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Efeitos da biodiversidade sobre a estrutura e funcionamento de ecossistemas em um cenário de mudança climática

São José do Rio Preto
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Tese apresentada como parte dos requisitos para obtenção do título de Doutor em Biologia Animal, junto ao Programa de Pós-Graduação em Biologia Animal, Área de Concentração – Ecologia e Comportamento, do Instituto de Biociências, Letras e Ciências Exatas da Universidade Estadual Paulista "Júlio de Mesquita Filho", Campus de São José do Rio Preto.

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Resumo

Mudanças climáticas e alterações na biodiversidade são as principais ameaças que os ecossistemas estão enfrentando na era atual. Mudanças na composição de espécies de plantas, juntamente com alterações nas suas características induzidas pelo clima, são esperados alterar a qualidade e a diversidade funcional dos detritos, o que pode gerar impactos diretos e indiretos sobre as comunidades associadas e o funcionamento ecossistêmico. Entretanto, pouco se sabe sobre como os atributos dos detritos e seus efeitos interativos com o aumento da temperatura podem afetar a estrutura de comunidades e processos ecossistêmicos. Neste estudo, nós investigamos os efeitos individuais e interativos do aquecimento e de mudanças na qualidade e diversidade funcional de detritos sobre a estrutura de comunidades de insetos aquáticos e sobre as taxas de decomposição dos detritos. Utilizando microcosmos aquáticos naturais (bromélias tanque), nós simulamos o efeito do aquecimento e manipulamos a qualidade e diversidade funcional de detritos. Nossos resultados mostram que o aquecimento pode afetar a riqueza e abundância de insetos aquáticos e mudar sua composição. Tanto a qualidade como a diversidade funcional dos detritos podem influenciar a estrutura das comunidades de insetos aquáticos. Além disso, o aquecimento e as alterações na qualidade e na diversidade funcional dos detritos podem afetar as taxas de decomposição, e esses efeitos podem ser explicados principalmente pelos conteúdos de ligninas e por variações nas quantidades de C, N and razões C:N. Nossos resultados ressaltam a importância de se conhecer como alterações na temperatura e na composição de espécies de plantas podem gerar efeitos sobre comunidades aquáticas que dependem desses recursos, a fim de prever os impactos do aquecimento global e das mudanças na biodiversidade sobre os ecossistemas.

Palavras-chave: Atributos funcionais. Aquecimentos global. Decomposição. Diversidade functional. Insetos aquáticos.

Abstract

Climate warming and biodiversity shifts are the main threats ecosystems are facing in current era. Changes in plant species composition, along with climate-induced alterations in plant traits, are expected to alter the quality and functional diversity of litter with direct or indirect impacts on the communities of consumers and ecosystem functioning. However, little is known on the importance of litter traits and how they interact with warming to affect the structuring of communities and ecosystem processes. In this study, we investigated the individual and interactive effects of warming and changes in litter quality and functional diversity on the structuring of aquatic invertebrate communities and decomposition process. Using a natural aquatic microecosystem (tank bromeliads), we simulated the effect of warming and manipulated litter quality and functional diversity. Our results shown that warming may affect richness and abundance of aquatic insects and change their composition. Both litter quality and functional diversity may affects the structure of insect communities. Moreover, warming and changes in litter quality and functional diversity may affect decomposition rates, and such changes can be explained mainly by specific traits, such as lignin contents and dissimilarities in C, N and C:N ratios. Our study highlight the importance in knowing the effects of increasing temperature and changes in plant composition on aquatic communities, in order to predict the effects of global warming and biodiversity shifts on ecosystems.

Keywords: Aquatic insects. Decomposition. Functional diversity. Functional traits. Global warming.

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1. INTRODUÇÃO GERAL

Biodiversidade, isto é, a variedade de genes, espécies e atributos funcionais, têm impacto no funcionamento ecossistêmico e, por consequência, nos serviços que os ecossistemas fornecem para a humanidade (Cardinale et al. 2012). Funcionamento ecossistêmico envolve os processos que controlam o fluxo de energia, nutrientes e matéria orgânica através do ambiente, como produtividade, ciclagem de nutrientes e decomposição (Loreau, Naeem & Inchausti 2002). Serviços ecossistêmicos são os benefícios que os ecossistemas fornecem para a humanidade, como ar, água, comida e regulação do clima (Millenium Ecosystem Assessment 2005). Relações entre biodiversidade, processos e serviços podem ser exemplificadas com questões como, por exemplo: Uma floresta terá maior depósito de carbono se possuir uma maior variedade de espécies de árvores? Um riacho terá maior capacidade de despoluição se houver maior diversidade de microorganismos? Ou, o controle biológico de pragas é mais eficaz se houver maior diversidade de predadores, parasitas e patógenos? (Cardinale et al. 2012). Conhecer as relações entre a biodiversidade e as funções ecossistêmicas é fundamental para prever os impactos que a perda de espécies pode causar nos ecossistemas.

Alterações no funcionamento dos ecossistemas podem ser explicadas por controles abióticos (e.g., temperatura, regime de chuva) e bióticos (e.g., diversidade e composição de espécies). Sabe-se atualmente que o papel da biodiversidade pode ser, ao menos, tão importante quanto o papel de fatores ambientais no controle de funções ecossistêmicas (Hooper et al. 2012; Tilman, Reich & Isbell 2012). Efeitos da biodiversidade podem ser atribuídos a dois tipos de mecanismos: complementaridade ou seleção (Loreau & Hector 2001). Por exemplo, se em uma mistura de espécies elas fazem o uso diferenciado dos recursos, de forma que o resultado final é o uso mais eficiente desses recursos, ocorreu o efeito de complementaridade entre espécies (Hooper et al. 2005). Complementaridade pode ocorrer também como interações de facilitação, onde uma espécie facilita a atividade de outra e, como resultado, aumenta as taxas do processo em questão (Tiunov & Scheu 2005). Seleção ocorre quando o efeito de uma mistura de espécies é causado pela presença de uma espécie que é altamente produtiva (Huston 1997; Loreau & Hector 2001). Embora a maior parte da teoria de biodiversidade e funcionamento de ecossistemas tenha sido fundamentada utilizando métricas de diversidade taxonômica, atualmente têm-se o consenso de que a composição de atributos funcionais é um melhor preditor de funcionamento ecossistêmico, porque atributos funcionais são conceitualmente mais relacionados aos mecanismos de complementaridade de nicho, facilitação e seleção (Diaz & Cabido 2001, Mason et al. 2005). Atributos funcionais são as características das espécies que influenciam propriedades ecossistêmicas ou as respostas das espécies para condições ambientais (Violle et al. 2007). Diversidade funcional refere-se à variação e valor dos atributos funcionais dos organismos que influenciam propriedades ecossistêmicas (Tilman 2001).

