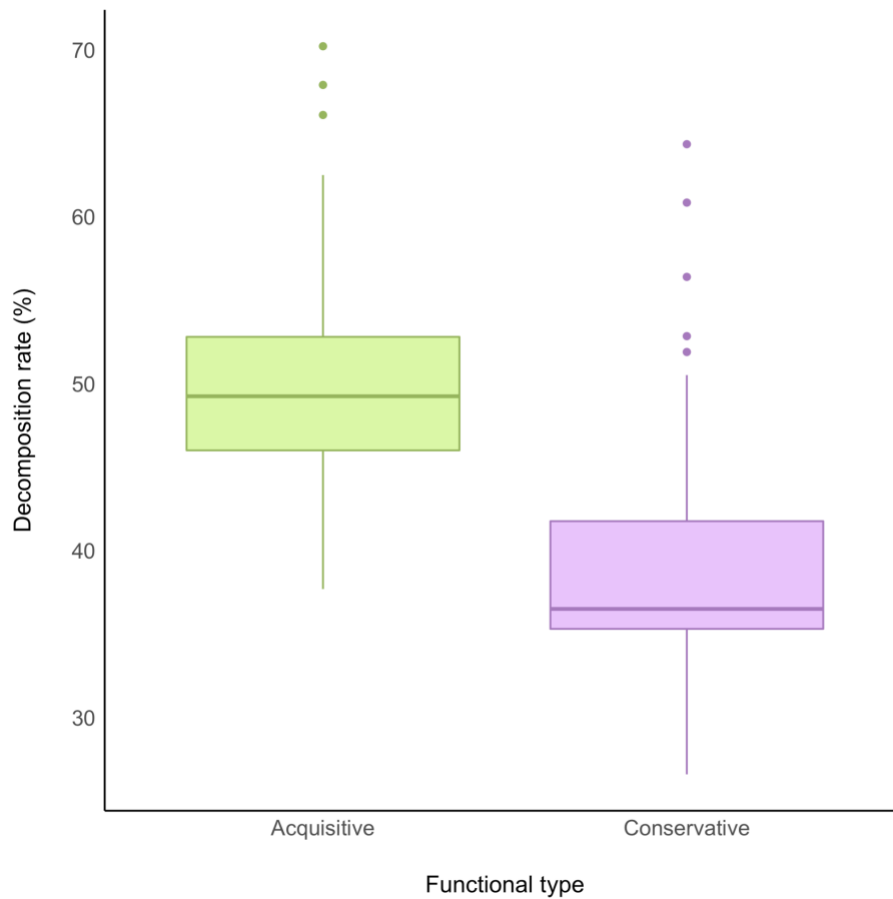


Figure 4. Boxplots of decomposition rates (%) along 120 days predicted by litter quality (acquisitive – for litter bags containing only leaves from the two acquisitive species and conservative – for bags containing only leaves from the two conservative species) ($p < 0.0001$).

Habitat of origin

Of our reciprocal leaf litter transplants with the two species combinations per forest type, we compared the ones in their habitat of origin and the ones put away from it. Contrary to our hypothesis, the Tukey test showed that the only group that significantly differed from the others was the one containing araucaria forest species at their habitat of origin (at “home”) ($p < 0.0001$) (Figure 5), meaning that home field advantage did not apply to our study.

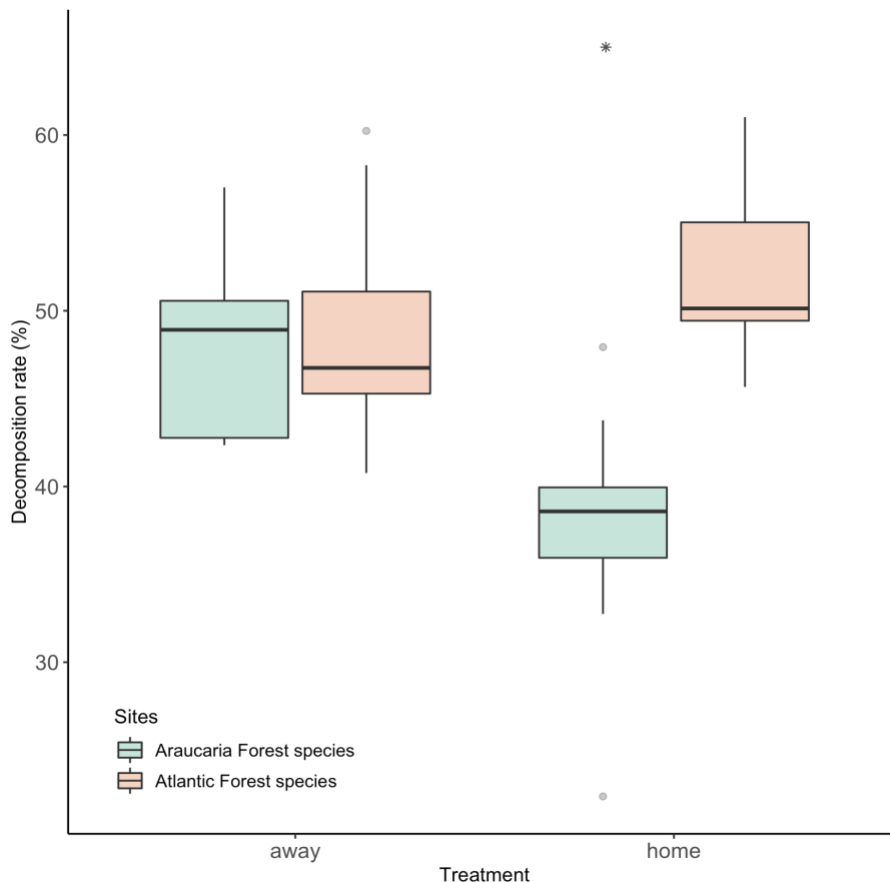


Figure 5. Boxplots of decomposition rates (%) along 120 days according to litter treatments of Atlantic forest species (light orange boxplots) or of Araucaria Forest species (light blue boxplots) at their habitat of origin (home) and away from it (away).

Diversity

The t-test comparing observed and expected litter mass decay (the expected being the arithmetic means of individual litter species included in each combined treatment) showed a significant difference between the observed and expected values in all the mixtures ($p < 0.01$), implying the presence of non-additive effects (Table A.3). Exploring the RME values, which represent these non-additive effects, we observed mostly antagonistic (negative) effects, with only the mixture of the two conservative species being synergistic (positive) (Figure 6). Although we confirmed non-additive effects in the mixtures, no statistical significance was observed for species richness per se on decomposition rates ($p = 0.723$) (Figure 7).

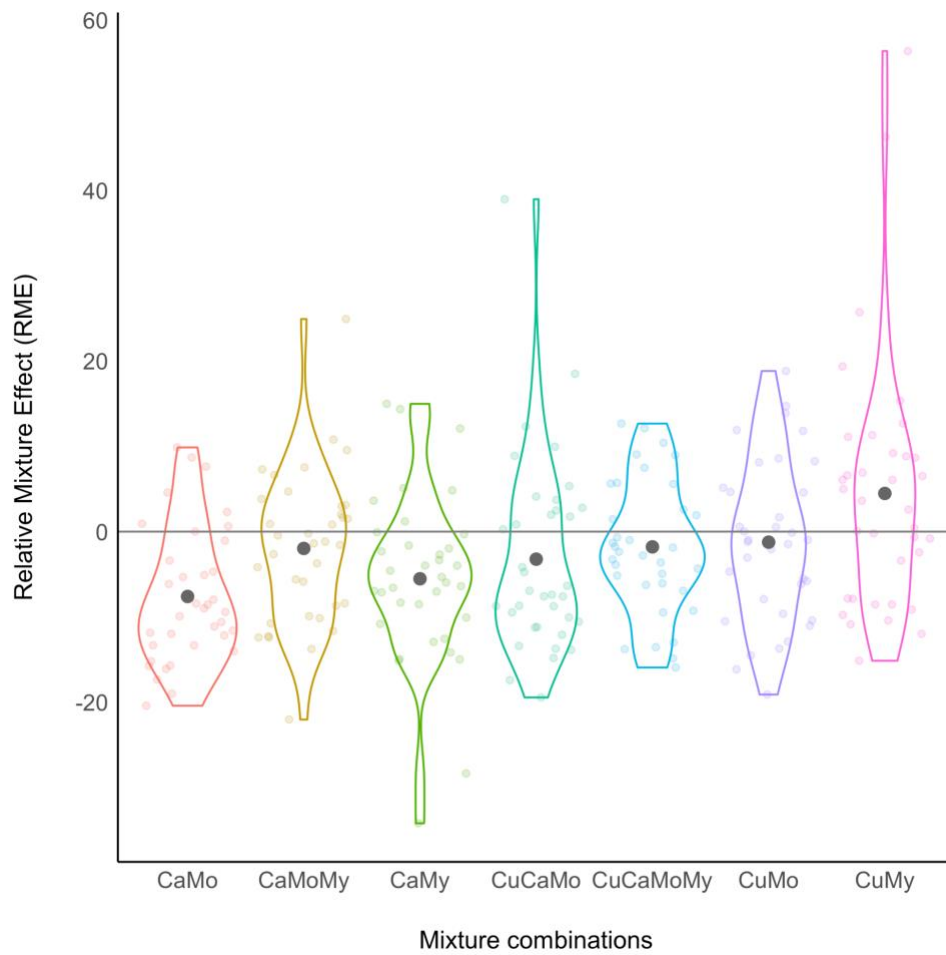


Figure 6. Violin graphs of the Relative Mixture Effect (RME) values of each mixture combination. Ca = *Campomanesia rhombea*; Cu = *Cupania vernalis*, Mo = *Mollinedia schottiana* and My = *Myrcia retorta*. Gray points are showing the mean values. All mixtures differed significantly from their expected values ($p < 0.01$) (see Table A.3).