1.1 Decomposição: definição, importância e fatores controladores

A decomposição de material vegetal é uma das principais funções ecossistêmicas, uma vez que envolve a quebra e transformação da matéria orgânica morta em energia para diversos organismos tanto em sistemas aquáticos como terrestres (Moore et al. 2004; Hätteschwiller, Tiunov & Scheu

2005; Gessner et al. 2010). Plantas terrestres produzem, a cada ano, em torno de 120 bilhões de toneladas de carbono orgânico (Beer et al. 2010), onde 90% não é consumido por herbívoros e acaba como matéria orgânica morta (Cebrian 1999). A quebra da matéria vegetal morta envolve a reciclagem de componentes de volta para suas formas inorgânicas enquanto a parte recalcitrante pode ser incorporada na matéria orgânica e armazenada por longos períodos (Cardinale et al. 2011). Detritos foliares correspondem a maior parte da matéria orgânica que passa pelo processo de decomposição (Moore et al. 2004). Dado que a diversidade de detritos foliares reflete a diversidade de plantas em um determinado local e que as diferenças em atributos funcionais das plantas enquanto vivas refletem nas características dos detritos, espera-se que os atributos funcionais dos detritos tenham um papel fundamental sobre a estrutura das comunidades detritívoras e decompositoras e, consequentemente, sobre o processo de decomposição (Gessner et al. 2010). A qualidade dos detritos, isto é, o conjunto de atributos físico-químicos que determinam a labilidade, palatabilidade, toxicidade e valor nutricional para detritívoros e decompositores, tem sido sugerido como o principal determinante da decomposição tanto em escalas locais como globais, superando até os efeitos do clima e das comunidades decompositoras (Cornwell et al. 2008; Makkonen et al. 2012). Por outro lado, estudos tem mostrado que a diversidade funcional, isto é, o grau de variação nos atributos dos detritos é o fator mais importante no controle da decomposição (Diaz et al. 2007). Maior variação nos tipos de detritos permite aos consumidores obter recursos de forma mais eficiente através do uso complementar, consequentemente, acelerando as taxas de decomposição (Heemsbergen et al. 2004; Barantal et al. 2014). A transferência de nutrientes entre detritos de diferentes qualidades, através de transferência passiva por lixiviação ou via transferência ativa por microorganismos (i.e., hifas de fungos), tem sido apontada como mecanismo de complementaridade de nicho envolvido no processo de decomposição foliar (Schimel & Hättenchwiller 2007; Gessner et al. 2010; Handa et al. 2014; García-Palacios et al. 2017). Compreender como fatores bióticos e abióticos controlam a decomposição é fundamental a fim entender como os ecossistemas funcionam e prever como responderão a perturbações como mudanças climáticas e alterações na biodiversidade.

1.2 Efeitos do aquecimento global sobre a estrutura de comunidades e funções ecossistêmicas em sistemas de água doce

A temperatura da superfície da Terra aumentou em torno de 0.8ºC durante o último século, e é previsto que aumente mais 2 a 4ºC até o ano de 2100 (IPCC 2013). Paralelamente com a superfícies, a temperatura de ecossistemas de água doce está aumentando, devido as relações físicas entre o ar e a temperatura da água (Webb and Nobilis 1997). Diversos estudos têm mostrado que o aquecimento global já está causando impactos severos em ecossistemas de água doce ao redor do globo. Como exemplo, pode-se citar as mudanças nos regimes de riachos causadas pelo degelo de glaciares de montanhas (Barnett et al. 2005). Além disso, o aquecimento tem alterado o relógio de importantes eventos biológicos levando a mudanças nas características (e.g., tamanho corporal) de organismos e comunidades (Walther et al. 2002; Parmesan 2006). Ecossistemas aquáticos, como de água doce, são particularmente vulneráveis ao aquecimento, uma vez que suas comunidades são basicamente formadas por organismos cujo as atividades fisiológicas são fortemente dependentes da temperatura (Pörtner and Farrel 2008). Além disso, muitas espécies que vivem nesses ambientes possuem capacidades de dispersão limitadas (Woodward, Perkins & Brown 2010). Uma vez que a temperatura é o principal controlador abiótico das taxas metabólicas dos organismos (Brown et al. 2004), deve-se esperar alterações no comportamento, reprodução, desenvolvimento e crescimento dos organismos (Woodward, Perkins & Brown 2010). Tais alterações ao nível de indivíduos devem refletir em níveis mais altos de organização, resultando em impactos na abundância de populações e na estrutura das comunidades (Woodward, Perkins & Brown 2010). Respostas ao nível de comunidades são mais complexas, uma vez que mudanças na temperatura podem diferentemente favorecer taxas vitais ou atributos demográficos de algumas espécies enquanto outras espécies são penalizadas (Elmendorf et al. 2012). São previstas, também, mudanças na força e no sinal de interações entre espécies, rompendo mutualismos, interações tróficas, hierarquias competitivas e, consequentemente, a coexistência de espécies (Zarnetske et al. 2012; Blois et al. 2013; Sorte & White 2013; Sentis et al. 2014).

Estudos investigando os efeitos do aquecimento sobre as relações entre biodiversidade e funcionamento de ecossistemas são relativamente escassos. Alguns dos primeiros experimentos a explorar tais relações em sistemas aquáticos foram realizados por Petchey e colaboradores (Petchey et al. 1999; Petchey 2000). Nesses estudos, através de experimentos com comunidades de protistas, foi constatado que grupos tróficos foram desproporcionalmente impactados pelo aquecimento, resultando em comunidades dominadas por grupos funcionais específicos e, consequentemente, o funcionamento ecossistêmico foi alterado. Dang et al. (2009) mostraram que o aquecimento alterou a composição das comunidades de fungos aquáticos e, por consequência, as taxas de decomposição de detritos. Recentemente, foi demonstrado que o aquecimento pode impactar o funcionamento de um ecossistema aquático ao enfraquecer interações interespecíficas entre os organismos da comunidade (Bernabé et al. 2018). Adicionalmente, um estudo que simulou o efeito do aquecimento e manipulou a perda de predadores de topo, mostrou que o aquecimento pode afetar diretamente o funcionamento do ecossistema, aumentando as taxas de produtividade e metabolismo. Além disso, foi observado que a perda de espécies de predadores pode ter fortes efeitos sobre a produtividade ecossistêmica (Antiqueira, Petchey & Romero 2018).

1.3 Sistema de estudo e objetivos

O uso de sistemas alternativos como modelo de estudo em ecologia já foi assunto de grandes debates (Carpenter 1996; Drenner & Mazumder 1999; Carpenter 1999). Modelos artificiais permitem experimentos rápidos, precisos e de alta replicabilidade porém são criticados em relação ao realismo (Carpenter 1996). Experimentos que envolvem ecossistemas como um todo, e.g., lagos e rios, apesar do realismo, dificultam a replicabilidade. Assim, o uso de sistemas-modelo que representam um equilíbrio entre realismo e viabilidade pode ser uma alternativa para evitar críticas (Srivastava et al. 2004). O uso de microcosmos naturais, como bromélias-tanque, plantas jarro e buracos de árvores, tem se tornado frequente na ecologia experimental. São sistemas de tamanho pequeno que permitem alta replicabilidade e manipulação de suas comunidades que podem ser formadas por complexas redes tróficas incluindo microorganismos decompositores e diversas espécies de detritívoros e predadores (Romero & Srivastava 2010).

No presente trabalho utilizamos bromélias-tanque como modelo de estudo para testar os efeitos individuais e interativos do aumento da temperatura e da variação na qualidade e diversidade funcional de detritos sobre a estrutura de comunidades e o funcionamento ecossistêmico. Especificamente, investigamos como as comunidades dos principais grupos de insetos colonizadores (filtradores, detritívoros e predadores) e as taxas de decomposição de detritos são afetados pelo aquecimento (de acordo com as predições para ao ano de 2100; IPCC 2013) e pela variação na qualidade e diversidade funcional de detritos foliares (simulação de mudança da biodiversidade). O estudo foi realizado no Parque Estadual Serra do Mar – Núcle Picinguaba, litoral norte do estado de São Paulo (Figura 1). O experimento foi conduzido em uma área de restinga fechada, onde os blocos experimentais contendo bromélias e coberturas de proteção foram instaladas sobre as bromélias (Figuras 2A-B). Para investigar os efeitos do aquecimento e da variação nos detritos (qualidade e diversidade funcional) sobre a taxas de decomposição, utilizamos pequenos sacos de detritos (litter bags) de 2 tamanhos de malhas (Figura 2D). Na malha grossa a decomposição é mediada pelos microorganismos e detritívoros, enquanto que na malha fina somente microorganismos controlam o processo. Para simular o efeito do aquecimento global, utilizamos um equipamento de controle automático programado para aumentar instantaneamente a temperatura ambiente em 4 ºC (Figura 2E-F e Figura 3), conforme as predições para o ano de 2100 (IPCC 2013).

No capítulo 1 investigamos os efeitos do aquecimento e da variação dos detritos em qualidade e diversidade funcional sobre a estrutura dos grupos dominantes de insetos aquáticos em bromélias, filtradores, detritívoros e predadores. Os resultados mostraram que tanto o aumento de conteúdos de lignina (efeito negativo) quanto o aumento nas variações de C, N e C:N (efeito positivo) dos detritos, afetam a abundância de filtradores e detritívoros. Além disso, observamos que essas mesmas características dos detritos podem gerar efeitos indiretos sobre predadores, ao afetar a abundância de suas presas (detritívoros e filtradores). Adicionalmente, observamos que o aquecimento pode reduzir a riqueza e equitabilidade de larvas filtradoras, enquanto que pode aumentar a abundância de detritívoros.

No capítulo 2, investigamos como o aquecimento combinado com a variação em qualidade e diversidade funcional dos detritos afeta as taxas de decomposição. Os resultados mostraram que tanto a qualidade como diversidade funcional controlam o processo de quebra dos detritos. Na decomposição total (microorganismos + detritívoros) observamos que o aumento nos conteúdos de lignina reduz as taxas de decomposição, enquanto que o aumento nas dissimilaridades de C, N e C:N aumenta as taxas. Na decomposição mediada por microorganismos apenas, além dos efeitos semelhantes a decomposição total descritos acima, observamos um efeito interativo do aquecimento com a qualidade. O aquecimento tendeu a aumentar a decomposição de detritos com altos conteúdos compostos secundários e C:N e a diminuir a decomposição de detritos com altos conteúdos de nutrientes. Além disso, verificamos a decomposição mediada somente por detritívoros aumenta positivamente com o aumento de conteúdos de N e P dos detritos.