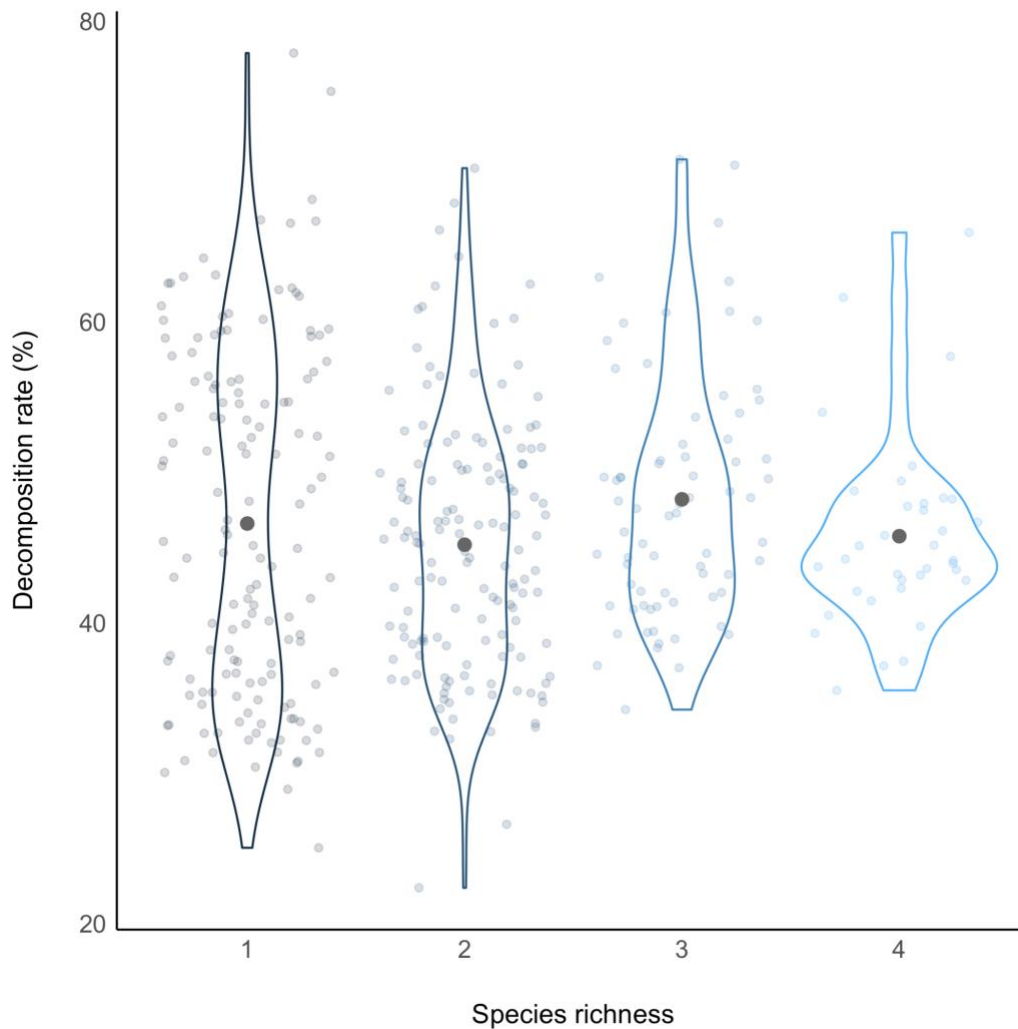


Figure 7. Violin graphs of the Decomposition rates (%) along 120 days of mixtures containing 1, 2, 3 and 4 species, respectively. The number of species represents species richness. Gray points are showing the mean values.

Discussion

We investigated litter decomposition of four functionally distinct tree species in several combinations and across 12 forest plots that varied in terms of altitude and, consequently, temperature. More specifically, we explored litter decomposability associated to (i) a range of temperature and humidity at the subtropical Atlantic Forest; (ii) litter functional traits; (iii) plant habitat of origin; and (iv) plant diversity in mixtures.

Concerning the natural temperature and humidity variation across the studied forests, we observed that temperature influences litter decay even in a subtle gradient (Figure 3), supporting conclusions of previous studies (Salinas et al. 2011; Esquivel et al. 2019; Zhou et

al. 2015). This relation possibly happens due to the influence of temperature on decomposer organisms (Bradford et al 2016) since higher temperatures increase metabolic activity of litter microbes (Schindlbacher et al. 2011) and that consequently accelerates decomposition (Tan et al. 2021). Given the small range of temperature registered between the forest plots (2.2° C), it is possible to say that even small temperature changes can affect the decomposition process. However, additional variables can be alternative or complementary to what we observed in relation to temperature, such as soil pH, radiation intensity, and fog, which vary in intensity along the studied plots and are more or less associated with the altitude (Bergamin et al. 2020). Concerning the temperature, our results suggest that further warming will accelerate decomposition and likely enhance carbon release from leaf litter (Hobbie et al. 1996) and that may have notable implications on projections of the Atlantic biome's productivity and its contributions to global carbon dynamics. Air humidity was not relevant in our study, since all plots had higher values (93-98%) during the study period, but in regions where precipitation mean or seasonality is more variable, it certainly affects decomposition patterns (Tan et al. 2021).

Although temperature has a great influence on the rate of mass decay in our experiment, the nature of the source plant material also showed notable importance on the decomposition process. The four different litter species included in our study varied greatly in their mass loss among species, supporting our initial hypothesis (Figure 2). In this study we classified our target species according to measured leaf traits (mainly SLA and LDMC, but also N, C and P content values) as being more acquisitive or more conservative, and used that to group into two litter quality treatments (Table 1). As hypothesized, we observed a relationship between decomposition rates and litter quality (i.e., the more acquisitive the species, the higher the decomposition rates), with conservative species decomposing more slowly than acquisitive ones (Figure 4). Our acquisitive species have higher Nitrogen content and SLA; and lower Carbon content and LDMC. These referred initial leaf traits are known to be positively correlated to decomposition rates (Fortunel et al. 2009; Szefer et al. 2017), due to the fact that conservative leaves are known to be unpalatable by having a more recalcitrant structure, associated with lower SLA and higher LDMC (Cornelissen 1996; Cornwell et al. 2008). Nitrogen has a stimulatory influence on the growth of decomposers communities; therefore it is usually linked with higher local decomposability (Palm and Rowland, 1997). Additionally, significant leaf strength is provided by carbon-rich structural components, such as lignin, which also affects leaf digestibility and litter breakdown (Choong et al. 1992; Pérez-Harguindeguy et al. 2000; Swift et al. 1979). Our results agree with those of Vaieretti et al. (2005), Vasconcelos

& Laurance (2005) and Makkonen et al. (2012), but we highlight the importance of evaluating broader intervals of individual values of these traits, using more species with a higher range of traits values to allow test their-relationship with decomposition rates.

In terms of habitat of origin, we tested the *home-field advantage* (HFA) of two litter mixtures from the two contrasting forest types in our study: two mixtures containing plants from the Atlantic Forest and two containing plants from the Araucaria Forest. In contrast to our hypothesis that litter produced in its origin site would have higher decomposition rates due to specialized soil fauna (Hunt et al. 1988), we couldn't find a significant effect of origin forest on litter decomposition in our study. We observed that, in general, litter from the Atlantic Forest had higher decomposition rates, regardless of place of incubation, but litter from Araucaria Forest had higher rates only away from home, i.e., when incubated in Atlantic Forest sites. This may reflect the predominance of climatic effects, where colder sites show greater disparities in environmental conditions that can possibly affect the decomposer community and therefore decomposition rates (Zhou et al. 2008). So the opposite could be true, and that might be the reason why warmer sites showed significantly higher decomposition rates, justifying why Araucaria Forest species had greater decomposition rates away from home, and not in sites of their habitat of origin. Concerning the HFA theory, the reasons we couldn't confirm our initial hypothesis for both groups of species origin (Araucaria and Atlantic Forest) are still not clear but might be associated with interactions with factors of climate and litter quality. Regarding species identity, for example, we did confirm that both Atlantic species here studied had overall higher decomposition rates irrespective of incubation site. In addition, another confounding factor may be associated with the fact that *C. vernalis* and *C. rhombea* had broader distribution patterns, with occurrence in both forest types. Overall, we can conclude that the HFA hypothesis concerning contrasting habitats at Araucaria Forest and Atlantic Forest *s.s.* deserves further attention, especially concerning that across the Atlantic Forest biome habitat transitions may follow a continuous of species composition turnover instead of abrupt changes (Bergamin et al. 2012; Oliveira-Filho et al. 2013). On the other hand, predicted warming will possibly accelerate decomposition of Araucaria Forest species, as observed when they were exposed to decomposition in Atlantic Forest sites, since temperatures there can rise to the same observed at the Atlantic sites (Bergamin et al. 2019).