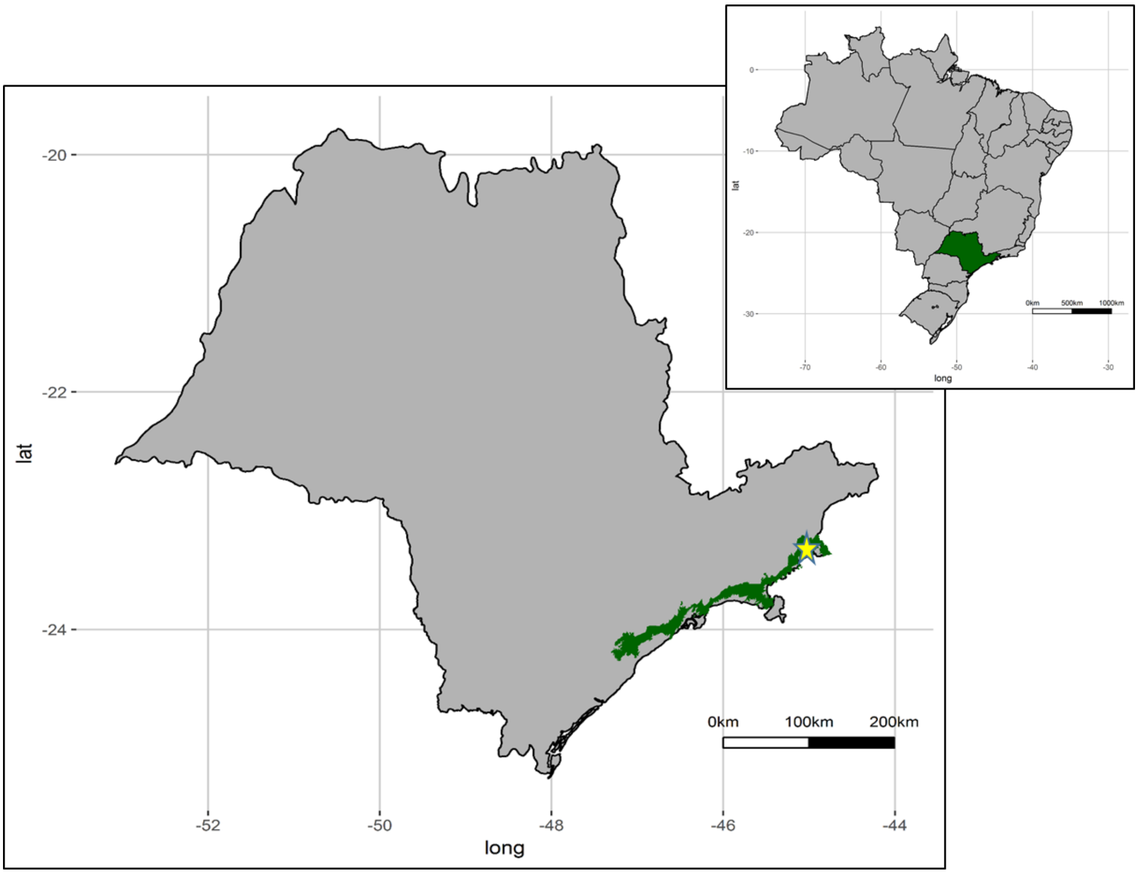

Figura 1. Mapa destacando a área do Parque Estadual Serra do Mar. A área de estudo corresponde ao Núcleo Picinguaba indicado pela estrela amarela.

Figura 2. (A-B) Área de restinga onde foi realizado o experimento destacando as coberturas de proteção das bromélias utilizadas nos blocos experimentais. (C) Bromélia com saco de detrito utilizado para medir a decomposição. (D) Sacos detritos de malha fina e grossa. Na malha fina somente microorganismos acessaram os detritos, enquanto que detritívoros juntamente com microorganismos tiveram acesso aos detritos na malha grossa. (E-F) Monitor de acesso as temperaturas de cada unidade experimental (bromélias) em cada bloco.

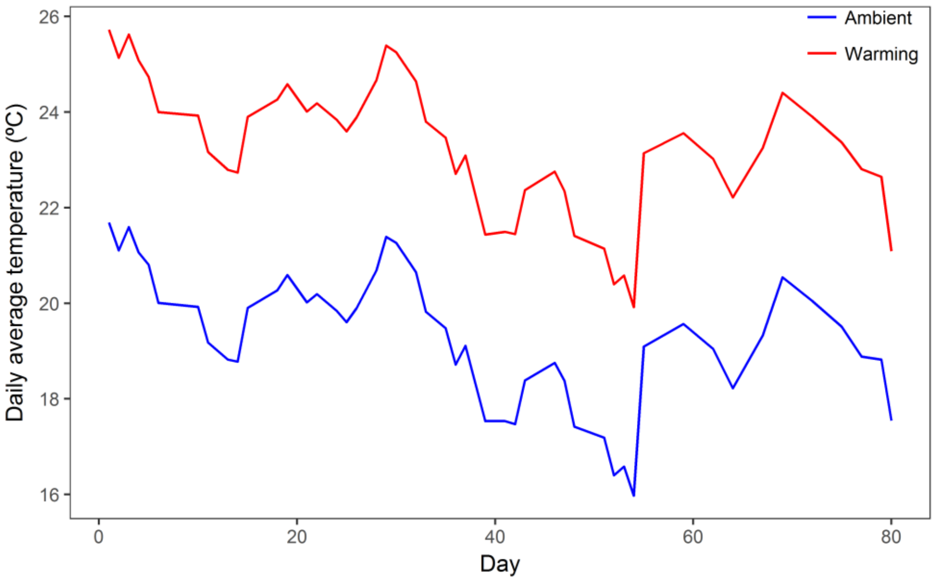

Figura 3. Média diária de temperatura mostrando a precisão do equipamento utilizado para simular o efeito do aquecimento. A linha azul representa a temperatura real do ambiente e a linha vermelha indica o aumento em 4ºC sobre a temperatura do ambiente.

1.4 REFERÊNCIAS

Antiqueira, P. A. P., O. L. Petchey, & G. Q. Romero. 2018. Warming and top predator loss drive ecosystem multifunctionality. Ecology Letters 21:72–82.

Barantal, S., H. Schimann, N. Fromin, & S. Hattenschwiler. 2014. C, N and P fertilization in an Amazonian rainforest supports stoichiometric dissimilarity as a driver of litter diversity effects on decomposition. Proceedings of the Royal Society B: Biological Sciences 281:20141682.

Barnett, T. P., J. C. Adam, & D. P. Lettenmaier. 2005. Potential impacts of a warming climate on water availability in snow-dominated regions. Nature 438:303–309.

Beer, C., et al. 2010. Terrestrial gross carbon dioxide uptake: global distribution and covariation with climate. Science 329:834–838.

Bernabé, T. N., P. M. de Omena, V. P. dos Santos, V. M. de Siqueira, V. M. de Oliveira, & G. Q. Romero. 2018. Warming weakens facilitative interactions between decomposers and detritivores, and modifies freshwater ecosystem functioning. Global Change Biology 24:3170–3186.

Blois, J. L., P. L. Zarnetske, M. C. Fitzpatrick, & S. Finnegan. 2013. Climate change and the past, present, and future of biotic interactions. Science 341:499–504.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, & G. B. West. 2004. Toward a metabolic theory of ecology. Ecology 85:1771–1789.

Cardinale, B. J., et al. 2012. Biodiversity loss and its impact on humanity. Nature 486:59–67.