Lastly, considering our diversity results, we couldn't corroborate our initial hypothesis that more diverse litter mixtures would have significantly higher decomposition rates. However, our test comparing observed and expected values of each mixture showed statistical difference between the pairs, indicating the presence of non-additive effects of species mixing

on decomposition rates, clearly observed through the patterns of Relative Mixture Effect (RME) of each mixture (Figure 6). RME values revealed slight antagonistic effects on most combinations, except for the mixture of the two conservative species (*C. vernalis* and *M. retorta*), demonstrating that most litter mixtures decomposed somewhat more slowly than what would be expected by observed means of each species individually. We expected more diverse mixtures to favor synergistic effects since they are chemically diverse and therefore support a higher diversity of soil fauna abundance (as it is shown by Xiao et al. 2020). Nonetheless, Zhou et al. (2020) and Bonanomi et al. (2010) also reported antagonistic effects in their litter mixtures. These effects can be a consequence of the interaction between different species that vary in their secondary compounds composition (e.g. lignin and polyphenols) restricting each other's mass decay (Hättenschwiler et al. 2005), but also due to the interactions with inhibitory fungal substances that can shape decomposer communities in forest floors (Gessner et al. 2010). Even though our RME values showed a great variability, from positive to negative values, we can conclude that our litter species had a potential inhibitory effect over one another which explains the several mixtures' antagonistic effects and the lack of direct response of diversity on litter decomposition rates. Further studies with more species, or with a better control on interacting effects of composition identity, diversity and climate, are probably needed to enhance our comprehension of richness effects on decomposability at the Atlantic Forest, as well as longer period decomposition experiments.

Conclusions

In this study we presented a decomposition experiment along an elevation gradient that, even with little variation of temperature, showed significant variance in decomposition rates along the gradient. Our findings confirm temperature as a primary factor controlling litter decomposition (Aerts 1997; Gholz et al. 2000) and emphasize the implications of global warming on leaf litter decomposition along habitats of the Atlantic Forest biome. Potentially, with the acceleration of decomposition rates, we can estimate alterations in mineralization rates, nutrient availability, and in the carbon cycle. A rise of carbon release through the decomposition rate can generate positive feedback for temperature elevation (Kirschbaum et al. 1995; Zhou et al. 2015), but complex interactions between primary productivity and tree mortality are further expected, also because of extreme climatic events (Brienen et al. 2015), and such feedbacks are hard to predict (Fernández-Martínez et al. 2023). Moreover, as climate changes may be influencing species distribution ranges and abundance along the Atlantic

forests (Bergamin et al. 2012), remnant sites can also have alterations in the decomposition related process due to changes in community species composition (Aerts 2006; Cornelissen 1996), especially when individuals of more tropical species advance over Araucaria Forests (Bergamin et al. 2019).

We also highlight the importance of leaf functional traits and species identity as predictors of litter decomposition. Our four species vary in a gradient of leaf quality and our results showed that they all differed in decomposition rates following this leaf quality gradient, i.e., the most conservative species having higher litter mass decay rates and the most acquisitive, lower. We also proved that the two functional groups of species combined significantly differ in decomposition rates. The combination of multiple leaf traits alters the environment in terms of soil processes, nutrient dynamics and plant succession; thus, they are likely to have major consequences at the ecosystem level such as in the decomposition process (Wardle et al. 1998). Changes in species composition due to anthropogenic impacts can directly influence litter decomposability through shifts in litter chemistry as well as the disappearance of particular plant-soil interactions, and that can cause feedbacks to the climate cycle (Chapin et al. 2005; Cornelissen et al. 2007*b*; Wieder et al. 2009); hence studies that elucidate the influence of leaf litter quality and identity on decomposition are crucial to understand these future patterns.

Contrary to what we expected, the impacts of species diversity on litter decomposition were often minimal; and the impacts of the habitat of origin were not observed at all. We did not observe any relation between diversity and decomposability, but an overall antagonistic effect associated with species identity of distinct litter mixtures. In addition, our results related to habitat of origin suggest that the other studied variables could be interfering (climate and leaf quality) as well as factors we didn't analyze (such as decomposers composition and activity). Overall, these two aspects need further research, along with evaluations of interactions between all variables contemplated here, to enhance forecasts of how human disturbances to tropical environments may affect litter decomposition and nutrient cycle.

References

Aerts R. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos* 79, 439–449 (1997).

Aerts, R. The freezer defrosting: global warming and litter decomposition rates in cold biomes. *Journal of Ecology* 94(4), 713–724 (2006).

- Ayres, E., H. Steltzer, B.L. Simmons, R.T. Simpson, J.M. Steinweg, et al. Home-field advantage accelerates leaf litter decomposition in forests. *Soil Biology and Biochemistry* 41, 606–610 (2009).
- Bakker M.A., Carreño-Rocabado G., Poorter L. Leaf economics traits predict litter decomposition of tropical plants and differ among land use types. *Funct Ecol* 25, 473–483 (2011).
- Bates, D., Maechler, M., Bolker, B., Walker, S. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* 67(1), 1-48 (2015).
- Bergamin, R.S., Debastiani, V., Joner, D.C., Lemes, P., Guimarães, T., Loyola, R.D., & Müller, S.C. Loss of suitable climatic areas for Araucaria forests over time. *Plant Ecology & Diversity* 12(2), 115–126 (2019).
- Bergamin, R.S., Müller, S.C., & Mello, R.S.P. Indicator species and floristic patterns in different forest formations in southern Atlantic rainforests of Brazil. *Community Ecology* 13(2), 162–170 (2012).
- Bonanomi, G., Incerti, G., Antignani, V., Capodilupo, M., & Mazzoleni, S. Decomposition and nutrient dynamics in mixed litter of Mediterranean species. *Plant and Soil* 331(1-2), 481–496 (2010).
- Bergamin, R.S., Seger, G.D.S., Carlucci, M.B., Molz, M., Mello, R.S.P., Martins, R., Jarenkow, J.A., Brack, P., Müller, S.C., & Duarte, L.D.S. Elevational shifts in phylogenetic diversity of angiosperm trees across the subtropical Brazilian Atlantic Forest. *Austral Ecology* 46(3), 486–495 (2020).
- Bond-Lamberty, B., Thomson, A. Temperature-associated increases in the global soil respiration record. *Nature* 464, 579–582 (2010).
- Bradford M.A., Berg B., Maynard D.S., Wieder W.R., & Wood S.A. Understanding the dominant controls on litter decomposition. *J Ecol* 104, 229–238 (2016).
- Brienen, R., Phillips, O., Feldpausch, T. et al. Long-term decline of the Amazon carbon sink. *Nature* 519, 344–348 (2015). <https://doi.org/10.1038/nature14283>

Butenschoen, O., Krashevskaya, V., Maraun, M., Marian, F., Sandmann, D., & Scheu, S. Litter mixture effects on decomposition in tropical montane rainforests vary strongly with time and turn negative at later stages of decay. *Soil Biology and Biochemistry* 77, 121–128 (2014).

Cadish, G. & Giller, K.E. *Driven by Nature: Plant Litter Quality and Decomposition*. CAB International, Wallingford XVI, 409p (1997).

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., & Naeem, S. Biodiversity loss and its impact on humanity. *Nature* 486, 59–67 (2012).

Chapin, F.S., Sturm, M., Serreze, M.C., McFadden, J.P., Key, J.R., Lloyd, A.H. *et al.* Role of land-surface changes in Arctic summer warming. *Science* 310, 657–660 (2005).

Chapman, S.K., Newman, G.S., Hart, S.C., Schweitzer, J.A., Koch, G.W. Leaf litter mixtures alter microbial community development: mechanisms for non-additive effects in litter decomposition. *PLoS One* 8 (4), e62671 (2013).

Chen, B.M., Peng, S.L., D'Antonio, C.M., Li, D.J., & Ren, W.T. Non-Additive Effects on Decomposition from Mixing Litter of the Invasive *Mikania micrantha* H.B.K. with Native Plants. *PLoS ONE* 8(6), e66289 (2013).

Cornelissen, J.H.C. An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. *Journal of Ecology* 84, 573–582 (1996).

Cornelissen, J.H.C., Van Bodegom, P.M., Aerts, R., Callaghan, T.V., Van Logtestijn, R.S.P., Alatalo, J., *et al.* Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. *Ecology Letters* 10, 619–627 (2007b).

Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., *et al.* Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters* 11(10), 1065–1071 (2008).

Choong, M.F., Lucas, P.W., Ong, J.S. Y., Pereira, B., Tan, H.T.W., & Turner, I.M. Leaf fracture toughness and sclerophylly: their correlations and ecological implications. *New Phytologist* 121(4), 597–610 (1992).

Davidson, E.A., Janssens, I.A. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440:165–173 (2006).

de la Riva, E.G., Prieto, I. & Villar, R. The leaf economic spectrum drives leaf litter decomposition in Mediterranean forests. *Plant Soil* 435, 353–366 (2019).

de Lima, R.A.F., Oliveira, A.A., Pitta, G.R. et al. The erosion of biodiversity and biomass in the Atlantic Forest biodiversity hotspot. *Nat Commun* 11, 6347 (2020).

Edwards, C.A., Reichle, D.E. & Crossley, D.A., Jr. The role of soil invertebrates in turnover of organic matter and nutrients. In: Reichle DE (Eds) *Analysis of Temperate Forest Ecosystems*. Springer-Verlag, New York pp 12–172 (1970).

Esquivel, J. , Park, B.B., Casanoves, F., Delgado, D., Park, G.E., & Finegan, B. Altitude and species identity drive leaf litter decomposition rates of ten species on a 2950 m altitudinal gradient in Neotropical rain forests. *Biotropica* 52, 11-21 (2019).

Gonçalves, E.T., & Souza, A.F. Floristic variation in ecotonal areas: Patterns, determinants and biogeographic origins of subtropical forests in South America. *Austral Ecology* 39(1), 122–134 (2013).

Fernández-Martínez, M., Peñuelas, J., Chevallier, F. et al. Diagnosing destabilization risk in global land carbon sinks. *Nature* 615, 848–853 (2023).

Freschet, G.T., Aerts, R., & Cornelissen, J.H.C. Multiple mechanisms for trait effects on litter decomposition: moving beyond home-field advantage with a new hypothesis. *Journal of Ecology* 100(3), 619–630 (2012).

Fortunel, C., Garnier, E., Joffre, R., Kazakou, E., Quested, H., Grigulis, K., ... Zarovali, M. Leaf traits capture the effects of land use changes and climate on litter decomposability of grasslands across Europe. *Ecology* 90(3), 598–611 (2009).

Galindo-Leal C., Câmara, I.G. Atlantic Forest hotspot status: an overview. In Galindo-Leal C, Câmara IG (eds). *The Atlantic Forest of South America*. Washington, DC: Center for Applied Biodiversity Science 3–11 (2003).

Garnier E., Shipley B., Roumet C., Laurent G. A standardized protocol for the determination of specific leaf area and leaf dry matter content. *Functional Ecology* 15, 688-695 (2001b).

Gartner, T. B., & Cardon, Z. G. Decomposition dynamics in mixed-species leaf litter. *Oikos* 104, 230–246 (2004).

Gessner, M.O., Swan, C.M., Dang, C.K., McKie, B.G., Bardgett, R.D., Wall, D.H., & Hättenschwiler, S. Diversity meets decomposition. *Trends in Ecology & Evolution* 25(6), 372–380 (2010).

Gholz, H.L., Wedin, D.A., Smitherman, S.M., Harmon, M.E. & Parton, W.J. Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. *Global Change Biology* 6, 751–765 (2000).

Hanson, P.J., Edwards, N.T., Garten, C.T., & Andrews, J.A. Separating root and soil microbial contributions to soil respiration: A review of methods and observations. *Biogeochemistry* 48, 115–146 (2000).

Hättenschwiler, S., Tiunov, A.V., & Scheu, S. Biodiversity and litter decomposition in terrestrial ecosystems. *Annu. Rev. Ecol. Evol. Syst.* 191–218 (2005).

Hijmans, R., Cameron, S., Parra, J., Jones, P., Jarvis, A., & Richardson, A. N. D. K. *Worldclim: Global climate data* (2011). Disponível em <http://www.worldclim.org>.

Hobbie, S.E. Temperature and Plant Species Control Over Litter Decomposition in Alaskan Tundra. *Ecological Monographs* 66(4), 503–522 (1996).

Hunt, H.W., Ingham, E.R., Coleman, D.C., Elliott, E.T. & Reid, C.P.P. Nitrogen limitation of production and decomposition in prairie, mountain meadow, and pine forest. *Ecology* 69, 1009–1016 (1988).

Kirschbaum, M.U.F. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. *Soil Biol. Biochem.* 27(6) 753-760 (1995).

Körner, C. CO₂ enrichment: effects on ecosystems. In: Munn T, ed. *Encyclopedia of global environmental change*, Vol 2. Weinheim, Germany: John Wiley & Sons Ltd, 215–224 (2002).

Kurokawa, H., & Nakashizuka, T. Leaf herbivory and decomposability in a malaysian tropical rain forest. *Ecology* 89(9), 2645–2656 (2008).

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B. lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software* 82(13), 1-26 (2017)

Lenth, R. Emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.8.1-1 (2022).

Liu, P., Sun, O.J., Huang, J. et al. Nonadditive effects of litter mixtures on decomposition and correlation with initial litter N and P concentrations in grassland plant species of northern China. *Biol Fertil Soils* 44, 211–216 (2007).

Makkonen, M., Berg, M.P., Handa, I.T., Hättenschwiler, S., van Ruijven, J., van Bodegom, P. M., & Aerts, R. Highly consistent effects of plant litter identity and functional traits on decomposition across a latitudinal gradient. *Ecology Letters* 15(9), 1033–1041 (2012).

Makkonen, M., Berg, M.P., van Logtestijn, R.S.P., van Hal, J.R., & Aerts, R. Do physical plant litter traits explain non-additivity in litter mixtures? A test of the improved microenvironmental conditions theory. *Oikos* 122(7), 987–997 (2013).

Manzoni, S., Schimel, J. P., & Porporato, A. Responses of soil microbial communities to water stress: results from a meta-analysis. *Ecology* 93(4), 930–938 (2012).

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., et al. *Vegan: Community Ecology Package*. R package version 2.6-2 (2022).

Oliveira, R.A.C., Marques, R., & Marques, M.C.M. Plant diversity and local environmental conditions indirectly affect litter decomposition in a tropical forest. *Applied Soil Ecology* 134, 45–53 (2018).

Oliveira-Filho, A.T., Budke, J.C., Jarenkow, J.A., Eisenlohr, P.V., & Neves, D.R.M. Delving into the variations in tree species composition and richness across South American subtropical Atlantic and Pampean forests. *Journal of Plant Ecology* 8(3), 242–260 (2013).

Oliveira-Filho, A.T., Budke, J.C., Jarenkow, J.A., Eisenlohr, P.V., & Neves, D.R.M. Delving into the variations in tree species composition and richness across South American subtropical Atlantic and Pampean forests. *Journal of Plant Ecology* 8(3), 242–260 (2013).

Palm, C.A. & Rowland, A.P. A minimum dataset for characterization of plant quality for decomposition. In *Driven by Nature: Plant Litter Quality and Decomposition*. Eds G Cadisch and K E Giller. CAB International-University Press, Cambridge pp 379–392 (1997).

Pérez-Harguindeguy, N., Díaz, S., Cornelissen, J.H.C., Vendramini, F., Cabido, M. & Castellanos, A. *Plant and Soil* 218/2(1/2), 21–30 (2000).

Purahong, W., Kahl, T., Krüger, D., Buscot, F., & Hoppe, B. Home-Field Advantage in Wood Decomposition Is Mainly Mediated by Fungal Community Shifts at “Home” Versus “Away.” *Microbial Ecology* (2019).

R Core Team. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL: <https://www.R-project.org/> (2022).

Raich, J.W. & W.H. Schlesinger. The global carbon dioxide flux in soil respiration and its relationship to climate. *Tellus* 44B, 81–99 (1992).

Reich, P.B., Walters, M.B., & Ellsworth, D.S. From tropics to tundra: Global convergence in plant functioning. *Proceedings of the National Academy of Sciences* 94(25), 13730–13734 (1997).

- Reich, P.B. The world-wide 'fast-slow' plant economics spectrum: A traits manifesto. *Journal of Ecology* 102, 275–301 (2014).
- Ruess, L. & Ferris, H. Decomposition pathways and successional changes. In: *Proceedings of the Fourth International Congress of Nematology*, 8-13 June 2002, Tenerife, Spain. 547–556 (2002).
- Salinas, N., Malhi, Y., Meir, P., Silman, M., Roman Cuesta, R., Huaman, J., Salinas, D., Huaman, V., Gibaja, A., Mamani, M. & Farfan, F. The sensitivity of tropical leaf litter decomposition to temperature: results from a large-scale leaf translocation experiment along an elevation gradient in Peruvian forests. *New Phytologist* 189, 967–77 (2011).
- Santiago, L.S. Extending the leaf economics spectrum to decomposition: evidence from a tropical forest. *Ecology* 88(5), 1126–1131 (2007).
- Scharlemann, J.P., Tanner, E.V., Hiederer, R., & Kapos, V. Global soil carbon: understanding and managing the largest terrestrial carbon pool. *Carbon Management* 5(1), 81–91 (2014).
- Schindlbacher, A., Rodler, A., Kuffner, M., Kitzler, B., Sessitsch, A., Zechmeister-Boltenstern, S. Experimental warming effects on the microbial community of a temperate mountain forest soil. *Soil Biol Biochem* 43(7), 1417-1425 (2011).
- Shipley, B., Vu, T.T. Dry matter content as a measure of dry matter concentration in plants and their parts. *New Phytologist* 153, 359-364 (2002).
- Sobral, M., Jarenkow, J.A., Brack, P., Irgang, B.E., Larocca, J., & Rodrigues, R.S. *Flora Arbórea e Arborescente Do Rio Grande Do Sul, Brasil*. Porto Alegre: Novo Ambiente (2006).
- Swift, M. J., O. W. Heal, and J. M. Anderson. *Decomposition in terrestrial ecosystems*. Blackwell, London, UK (1979).
- Szefer, P., Carmona, C. P., Chmel, K., Konečná, M., Libra, M., Molem, K., *et al.* Determinants of litter decomposition rates in a tropical forest: functional traits, phylogeny and ecological succession. *Oikos* 126(8), 1101–1111 (2017).
- Tan, B., Yin, R., Zhang, J. et al. Temperature and Moisture Modulate the Contribution of Soil Fauna to Litter Decomposition via Different Pathways. *Ecosystems* 24, 1142–1156 (2021).
- Vaieretti, M. V., Harguindeguy, N. P., Gurvich, D. E., Cingolani, A. M., & Cabido, M.. Decomposition Dynamics and Physico-chemical Leaf Quality of Abundant Species in a Montane Woodland in Central Argentina. *Plant and Soil* 278(1-2), 223–234 (2005).