Cardinale, B. J., K. L. Matulich, D. U. Hooper, J. E. Byrnes, E. Duffy, L. Gamfeldt, P. Balvanera, M. I. O’Connor, & A. Gonzalez. 2011. The functional role of producer diversity in ecosystems. American Journal of Botany 98:572–592.

Carpenter, S. R. 1996. Microcosm Experiments have Limited Relevance for Community and Ecosystem Ecology. Ecology 77:677–680.

Carpenter, S. 1999. Microcosm experiments have limited relevance for community and ecosystem ecology: comment. Ecology 80:1085-1088.

Cebrian, J. 1999. Patterns in the Fate of Production in Plant Communities. The American Naturalist 154:449–468.

Cornwell, W. K., et al. 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecology Letters 11:1065–1071.

Drenner, R. W. & A. Mazumder. 1999. Microcosm experiments have limited relevance for community and ecosystem ecology: comment. Ecology 80:1081-1085

Dang, C. K., M. Schindler, E. Chauvet, & M. O. Gessner. 2009. Temperature oscillation coupled with fungal community shifts can modulate warming effects on litter decomposition. Ecology 90:122–131.

Diaz, S., S. Lavorel, F. de Bello, F. Quetier, K. Grigulis, & T. M. Robson. 2007. Incorporating plant functional diversity effects in ecosystem service assessments. Proceedings of the National Academy of Sciences 104:20684–20689.

Díaz, S., & M. Cabido. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. Trends in Ecology & Evolution 16:646–655.

Elmendorf, S. C., et al. 2012. Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. Ecology Letters 15:164–175.

García-Palacios, P., E. A. Shaw, D. H. Wall, & S. Hättenschwiler. 2017. Contrasting mass-ratio vs. niche complementarity effects on litter C and N loss during decomposition along a regional climatic gradient. Journal of Ecology 105:968–978.

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

Handa, I. T., et al. 2014. Consequences of biodiversity loss for litter decomposition across biomes. Nature 509:218–221.

Hättenschwiler, S., A. V. Tiunov, & S. Scheu. 2005. Biodiversity and litter decomposition in terrestrial ecosystems. Annual Review of Ecology, Evolution, and Systematics 36:191–218.

Heemsbergen, D. A., M. P. Berg, M. Loreau, J. R. van Hal, J. H. Faber, & H. A. Verhoef. 2004. Biodiversity effects on soil processes explained by interspecific functional dissimilarity. Science 306:1019–1020.

Hooper, D. U., E. C. Adair, B. J. Cardinale, J. E. K. Byrnes, B. A. Hungate, K. L. Matulich, A. Gonzalez, J. E. Duffy, L. Gamfeldt, & M. I. O'Connor. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486:105–108.

Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä, A. J. Symstad, J. Vandermeer, & D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75:3–35.

Huston, M. A. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. Oecologia 110:449–460.

Loreau, M., & A. Hector. 2001. Partitioning selection and complementarity in biodiversity experiments. Nature 412:72–76.

Loreau, M., S. Naeem, & P. Inchausti, editors. 2002. Biodiversity and ecosystem functioning: synthesis and perspectives. Oxford University Press, Oxford.

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

Mason, N. W. H., D. Mouillot, W. G. Lee, & J. B. Wilson. 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111:112–118.

Millennium Ecosystem Assessment. 2005. Ecosystems and Human Well-being: Biodiversity Synthesis. World Resources Institute, Washington, DC.

Moore, J. C., et al. 2004. Detritus, trophic dynamics and biodiversity: Detritus, trophic dynamics and biodiversity. Ecology Letters 7:584–600.

Parmesan, C. 2006. Ecological and Evolutionary Responses to Recent Climate Change. Annual Review of Ecology, Evolution, and Systematics 37:637–669.

Petchey, O. L. 2000. Prey diversity, prey composition, and predator population dynamics in experimental microcosms. Journal of Animal Ecology 69:874–882.

Petchey, O. L., P. T. McPhearson, T. M. Casey, & P. J. Morin. 1999. Environmental warming alters food-web structure and ecosystem function. Nature 402:69–72.

Portner, H. O., and A. P. Farrell. 2008. Physiology and climate change. Science 322:690–692.

Romero, G. Q., & D. S. Srivastava. 2010. Food-web composition affects cross-ecosystem interactions and subsidies. Journal of Animal Ecology 79:1122–1131.

Schimel, J. P., & S. Hättenschwiler. 2007. Nitrogen transfer between decomposing leaves of different N status. Soil Biology and Biochemistry 39:1428–1436.

Sentis, A., J.-L. Hemptinne, & J. Brodeur. 2014. Towards a mechanistic understanding of temperature and enrichment effects on species interaction strength, omnivory and food-web structure. Ecology Letters 17:785–793.

Sorte, C. J. B., & J. W. White. 2013. Competitive and demographic leverage points of community shifts under climate warming. Proceedings of the Royal Society B: Biological Sciences 280:20130572–20130572.

Srivastava, D. S., J. Kolasa, J. Bengtsson, A. Gonzalez, S. P. Lawler, T. E. Miller, P. Munguia, T. Romanuk, D. C. Schneider, & M. K. Trzcinski. 2004. Are natural microcosms useful model systems for ecology? Trends in Ecology & Evolution 19:379–384.

Stocker, T., editor. 2014. Climate change 2013: the physical science basis: Working Group I contribution to the Fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York.

Tilman, D. 2001. Functional diversity. - In: Levin, S. A. (ed.), Encyclopedia of biodiversity. Academic Press, pp. 109-120.

Tilman, D., P. B. Reich, & F. Isbell. 2012. Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. Proceedings of the National Academy of Sciences 109:10394–10397.

Tiunov, A. V., & S. Scheu. 2005. Facilitative interactions rather than resource partitioning drive diversity-functioning relationships in laboratory fungal communities. Ecology Letters 8:618–625.

Violle, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, & E. Garnier. 2007. Let the concept of trait be functional! Oikos 116:882–892.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, & F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389–395.

Webb, B. W., & F. Nobilis. 1997. Long-term perspective on the nature of the air–water temperature relationship: a case study. Hydrological Processes 11:137–147.

Woodward, G., D. M. Perkins, & L. E. Brown. 2010. Climate change and freshwater ecosystems: impacts across multiple levels of organization. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2093–2106.

Zarnetske, P. L., D. K. Skelly, & M. C. Urban. 2012. Biotic multipliers of climate change. Science 336:1516–1518.