- van de Weg, M.J., Meir, P., Grace, J., Atkin, O. Altitudinal variation in LMA, leaf tissue density and foliar nitrogen and phosphorus along an Andes–Amazon gradient in Peru. *Plant Ecology and Diversity* 2, 243–254 (2009).
- Vivanco, L. & Austin, A.T. Tree species identity alters forest litter decomposition through long-term plant and soil interactions in Patagonia, Argentina. *Journal of Ecology* 96(4), 727–736 (2008).
- Wardle, D., Bonner, K., & Nicholson, K. Biodiversity and plant litter: Experimental evidence which does not support the view that enhanced species richness improves ecosystem function. *Oikos* 247–258 (1997).
- Wardle, D.A., Barker, G.M., Bonner, K. I., & Nicholson, K.S. Can comparative approaches based on plant ecophysiological traits predict the nature of biotic interactions and individual plant species effects in ecosystems? *Journal of Ecology* 86, 405–420 (1998).
- Wall, D.H., Bradford, M.A., St. John, M.G., Trofymow, J.A., Behan-Pelletier, V., Bignell, D.E., *et al.* Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. *Global Change Biology* 14, 2661–2677 (2008).
- Wickham, H. *Ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York (2016).
- Wieder, W.R., Cleveland, C.C., & Townsend, A.R. Controls over leaf litter decomposition in wet tropical forests. *Ecology* 90(12), 3333–3341 (2009).
- Wright, I.J., P.B., Reich, M., Westoby, D.D., Ackerly, Z., Baruch, F., Bongers, J., Cavender-Bares, T., Chapin, J.H.C., Cornelissen, M., *et al.* The worldwide leaf economics spectrum. *Nature* 498, 821–827 (2004).
- Xiao, W., Chen, C., Chen, X., Huang, Z., & Chen, H.Y.H. Functional and phylogenetic diversity promote litter decomposition across terrestrial ecosystems. *Global Ecology and Biogeography* 29(12), 2261–2272 (2020).
- Yuan, X., Niu, D., Wang, Y., Boydston, A., Guo, D., Li, X., Wen, H., Qin, Y., Fu, H. Litter decomposition in fenced and grazed grasslands: A test of the home-field advantage hypothesis. *Geoderma* 354, 113876 (2019).
- Zhang, D.Q., Hui, D.F., Luo, Y.Q., Zhou, G.Y. Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. *J Plant Ecol* 1, 85–93 (2008).
- Zhou, G., Guan, L., Wei, X., Tang, X., Liu, S., Liu, J., Zhang, D., Yan, J. Factors influencing leaf litter decomposition: an intersite decomposition experiment across China. *Plant and Soil*, 311(1-2), 61–72 (2008).

Zhou, Y., Clark, M., Su, J., Xiao, C. Litter decomposition and soil microbial community composition in three Korean pine (*Pinus koraiensis*) forests along an altitudinal gradient. *Plant Soil* 386, 171–183 (2015).

Zhou, S., Butenschoen, O., Barantal, S., Handa, I. T., Makkonen, M., Vos, V., Aerts, R., Berg, M.P., McKie, B., Ruijven, J.V., Hättenschwiler, S., & Scheu, S. Decomposition of leaf litter mixtures across biomes: The role of litter identity, diversity and soil fauna. *Journal of Ecology* 00, 1-15 (2020).

Considerações finais

Neste trabalho, confirmamos o efeito da temperatura sobre taxas de decomposição de espécies nativas da Mata Atlântica, o que implica consequências importantes sobre ciclos globais de carbono e nutrientes. Demonstramos também a importância das características funcionais foliares da serapilheira na decomposição e a identidade das espécies. Portanto, este estudo contribuiu para a compreensão de alguns controles do processo de decomposição de espécies nativas funcionalmente diferentes ao longo de um gradiente climático, nos permitindo inferir informações relevantes sobre o funcionamento deste processo no bioma Mata Atlântica. Apesar de não termos encontrado evidências da influência do habitat de origem e da diversidade de serapilheira sobre a decomposição, estudos posteriores que aprimorem os métodos utilizados neste trabalho (e.g. utilizando um maior número de espécies) são pertinentes para o melhor entendimento desses fatores sobre a decomposição. Com os nossos resultados, avançamos no conhecimento sobre como processos ecossistêmicos podem ser influenciados por alterações climáticas e de biodiversidade em florestas subtropicais.

Material Suplementar

Apêndice 1 - Taxas de decomposição dos tratamentos

Tabela A.1: Taxa de decomposição (%) de todos os tratamentos e em todos os locais de estudo. P indica PARNA, PM indica Pró-Mata, AR indica Aratinga e M indica Maquiné. T1, T2 e T3 indicam as 3 replicatas utilizadas no experimento.

Locais	Cupania	Campomanesia	Mollinedia	Myrcia	Funcional 1	Funcional 2	Origem 1	Origem 2	Diversidade 1	Diversidade 2	Mix
P1 T1	39.2	50.4	59.1	31.3	51.9	32.2	48.1	35.7	44.3	45.2	44.2
P1 T2	42.5	40.3	61.7	32.0	46.7	37.2	58.2	34.2	46.0	50.7	43.7
P1 T3	48.6	46.1	52.3	33.1	49.5	36.4	42.3	38.3	43.2	49.4	42.8
P2 T1	33.6	36.6	48.9	31.3	37.7	35.3	40.7	22.3	39.7	34.2	37.1
P2 T2	34.6	43.0	51.7	32.6	46.8	35.3	46.6	39.2	41.9	41.0	44.1
P2 T3	36.7	49.6	54.6	33.4	44.8	35.9	45.9	38.5	41.3	41.7	46.1
P3 T1	44.6	43.73	50.7	33.2	40.9	34.9	51.6	32.7	42.0	44.4	40.4
P3 T2	38.8	44.2	56.0	34.0	43.4	33.5	42.8	35.2	39.2	38.3	37.4
P3 T3	36.0	35.3	59.4	30.7	45.7	35.4	41.2	33.0	42.5	60.6	39.2
PM1 T1	36.5	44.83	57.7	25.0	43.0	34.7	47.1	36.3	37.1	39.3	43.2
PM1 T2	38.1	48.0	56.2	33.2	48.9	35.4	46.5	39.0	40.8	41.1	39.7
PM1 T3	39.9	56.1	57.3	32.2	62.3	36.2	55.8	37.5	60.7	47.8	43.5

PM2T 1	47.8	55.5	59.5	35.9	45.7	41.9	49.4	32.7	39.2	43.7	45.1
PM2 T2	41.2	60.3	63.0	37.5	49.9	39.0	56.5	42.6	52.2	48.7	43.9
PM2 T3	46.8	45.8	54.5	32.6	50.2	36.1	60.2	38.4	47.5	43.8	50.4
PM3 T1	52.5	60.1	55.2	35.3	51.5	64.3	48.3	43.7	51.0	50.6	48.2
PM3 T2	39.9	62.5	56.6	35.1	52.9	41.7	50.5	41.4	49.5	49.6	46.6
PM3T 3	37.8	40.1	54.6	30.8	51.0	36.5	46.1	39.7	37.0	41.1	41.4
PM4T 1	51.2	60.1	66.5	34.5	53.1	37.7	50.3	47.9	48.3	54.8	45.8
PM4 T2	44.9	53.7	54.3	34.3	47.5	42.2	46.7	42.0	47.8	55.5	47.7
PM4 T3	42.2	45.1	58.9	30.4	52.5	38.8	45.2	39.6	49.6	50.5	48.7
AR1 T1	39.5	53.0	56.3	35.1	46.0	36.4	45.3	37.8	44.1	45.3	45.1
AR1 T2	38.7	51.0	54.5	36.5	46.3	34.6	53.1	41.0	44.6	44.5	42.0
AR1 T3	40.6	45.4	53.5	37.2	47.1	35.1	46.6	38.6	49.7	40.8	42.2
AR2 T1	30.0	41.6	57.9	32.6	44.0	26.6	44.7	36.1	38.6	39.4	43.6
AR2 T2	30.6	51.2	53.4	33.6	47.4	33.3	44.0	38.7	42.0	38.9	35.5
AR2 T3	37.4	51.4	56.0	32.1	45.5	38.7	52.3	40.1	48.3	57.2	42.8
M1 T1	41.1	53.6	62.2	37.4	52.7	35.9	50.1	42.3	50.8	53.6	48.3
M1	38.2	52.4	55.8	33.4	48.7	38.9	49.4	42.7	47.1	49.6	47.4

T2											
M1 T3	51.9	60.5	58.9	31.3	62.5	40.2	49.3	42.7	51.8	58.7	43.1
M2 T1	59.4	75.3	68.1	32.2	67.9	52.8	51.6	50.5	62.9	70.4	57.7
M2 T2	61.9	77.8	59.4	34.8	70.2	60.8	61.0	55.4	60.0	66.5	65.9
M2 T3	62.1	66.7	64.2	32.9	59.9	51.9	55.0	57.0	55.1	70.8	61.6
M3 T1	54.6	59.0	62.5	28.9	66.1	44.3	55.8	50.5	43.2	59.9	49.4
M3 T2	36.2	63.1	61.0	35.8	57.1	56.4	45.6	48.3	56.9	48.1	47.9
M3 T3	41.6	66.7	59.1	43.0	52.0	50.5	49.8	48.9	53.9	62.7	53.9

Apêndice 2 - Temperatura e umidade dos plots florestais

Tabela A.2: Valores de temperatura (° C) e umidade (%) de todas as localidades de estudo utilizadas nas análises. P = PARNA, PM = Pró-Mata, AR = Aratinga e M = Maquiné.

Site	Mean temperature (° C)	Mean moisture (%)
P1	15.3207518	96.1366513
P2	15.3960491	98.5782125
P3	15.3584005	97.3574319
PM3	15.5779056	95.6681626
PM2	16.1063099	93.930514
PM1	16.4870733	93.2804565
PM4	16.0570963	94.2930444

AR2	15.5232643	96.2668393
AR1	15.5012275	94.7957039
M1	17.1506736	98.544715
M2	17.5798446	96.9629534
M3	17.3652591	97.7538342

Apêndice 3 - Taxas de decomposição esperadas e observadas das misturas de tratamentos

Tabela A.3: Taxa de decomposição (%) observada (Mobs) e esperada (Mesp) das misturas de tratamentos, em todos os locais de estudo e em todas as replicatas; bem como valores de “*Relative Mixture Effect*” (RME), número de espécies em cada mistura (Num_sp), o respectivo tratamento (Treatment), a identidade das espécies dentro de cada mistura (Id) e o valor de p do teste-t realizado entre o valor observado e esperado de cada mistura (p_value). P indica PARNA, PM indica Pró-Mata, AR indica Aratinga e M indica Maquiné. T1, T2 e T3 indicam as 3 replicatas utilizadas no experimento. “Cu” representa a espécie *Cupania vernalis*; “Ca” representa a espécie *Campomanesia rhombea*; “Mo” representa a espécie *Mollinedia schottiana*; e “My” representa a espécie *Myrcia retorta*. O RME foi calculado conforme descrito no texto.

Site	Sample	Mobs	Mesp	RME	Num_sp	Treatment	Id	p_value
P1	P1T1	44.233	45.025	-1.7582824	4	mix	CuCaMoMy	1.06E-05
P1	P1T2	43.717	44.1583333	-1.0001887	4	mix	CuCaMoMy	1.06E-05
P1	P1T3	42.850	45.0833333	-4.9537893	4	mix	CuCaMoMy	1.06E-05
P2	P2T1	37.133	37.6291667	-1.3176835	4	mix	CuCaMoMy	1.06E-05
P2	P2T2	44.133	40.5	8.97119342	4	mix	CuCaMoMy	1.06E-05

P2	P2T3	46.100	43.6041667	5.72384138	4	mix	CuCaMoMy	1.06E-05
P3	P3T1	40.483	43.1041667	-6.080232	4	mix	CuCaMoMy	1.06E-05
P3	P3T2	37.433	43.3	-13.548884	4	mix	CuCaMoMy	1.06E-05
P3	P3T3	39.283	40.4125	-2.7941025	4	mix	CuCaMoMy	1.06E-05
P M 1	PM1T1	43.217	40.9083333	5.64269709	4	mix	CuCaMoMy	1.06E-05
P M 1	PM1T2	39.750	43.9125	-9.4790777	4	mix	CuCaMoMy	1.06E-05
P M 1	PM1T3	43.517	46.425	-6.2645845	4	mix	CuCaMoMy	1.06E-05
P M 2	PM2T1	45.117	49.7333333	-9.2828418	4	mix	CuCaMoMy	1.06E-05
P M 2	PM2T2	43.950	50.5208333	-13.006186	4	mix	CuCaMoMy	1.06E-05
P M 2	PM2T3	50.417	44.9625	12.1304791	4	mix	CuCaMoMy	1.06E-05
P M 3	PM3T1	48.217	50.8375	-5.1553151	4	mix	CuCaMoMy	1.06E-05
P M 3	PM3T2	46.683	48.575	-3.8943215	4	mix	CuCaMoMy	1.06E-05

P M 3	PM3T3	41.450	40.8583333	1.448093	4	mix	CuCaMoMy	1.06E-05
P M 4	PM4T1	45.800	53.125	-13.788235	4	mix	CuCaMoMy	1.06E-05
P M 4	PM4T2	47.733	46.8291667	1.93077676	4	mix	CuCaMoMy	1.06E-05
P M 4	PM4T3	48.767	44.1625	10.4255118	4	mix	CuCaMoMy	1.06E-05
A R1	AR1T1	45.150	46.0125	-1.8744906	4	mix	CuCaMoMy	1.06E-05
A R1	AR1T2	42.083	45.2208333	-6.9381738	4	mix	CuCaMoMy	1.06E-05
A R1	AR1T3	42.283	44.2083333	-4.3543827	4	mix	CuCaMoMy	1.06E-05
A R2	AR2T1	43.600	40.5625	7.48844376	4	mix	CuCaMoMy	1.06E-05
A R2	AR2T2	35.500	42.2333333	-15.943173	4	mix	CuCaMoMy	1.06E-05
A R2	AR2T3	42.817	44.2625	-3.2664972	4	mix	CuCaMoMy	1.06E-05
M 1	M1T1	48.300	48.6291667	-0.6768914	4	mix	CuCaMoMy	1.06E-05
M 1	M1T2	47.467	44.9541667	5.58902586	4	mix	CuCaMoMy	1.06E-05
M 1	M1T3	43.167	50.7083333	-14.872638	4	mix	CuCaMoMy	1.06E-05
M 2	M2T1	57.700	58.775	-1.8290089	4	mix	CuCaMoMy	1.06E-05

M 2	M2T2	65.933	58.5166667	12.6744517	4	mix	CuCaMoMy	1.06E-05
M 2	M2T3	61.633	56.5166667	9.05337659	4	mix	CuCaMoMy	1.06E-05
M 3	M3T1	49.433	51.2958333	-3.6308992	4	mix	CuCaMoMy	1.06E-05
M 3	M3T2	47.917	49.0791667	-2.3686221	4	mix	CuCaMoMy	1.06E-05
M 3	M3T3	53.983	52.6166667	2.5974026	4	mix	CuCaMoMy	1.06E-05
P1	P1T1	44.333	46.9666667	-5.6068133	3	div1	CaMoMy	2.37E-05
P1	P1T2	46.033	44.7	2.98284862	3	div1	CaMoMy	2.37E-05
P1	P1T3	43.200	43.8888889	-1.5696203	3	div1	CaMoMy	2.37E-05
P2	P2T1	39.750	38.9666667	2.01026518	3	div1	CaMoMy	2.37E-05
P2	P2T2	41.967	42.4611111	-1.1644642	3	div1	CaMoMy	2.37E-05
P2	P2T3	41.350	45.9055556	-9.9237565	3	div1	CaMoMy	2.37E-05
P3	P3T1	42.000	42.5888889	-1.3827289	3	div1	CaMoMy	2.37E-05
P3	P3T2	39.217	44.7722222	-12.408487	3	div1	CaMoMy	2.37E-05
P3	P3T3	42.550	41.8555556	1.65914521	3	div1	CaMoMy	2.37E-05
P M 1	PM1T1	37.150	42.35	-12.27863	3	div1	CaMoMy	2.37E-05
P M 1	PM1T2	40.883	45.8222222	-10.778371	3	div1	CaMoMy	2.37E-05

P M 1	PM1T3	60.700	48.5833333	24.9399657	3	div1	CaMoMy	2.37E-05
P M 2	PM2T1	39.250	50.35	-22.04568	3	div1	CaMoMy	2.37E-05
P M 2	PM2T2	52.200	53.6222222	-2.6523	3	div1	CaMoMy	2.37E-05
P M 2	PM2T3	47.583	44.3444444	7.30393385	3	div1	CaMoMy	2.37E-05
P M 3	PM3T1	51.017	50.2555556	1.51448154	3	div1	CaMoMy	2.37E-05
P M 3	PM3T2	49.550	51.4666667	-3.7240933	3	div1	CaMoMy	2.37E-05
P M 3	PM3T3	37.000	41.8777778	-11.647652	3	div1	CaMoMy	2.37E-05
P M 4	PM4T1	48.300	53.7611111	-10.158107	3	div1	CaMoMy	2.37E-05
P M 4	PM4T2	47.883	47.4611111	0.88961723	3	div1	CaMoMy	2.37E-05
P M 4	PM4T3	49.650	44.8111111	10.7984131	3	div1	CaMoMy	2.37E-05
A R1	AR1T1	44.117	48.1666667	-8.4083045	3	div1	CaMoMy	2.37E-05

A R1	AR1T2	44.600	47.3777778	-5.8630394	3	div1	CaMoMy	2.37E-05
A R1	AR1T3	49.750	45.4111111	9.55468559	3	div1	CaMoMy	2.37E-05
A R2	AR2T1	38.600	44.0722222	-12.416488	3	div1	CaMoMy	2.37E-05
A R2	AR2T2	42.083	46.0888889	-8.6909354	3	div1	CaMoMy	2.37E-05
A R2	AR2T3	48.317	46.5333333	3.83237822	3	div1	CaMoMy	2.37E-05
M 1	M1T1	50.883	51.1166667	-0.4564721	3	div1	CaMoMy	2.37E-05
M 1	M1T2	47.100	47.2055556	-0.2236083	3	div1	CaMoMy	2.37E-05
M 1	M1T3	51.867	50.2944444	3.12603557	3	div1	CaMoMy	2.37E-05
M 2	M2T1	62.967	58.55	7.54341019	3	div1	CaMoMy	2.37E-05
M 2	M2T2	60.083	57.3777778	4.71533695	3	div1	CaMoMy	2.37E-05
M 2	M2T3	55.100	54.6444444	0.83367222	3	div1	CaMoMy	2.37E-05
M 3	M3T1	43.267	50.1777778	-13.773251	3	div1	CaMoMy	2.37E-05
M 3	M3T2	56.900	53.3555556	6.64306539	3	div1	CaMoMy	2.37E-05
M 3	M3T3	53.933	56.2833333	-4.1753035	3	div1	CaMoMy	2.37E-05
P1	P1T1	45.250	49.5777778	-8.7292694	3	div2	CuCaMo	8.57E-06
P1	P1T2	50.783	48.2055556	5.34747032	3	div2	CuCaMo	8.57E-06