2. CAPÍTULO 1

WARMING, LITTER QUALITY AND FUNCTIONAL DIVERSITY SHAPE COMMUNITY STRUCTURE IN A FRESHWATER ECOSYSTEM

Warming, litter quality and functional diversity shape community structure in a freshwater ecosystem

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2.1 Abstract

Climate warming and biodiversity shifts are the main threats ecosystems are facing in current era. Changes in plant species composition, along with climate-induced alterations in plant traits, are expected to alter the quality and functional diversity of litter with direct or indirect impacts on the communities of consumers. However, little is known on the importance of litter traits and how they interact with warming to affect the structuring of communities. In this study, we used natural aquatic microcosms to investigate the individual and interactive effects of warming and changes in litter quality and functional diversity on richness, abundance, evenness and composition of aquatic invertebrates. Warming reduced richness and evenness of filter feeders (Culicidae) while increased abundance of detritivores. Both filter feeders and detritivores abundance negatively correlated with increasing litter lignin, but positively correlated with increasing litter functional diversity, as represented by higher dissimilarities in C, N and C:N ratio. Litter quality and functional diversity indirectly affected predators via detritivores (detritivores + filter feeders) abundance. In addition, litter quality, represented by high contents of N, P as opposed to high contents of secondary compounds, explained variation in insect composition. Our results demonstrate that warming, along with the distinct aspects of litter traits drive the structure of detrital-based communities.

Keywords: climate change, leaf litter diversity, resource complementarity, litter traits, aquatic microcosms, aquatic invertebrates

2.2 Introduction

Earth surface temperature increased by around 0.8ºC over the last century and it is expected to rise more 2-4ºC by the year 2100 (IPCC 2013). Climate warming is expected to have strong impacts on organisms, by changing their body size, distribution, phenology and abundance, and hence affecting species interactions (Petchey et al. 1999; Walther et al. 2002; Parmesan 2006; Dawson et al. 2011; Gardner et al. 2011). Since temperature play a key role in determining ecological communities, it should be expected substantial impacts of warming in the structure of communities and food webs (Woodward et al. 2010).

Aquatic environments, such as freshwater ecosystems, are particularly vulnerable to warming, since their communities are mainly composed by organisms whose physiological activities are directly dependent on temperature (Pörtner and Farrell 2008) and indirectly on oxygen concentrations (Foster, Hirst and Atkinson 2012). Moreover, temperature plays a key role in controlling individual metabolic rate (Brown et al. 2004), so it could be expected that climate warming would profoundly affect reproduction, development, growth and behavior of several organisms, with cascading effects to ecosystem functioning (Woodward et al. 2010). Indeed, experimental studies using protist assemblages revealed substantial effects of warming on community structure, which influenced the ecosystem functioning due to changes in the relative abundance of functional groups (Petchey et al. 1999; Petchey et al. 2000). Similarly, Dang et al. (2009) have shown that warming altered litter decomposition through shifts in fungal communities. Although the effects of increasing temperature are relatively well known at the organismal level, little is known about their effects at higher levels of ecological organization, such as communities and ecosystems (Woodward et al. 2010). Understanding how climate warming affects community structuring is essential in order to predict the responses in ecosystem functions and services.

In many aquatic ecosystems, such as streams, ponds and phytotelmata, the main energy source are the allochthonous inputs of organic material, such as leaf litter, which fuels complex food webs and ecosystem processes (Cummins 1974; Oertli 1993; Polis et al. 1997; Romero and Srivastava 2010). Since plant species differ in chemical and physical traits and these differences remain in the dead parts of plants, as in leaf litter, one should expect contrasting effects of such interspecific variations on litter consumers, and hence on decomposition process and energy flow (Gessner et al. 2010 and citations therein). While some litter species are soft and nutrient-rich, others have high contents of lignin and secondary compounds (Gessner et al. 2010). This suite of characteristics determines the litter quality and have been shown to play a key role in the structuring of communities and decomposition, at both aquatic and terrestrial environments (Rubbo and Kiesecker 2004; Ilieva-Makulec et al. 2006). Indeed, studies addressing different questions on community structure (e.g., growth, development or survival) of aquatic invertebrates and vertebrates revealed substantial impacts of litter quality (Cohen et al. 2014; Stoler and Relyea 2013, 2016; Migliorini et al. 2018). However, it has been argued that litter functional diversity drive the structure of detritivores and decomposer communities, as increased dissimilarity of litter traits would reduce niche overlap and allow species to avoid competition for the resource pool (Tilman 1999; Grime 2006; Cardinale et al. 2011). Although several studies evaluated the role of quality or functional diversity of leaf litter on decomposition (Heemsberg et al. 2004; Cornwell et al. 2008; Makkonen et al. 2012; Barantal et al. 2014; Frainer et al. 2015; García-Palacios et al. 2015), few investigated the contrasting effects of litter quality and functional diversity on community structuring (Reiskind et al. 2009; Stoler and Relyea 2013, 2016; Migliorini et al. 2018). It is more common to find studies that sought to contrast mass-ratio hypothesis and functional diversity on decomposition (Bilá et al. 2014; García-Palacios et al 2017). However, to account for the mass-ratio hypothesis it is necessary to have real differences in litter species abundances (Grime 1998). Understanding how litter traits affect detritus-based communities is of crucial importance to predict the impacts of biodiversity loss and climate change in both aquatic and terrestrial environments.

The predicted increase of atmospheric carbon dioxide (CO_2), which is one of the main drivers of climate warming, is expected to alter the chemical and physical characteristics of plant leaves, and such changes should be reflected in leaf litter (Tuchman et al. 2002). Studies examining the CO_2-induced shifts in leaf traits observed a decrease in nutrient contents (e.g., nitrogen) and an increase in the contents of structural and secondary compounds (Lambers 1993; Cotrufo et al. 1998). Thus, besides the modifications in plant species composition caused by biodiversity loss, the CO_2-induced changes in plant traits could further strengthen the impacts on detrital-based food webs.

Since climate warming and changes in litter composition occurs simultaneously, understanding their interactive effects on community structuring is essential in order to predict the impacts on ecosystem functioning. In this study, we tested the individual and interactive effect of warming and changes in litter composition (quality and functional diversity) on the structuring of three different trophic levels of aquatic insects (filter feeders, detritivores and predators). We used a trait-based approach to evaluate the role of quality and functional diversity of leaf litter on the abundance, richness, evenness and composition of aquatic invertebrates. As model system, we used tank bromeliads, which is a very suitable model for ecological experiments, because their small size allow high replicability and manipulation, while houses complex food webs (Srivastava et al. 2004). We hypothesized that both quality and functional diversity would explain the structure of filter feeders and detritivores, and warming should affect such responses. Specifically, we predicted that increasing litter quality (e.g., high contents of N and P) would positively correlate with invertebrate abundance, richness and evenness, as opposed to litter with high lignin contents and secondary compounds (Gessner et al. 2010 and citations therein). On the other hand, higher litter functional diversity (i.e., trait dissimilarity) would increase invertebrate abundance, richness and evenness mainly by increasing the variety of resources and reducing niche overlap and competition (Tilman 1999, Grime 2006). However, warming may negatively affect filter feeders and detritivores by changing species interactions, such as increased predator pressure (Blois et al. 2013). For predators, we predict indirect effects of litter components mediated by filter feeders and detritivores, and a direct effect of warming, as higher trophic levels may be more vulnerable to changes in temperature (Petchey et al. 1999; Estes et al. 2011). We also predicted that warming and litter components would explain differences in invertebrate composition.

2.3 Methods

Study area and model system

Our study took place from April to July 2015 in a coastal sand-based (i.e., *Restinga*) forest at Serra do Mar State Park - Núcleo Picinguaba (23°21’27” S, 44°51’01” W), an Atlantic forest conservation area in the north coast of São Paulo state, Brazil. The restinga forest at our site is composed by trees of about 15 m tall sharing the substrate mainly with bromeliads and orchids. One of the most abundant tank bromeliad, *Neoregelia johannis* (Carriére) L. B. Smith. (Bromeliaceae) can hold more than two liters of water in the tanks formed by their leaves (Cogliatti-Carvalho et al. 2010). Bromeliads are very suitable ecosystem models to test various ecological theories, from communities to ecosystem level (Srivastava et al. 2004). This plant grows on the ground or as epiphytic on trees, accumulating water and organic material (e.g., leaf litter) that fall from the surrounding trees. Leaf litter is the main resource for decomposers and detritivorous insects living in bromeliads at our site. A wide diversity of micro and macroorganisms house this aquatic microecosystem, mainly insect larvae from different functional groups, like predators, detritivores and filter-feeders (Romero and Srivastava 2010; Migliorini et al. 2018).

Leaf litter collecting and chemical analysis

We chose 12 native tree species from closed restinga that are abundant at the fieldsite. The included species were *Jacaranda puberula* (Cham.), *Inga subnuda* (Salzm.), *Alchornea triplinervia* (Spreng.), *Pera glabrata* (Schott), *Myrcia glabra* (O. Berg), *Myrcia racemosa* (O. Berg), *Andira anthelmia* (Vell.), *Abarema brachystachia* (DC.), *Cupania oblongifolia* (Mart.), *Miconia* sp., *Lacistema* *pubescens* (Mart.), *Inga edulis* (Mart.). We cut branches of each species and air-dried at room temperature until the leaves fall for use in the chemical analysis and in the experiment. Carbon and nitrogen content were quantified by dry combustion in an elemental analyser (Perkin Elmer 2400 II CHN) and phosphorus content through colorimetry by vanadate-molybdate method (Sarruge and Haag 1974). Using this data we calculated C:N and N:P ratios for each litter species. We quantified lignin content with the acid-detergent method (Robertson and Van Soest 1981). In addition, we quantified litter tannins and phenolics using the Folin-Ciocalteu method, as described by Makkar et al. (1993). Carbon and nitrogen analysis were performed at the Analytical Center of the Institute of Chemistry – University of Campinas. Lignin, phosphorus, tannins and phenolics were analyzed at the Center of Nuclear Energy in Agriculture (CENA) – University of São Paulo.

Defining litter treatments and accessing quality and functional diversity

In order to visualize differences in terms of traits between litter species, we conducted a principal component analysis (PCA; Appendix S1: Fig. S1; Appendix S2: Table S1), by which it was possible to determine five litter treatments (hereafter LT; each one containing four litter species) according to the position of each litter species in the trait space. We selected our LTs following a gradient of quality (i.e., resource ranging from low to high quality for consumers) based on traits where high concentrations would be positive or detrimental for litter consumers. The LT1 included *C. oblongifolia*, *P. glabrata*, *A. triplinervia* and *Miconia* sp., LT2 included *L. pubescens*, *M. glabra*, *J. puberula* and *M. racemosa*. The LT3 was composed by *L. pubescens*, *J.*

puberula, *A. brachystachia* and *M. racemosa*. LT4 contained *C. oblongifolia*, *J. puberula*, *I. subnuda*, *A. brachystachia*. Finally, the LT5 included *I. subnuda*, *A. anthelmia*, *A. brachystachia* and *I. edulis*.

To evaluate the role of litter quality in shaping invertebrate communities, we calculated the mean trait values of each trait in each litter treatment and standardized the values using *Z*-scores. Then we conducted a principal component analysis (PCA) using our mean trait matrix (Fig. 1a). The quality of each LT was then assessed by retaining the first two PCA axes, which captures most of the variance in mean trait values. The first principal component of quality (hereafter Quality1) had a positive loading of N and P, and negative loadings of phenolics, tannins and C:N ratios. The second principal component of quality (hereafter Quality2) was positively loaded by lignin and negatively loaded by N:P ratio. To assess the importance of litter functional diversity in structuring invertebrate communities, we calculated Rao's quadratic entropy (Rao's Q) for each trait in each LT followed by a PCA on *Z*-scored Rao's Q values and then retaining the first two axes (Fig. 1b). Using this metric of functional diversity, we assume that trait differences between litter species shapes aquatic invertebrate communities through niche differentiation related to resource availability (Tilman 1999; Botta-Dukat 2005).