P1	P1T3	49.467	49.0555556	0.8380521	3	div2	CuCaMo	8.57E-06
P2	P2T1	34.217	39.7222222	-13.86014	3	div2	CuCaMo	8.57E-06
P2	P2T2	41.067	43.1166667	-4.7545419	3	div2	CuCaMo	8.57E-06
P2	P2T3	41.717	47	-11.241135	3	div2	CuCaMo	8.57E-06
P3	P3T1	44.450	46.3833333	-4.1681639	3	div2	CuCaMo	8.57E-06
P3	P3T2	38.317	46.4	-17.420977	3	div2	CuCaMo	8.57E-06
P3	P3T3	60.633	43.6222222	38.996434	3	div2	CuCaMo	8.57E-06
P M 1	PM1T1	39.350	46.2	-14.82684	3	div2	CuCaMo	8.57E-06
P M 1	PM1T2	41.117	47.4833333	-13.408213	3	div2	CuCaMo	8.57E-06
P M 1	PM1T3	47.283	51.1666667	-7.5895765	3	div2	CuCaMo	8.57E-06
P M 2	PM2T1	43.750	54.3166667	-19.45382	3	div2	CuCaMo	8.57E-06
P M 2	PM2T2	48.717	54.8555556	-11.191007	3	div2	CuCaMo	8.57E-06
P M 2	PM2T3	43.883	49.0666667	-10.563859	3	div2	CuCaMo	8.57E-06
P M 3	PM3T1	50.683	55.9888889	-9.4760865	3	div2	CuCaMo	8.57E-06

P M 3	PM3T2	49.667	53.0444444	-6.3678257	3	div2	CuCaMo	8.57E-06
P M 3	PM3T3	41.133	44.2	-6.9381599	3	div2	CuCaMo	8.57E-06
P M 4	PM4T1	54.800	59.3111111	-7.6058449	3	div2	CuCaMo	8.57E-06
P M 4	PM4T2	55.517	50.9833333	8.8917947	3	div2	CuCaMo	8.57E-06
P M 4	PM4T3	50.567	48.75	3.72649573	3	div2	CuCaMo	8.57E-06
A R1	AR1T1	45.333	49.65	-8.6941927	3	div2	CuCaMo	8.57E-06
A R1	AR1T2	44.550	48.1111111	-7.4018476	3	div2	CuCaMo	8.57E-06
A R1	AR1T3	40.883	46.5166667	-12.110355	3	div2	CuCaMo	8.57E-06
A R2	AR2T1	39.417	43.1944444	-8.7459807	3	div2	CuCaMo	8.57E-06
A R2	AR2T2	38.917	45.1111111	-13.731527	3	div2	CuCaMo	8.57E-06
A R2	AR2T3	57.233	48.2944444	18.5091453	3	div2	CuCaMo	8.57E-06
M 1	M1T1	53.667	52.3666667	2.48249523	3	div2	CuCaMo	8.57E-06
M 1	M1T2	49.667	48.8055556	1.76437109	3	div2	CuCaMo	8.57E-06

M 1	M1T3	58.750	57.15	2.79965004	3	div2	CuCaMo	8.57E-06
M 2	M2T1	70.417	67.6333333	4.11532775	3	div2	CuCaMo	8.57E-06
M 2	M2T2	66.583	66.4	0.27610442	3	div2	CuCaMo	8.57E-06
M 2	M2T3	70.800	64.3833333	9.9663474	3	div2	CuCaMo	8.57E-06
M 3	M3T1	59.917	58.7555556	1.97617247	3	div2	CuCaMo	8.57E-06
M 3	M3T2	48.100	53.4777778	-10.056098	3	div2	CuCaMo	8.57E-06
M 3	M3T3	62.700	55.8166667	12.3320394	3	div2	CuCaMo	8.57E-06
P1	P1T1	51.983	54.7666667	-5.0821668	2	func1	CaMo	1.29E-06
P1	P1T2	46.733	51.0416667	-8.4408163	2	func1	CaMo	1.29E-06
P1	P1T3	49.567	49.25	0.642978	2	func1	CaMo	1.29E-06
P2	P2T1	37.700	42.775	-11.864407	2	func1	CaMo	1.29E-06
P2	P2T2	46.867	47.3666667	-1.0555947	2	func1	CaMo	1.29E-06
P2	P2T3	44.833	52.15	-14.030042	2	func1	CaMo	1.29E-06
P3	P3T1	40.950	47.25	-13.333333	2	func1	CaMo	1.29E-06
P3	P3T2	43.467	50.1583333	-13.341087	2	func1	CaMo	1.29E-06
P3	P3T3	45.783	47.3916667	-3.3937049	2	func1	CaMo	1.29E-06
P M 1	PM1T1	43.000	51.0083333	-15.700049	2	func1	CaMo	1.29E-06

P M 1	PM1T2	48.933	52.1333333	-6.1381074	2	func1	CaMo	1.29E-06
P M 1	PM1T3	62.383	56.775	9.87817408	2	func1	CaMo	1.29E-06
P M 2	PM2T1	45.783	57.5333333	-20.422943	2	func1	CaMo	1.29E-06
P M 2	PM2T2	49.950	61.675	-19.010944	2	func1	CaMo	1.29E-06
P M 2	PM2T3	50.200	50.1916667	0.01660302	2	func1	CaMo	1.29E-06
P M 3	PM3T1	51.567	57.6916667	-10.616785	2	func1	CaMo	1.29E-06
P M 3	PM3T2	52.983	59.6166667	-11.126642	2	func1	CaMo	1.29E-06
P M 3	PM3T3	51.017	47.4	7.63009845	2	func1	CaMo	1.29E-06
P M 4	PM4T1	53.150	63.3583333	-16.112061	2	func1	CaMo	1.29E-06
P M 4	PM4T2	47.533	54.0083333	-11.988891	2	func1	CaMo	1.29E-06
P M 4	PM4T3	52.500	52.0166667	0.92918936	2	func1	CaMo	1.29E-06

A R1	AR1T1	46.083	54.7	-15.75259	2	func1	CaMo	1.29E-06
A R1	AR1T2	46.367	52.7916667	-12.170481	2	func1	CaMo	1.29E-06
A R1	AR1T3	47.150	49.475	-4.6993431	2	func1	CaMo	1.29E-06
A R2	AR2T1	44.000	49.775	-11.60221	2	func1	CaMo	1.29E-06
A R2	AR2T2	47.400	52.3333333	-9.4267516	2	func1	CaMo	1.29E-06
A R2	AR2T3	45.550	53.7166667	-15.203227	2	func1	CaMo	1.29E-06
M 1	M1T1	52.750	57.9666667	-8.999425	2	func1	CaMo	1.29E-06
M 1	M1T2	48.733	54.1083333	-9.9337748	2	func1	CaMo	1.29E-06
M 1	M1T3	62.500	59.75	4.60251046	2	func1	CaMo	1.29E-06
M 2	M2T1	67.900	71.725	-5.3328686	2	func1	CaMo	1.29E-06
M 2	M2T2	70.217	68.6333333	2.30694512	2	func1	CaMo	1.29E-06
M 2	M2T3	59.900	65.5083333	-8.5612517	2	func1	CaMo	1.29E-06
M 3	M3T1	66.100	60.8083333	8.70220639	2	func1	CaMo	1.29E-06
M 3	M3T2	57.133	62.0916667	-7.9855053	2	func1	CaMo	1.29E-06
M 3	M3T3	52.000	62.9166667	-17.350993	2	func1	CaMo	1.29E-06

P1	P1T1	32.267	35.2833333	-8.5498347	2	func2	CuMy	0.01178
P1	P1T2	37.200	37.275	-0.2012072	2	func2	CuMy	0.01178
P1	P1T3	36.467	40.9166667	-10.875764	2	func2	CuMy	0.01178
P2	P2T1	35.300	32.4833333	8.67111339	2	func2	CuMy	0.01178
P2	P2T2	35.317	33.6333333	5.0049554	2	func2	CuMy	0.01178
P2	P2T3	35.967	35.0583333	2.5909199	2	func2	CuMy	0.01178
P3	P3T1	34.900	38.9583333	-10.417112	2	func2	CuMy	0.01178
P3	P3T2	33.583	36.4416667	-7.8435856	2	func2	CuMy	0.01178
P3	P3T3	35.467	33.4333333	6.08175474	2	func2	CuMy	0.01178
P M 1	PM1T1	34.717	30.8083333	12.6859616	2	func2	CuMy	0.01178
P M 1	PM1T2	35.467	35.6916667	-0.6303993	2	func2	CuMy	0.01178
P M 1	PM1T3	36.233	36.075	0.43890044	2	func2	CuMy	0.01178
P M 2	PM2T1	41.967	41.9333333	0.07949126	2	func2	CuMy	0.01178
P M 2	PM2T2	39.050	39.3666667	-0.804403	2	func2	CuMy	0.01178
P M 2	PM2T3	36.100	39.7333333	-9.1442953	2	func2	CuMy	0.01178

P M 3	PM3T1	64.350	43.9833333	46.3054187	2	func2	CuMy	0.01178
P M 3	PM3T2	41.700	37.5333333	11.1012433	2	func2	CuMy	0.01178
P M 3	PM3T3	36.550	34.3166667	6.5080136	2	func2	CuMy	0.01178
P M 4	PM4T1	37.750	42.8916667	-11.987566	2	func2	CuMy	0.01178
P M 4	PM4T2	42.267	39.65	6.59941152	2	func2	CuMy	0.01178
P M 4	PM4T3	38.817	36.3083333	6.90842323	2	func2	CuMy	0.01178
A R1	AR1T1	36.417	37.325	-2.4335789	2	func2	CuMy	0.01178
A R1	AR1T2	34.683	37.65	-7.8795927	2	func2	CuMy	0.01178
A R1	AR1T3	35.133	38.9416667	-9.7795848	2	func2	CuMy	0.01178
A R2	AR2T1	26.600	31.35	-15.151515	2	func2	CuMy	0.01178
A R2	AR2T2	33.300	32.1333333	3.63070539	2	func2	CuMy	0.01178
A R2	AR2T3	38.750	34.8083333	11.3239167	2	func2	CuMy	0.01178
M 1	M1T1	35.933	39.2916667	-8.5471898	2	func2	CuMy	0.01178

M 1	M1T2	38.967	35.8	8.84543762	2	func2	CuMy	0.01178
M 1	M1T3	40.250	41.6666667	-3.4	2	func2	CuMy	0.01178
M 2	M2T1	52.850	45.825	15.33006	2	func2	CuMy	0.01178
M 2	M2T2	60.850	48.4	25.7231405	2	func2	CuMy	0.01178
M 2	M2T3	51.900	47.525	9.20568122	2	func2	CuMy	0.01178
M 3	M3T1	44.317	41.7833333	6.06302353	2	func2	CuMy	0.01178
M 3	M3T2	56.400	36.0666667	56.3770795	2	func2	CuMy	0.01178
M 3	M3T3	50.517	42.3166667	19.3777078	2	func2	CuMy	0.01178
P1	P1T1	48.150	49.1583333	-2.0511951	2	ori1	CuMo	0.02382
P1	P1T2	58.283	52.125	11.8145484	2	ori1	CuMo	0.02382
P1	P1T3	42.333	50.4916667	-16.157782	2	ori1	CuMo	0.02382
P2	P2T1	40.767	41.2583333	-1.1916784	2	ori1	CuMo	0.02382
P2	P2T2	46.683	43.175	8.12584443	2	ori1	CuMo	0.02382
P2	P2T3	45.917	45.6666667	0.54744526	2	ori1	CuMo	0.02382
P3	P3T1	51.650	47.7083333	8.26200873	2	ori1	CuMo	0.02382
P3	P3T2	42.883	47.4583333	-9.6400351	2	ori1	CuMo	0.02382
P3	P3T3	41.200	47.75	-13.717277	2	ori1	CuMo	0.02382

P M 1	PM1T1	47.167	47.1583333	0.01767097	2	ori1	CuMo	0.02382
P M 1	PM1T2	46.500	47.1916667	-1.4656542	2	ori1	CuMo	0.02382
P M 1	PM1T3	55.833	48.6583333	14.7456756	2	ori1	CuMo	0.02382
P M 2	PM2T1	49.450	53.7	-7.9143389	2	ori1	CuMo	0.02382
P M 2	PM2T2	56.583	52.1083333	8.58787782	2	ori1	CuMo	0.02382
P M 2	PM2T3	60.233	50.6833333	18.842486	2	ori1	CuMo	0.02382
P M 3	PM3T1	48.317	53.9333333	-10.414091	2	ori1	CuMo	0.02382
P M 3	PM3T2	50.533	48.2833333	4.6599931	2	ori1	CuMo	0.02382
P M 3	PM3T3	46.183	46.2416667	-0.1261489	2	ori1	CuMo	0.02382
P M 4	PM4T1	50.333	58.8833333	-14.520238	2	ori1	CuMo	0.02382
P M 4	PM4T2	46.750	49.625	-5.7934509	2	ori1	CuMo	0.02382

P M 4	PM4T3	45.250	50.5666667	-10.514173	2	ori1	CuMo	0.02382
A R1	AR1T1	45.317	47.9666667	-5.5246699	2	ori1	CuMo	0.02382
A R1	AR1T2	53.117	46.6416667	13.882437	2	ori1	CuMo	0.02382
A R1	AR1T3	46.617	47.075	-0.9736237	2	ori1	CuMo	0.02382
A R2	AR2T1	44.733	43.9916667	1.68592536	2	ori1	CuMo	0.02382
A R2	AR2T2	44.000	42.0666667	4.59587956	2	ori1	CuMo	0.02382
A R2	AR2T3	52.300	46.7333333	11.9115549	2	ori1	CuMo	0.02382
M 1	M1T1	50.133	51.7083333	-3.0459307	2	ori1	CuMo	0.02382
M 1	M1T2	49.433	47.0083333	5.15865981	2	ori1	CuMo	0.02382
M 1	M1T3	49.333	55.45	-11.030959	2	ori1	CuMo	0.02382
M 2	M2T1	51.600	63.7916667	-19.111692	2	ori1	CuMo	0.02382
M 2	M2T2	61.017	60.6666667	0.57692308	2	ori1	CuMo	0.02382
M 2	M2T3	55.033	63.1833333	-12.898971	2	ori1	CuMo	0.02382
M 3	M3T1	55.867	58.6166667	-4.6914984	2	ori1	CuMo	0.02382
M 3	M3T2	45.667	48.6583333	-6.1483131	2	ori1	CuMo	0.02382

M 3	M3T3	49.883	50.375	-0.9760132	2	ori1	CuMo	0.02382
P1	P1T1	35.750	40.8916667	-12.573874	2	ori2	CaMy	5.71E-08
P1	P1T2	34.267	36.1916667	-5.318904	2	ori2	CaMy	5.71E-08
P1	P1T3	38.350	39.675	-3.3396345	2	ori2	CaMy	5.71E-08
P2	P2T1	22.367	34	-34.215686	2	ori2	CaMy	5.71E-08
P2	P2T2	39.200	37.825	3.63516193	2	ori2	CaMy	5.71E-08
P2	P2T3	38.583	41.5416667	-7.1213641	2	ori2	CaMy	5.71E-08
P3	P3T1	32.750	38.5	-14.935065	2	ori2	CaMy	5.71E-08
P3	P3T2	35.200	39.1416667	-10.070258	2	ori2	CaMy	5.71E-08
P3	P3T3	33.050	33.075	-0.0755858	2	ori2	CaMy	5.71E-08
P M 1	PM1T1	36.333	34.6583333	4.83289252	2	ori2	CaMy	5.71E-08
P M 1	PM1T2	39.017	40.6333333	-3.978671	2	ori2	CaMy	5.71E-08
P M 1	PM1T3	37.567	44.1916667	-14.991514	2	ori2	CaMy	5.71E-08
P M 2	PM2T1	32.783	45.7666667	-28.368536	2	ori2	CaMy	5.71E-08
P M 2	PM2T2	42.600	48.9333333	-12.942779	2	ori2	CaMy	5.71E-08

P M 2	PM2T3	38.467	39.2416667	-1.9749416	2	ori2	CaMy	5.71E-08
P M 3	PM3T1	43.767	47.7416667	-8.3260604	2	ori2	CaMy	5.71E-08
P M 3	PM3T2	41.467	48.8666667	-15.143247	2	ori2	CaMy	5.71E-08
P M 3	PM3T3	39.767	35.475	12.0977214	2	ori2	CaMy	5.71E-08
P M 4	PM4T1	47.933	47.3666667	1.19634061	2	ori2	CaMy	5.71E-08
P M 4	PM4T2	42.017	44.0333333	-4.5798637	2	ori2	CaMy	5.71E-08
P M 4	PM4T3	39.683	37.7583333	5.09821232	2	ori2	CaMy	5.71E-08
A R1	AR1T1	37.817	44.0583333	-14.166824	2	ori2	CaMy	5.71E-08
A R1	AR1T2	41.000	43.8	-6.3926941	2	ori2	CaMy	5.71E-08
A R1	AR1T3	38.617	41.3416667	-6.591413	2	ori2	CaMy	5.71E-08
A R2	AR2T1	36.133	37.1333333	-2.6929982	2	ori2	CaMy	5.71E-08
A R2	AR2T2	38.783	42.4	-8.5298742	2	ori2	CaMy	5.71E-08

A R2	AR2T3	40.133	41.7916667	-3.9680957	2	ori2	CaMy	5.71E-08
M 1	M1T1	42.350	45.55	-7.025247	2	ori2	CaMy	5.71E-08
M 1	M1T2	42.767	42.9	-0.3108003	2	ori2	CaMy	5.71E-08
M 1	M1T3	42.767	45.9666667	-6.9615664	2	ori2	CaMy	5.71E-08
M 2	M2T1	50.550	53.7583333	-5.968067	2	ori2	CaMy	5.71E-08
M 2	M2T2	55.450	56.3666667	-1.6262567	2	ori2	CaMy	5.71E-08
M 2	M2T3	57.017	49.85	14.3764627	2	ori2	CaMy	5.71E-08
M 3	M3T1	50.567	43.975	14.9895774	2	ori2	CaMy	5.71E-08
M 3	M3T2	48.350	49.5	-2.3232323	2	ori2	CaMy	5.71E-08
M 3	M3T3	48.917	54.8583333	-10.830928	2	ori2	CaMy	5.71E-08