Experimental design

We explored the effects of warming and litter differing in quality and functional diversity on the assemblage of aquatic invertebrate communities associated to bromeliads. To simulate global warming we used an electronic heating system composed by pre-programmed controllers connected to a digital display for temperature monitoring. The heating equipment was composed of five boxes (containing the electronic components) connected one to another. Each component box represented an experimental block and was responsible for accessing and controlling the temperature of 10 bromeliads (five with ambient temperature and five warmed). We used submersible water heaters (1W) in half of bromeliads of each block to maintain a continuous 4 °C increase above the ambient temperature of unheated bromeliads. This increase in the temperature was achieved by submersible sensors in the unheated bromeliads, which switched on and off the heaters through the controllers. The temperature difference used in this experiment followed the projections of temperature increase in the southeastern region of Brazil over the next century (IPCC 2013). We used 50 tank-bromeliads *Neoregelia johannis* acquired from a greenhouse in order to ensure all plants had similar sizes and water storage capacities and were virtually free of colonizing organisms. Before starting the experiment, we washed the bromeliads with spring water and solutions of antibiotics and 5% sodium hypochlorite to remove undesirable invertebrates and bacteria. We planted the bromeliads in the ground of the restinga following a randomized block design (n =5) and installed plastic roofs over each plant to prevent any input of rain and organic matter like branches and fallen leaves from trees. To keep the water level constant, we watered the bromeliads at 1-day intervals. In each block, we placed four grams of oven-dried litter (60ºC; 1 ± 0.05 g of each species of each LT) in the bromeliads wells, repeating the treatment in warmed and ambient bromeliads.

Data analysis

All data analyzes were carried out using R version 3.2.2 (R Core Team, 2016). To investigate how warming, litter quality and functional diversity affected the structure of aquatic invertebrate communities, we used linear mixed effects models using lme function in *nlme* package. Specifically, we used different analyses to evaluate the effects of our predictor variables on the richness, evenness and abundance of filter feeders (Culicidae), detritivores (e.g., Chironomidae, Ceratopogonidae and Scirtidae), and predators (e.g., Coenagrionidae and Dytiscidae). We analyzed these three groups of invertebrates separately because they represent different compartments of bromeliad food webs. Because quality and functional diversity components are mathematically related, as they represent mean and dispersion (Ricotta and Moretti 2011), we conducted separate models for each metric to better evaluate their effects on community structuring. Filter feeders and detritivores models were composed by the additive terms for litter effects (quality or functional diversity component axes) and temperature, and interaction of litter effects and temperature. Models were tested with type-III Anova implemented in the *car* package. For predators, we fitted piecewise structural equation models (Lefcheck 2016) to each community response and each litter effect (quality and functional diversity). Specifically, we use piecewiseSEM R-package to investigate whether warming, litter quality and functional diversity affected abundance, richness and evenness of predators. Warming was included as direct effect, but the effects of litter components were investigated as indirect effects by influencing detritivores abundance and richness (detritivores + filter feeders). SEM models were fitted using linear mixed effect models (lme) with block as random effect. We presented the standardized coefficient for each path and estimated the indirect effects through coefficient multiplication. We assessed the fit of the piecewiseSEM by using Shipley's test of d-separation through Fisher's C statistic and AIC.

To access the importance of each litter effect (quality and FD), we compared the AIC values of each model when both had significant litter effects. Before conducting the analyses, we verified normality and homoscedasticity of data, removing influential data when detected.

To test and visualize effects of warming and litter component axes on the composition of macroinvertebrates, we conducted canonical correspondence analyses (CCA) using the *vegan* package.

2.4 Results

We collected 5462 individuals of aquatic macroinvertebrates distributed in 34 morphospecies (Appendix S2: Table S2). Our results shown that warming reduced richness and evenness of filter feeders, but increased the abundance of detritivores (Figs. 2a-c; Table 2). Filter feeders and detritivores abundance negatively correlated with increasing litter lignin (Quality2: r = -0.28; Fig. 3a and r = -0.34; Fig. 3c, respectively; Table 2) and positively correlated with increasing litter C, N and C:N ratios dissimilarities (FD1: r = 0.27; Fig. 3b and r = 0.29; Fig. 3d, respectively; Table 2). Similarly, detritivores abundance was negatively affected by increasing litter lignin (Quality2: r = -0.34; Fig. 3c; Table 2) and positively affected by with increasing litter C, N and C:N ratios dissimilarities (r = 0.29; Fig. 3d; Table 2). Moreover, we found that increasing litter lignin (quality2) indirectly affected predators abundance by reducing detritivores abundance (r = -0.15; Fig.4a). Besides that, we found that increasing litter dissimilarities in C, N and C:N ratio (FD1), indirectly increased predators abundance by increasing abundance of detritivores (*r* = 0.14; Fig. 4b). Additionally, quality2 and FD1 indirectly affected detritivores richness by affecting detritivores abundance (Figs. 4a-b). Predator richness and evenness were not affected in the SEM models (Figs. 4c-d). Increasing litter lignin positively correlated with detritivores richness (fig. 4a), while increasing litter dissimilarities in C, N and C:N ratios negatively correlated with detritivores richness (Fig. 4b). Litter quality was the strongest driver of differences in detritivores abundance (quality AIC: 430.7 v.s FD AIC: 434.5). For filter feeders abundance, quality and functional diversity had similar importance (AIC: 393.5 and 394.5, respectively). Finally, we examined whether our litter effects and warming determined the composition of aquatic invertebrates. The CCA model for litter quality revealed that the quality1 axis (permutational anova on CCA, $F_{1,44}$ = 1.57, *p* = 0.01; Fig. 5), but not quality2 ($F_{1,44}$ = 1.22, *p* = 0.17), explained variation in macroinvertebrate composition. The CCA model for litter functional diversity showed no effect of FD axes on insect composition (FD1: $F_{1,46}$ = 1.27, *p* = 0.09; FD2: $F_{1,42}$ = 1.08, *p* = 0.38), but a significant effect of temperature ($F_{1,46}$ = 2.39, *p* = 0.001).

2.5 Discussion

Our study shows that warming and leaf litter composition can have substantial impacts on freshwater invertebrate communities. Partitioning litter effects in quality and functional diversity by summarizing their trait syndromes along two trait axes allowed understanding differences in richness, abundance, evenness and composition of aquatic insects. Overall, both litter effects explained patterns of community structure in bromeliad communities, but their importance may depend on the organisms involved. To our knowledge, this is the first study exploring the interactive effects of warming and changes in litter composition on the structure of aquatic communities.

Although the effects of litter diversity on decomposition are well documented (Gessner et al. 2010 and citations therein), few studies investigated how litter traits shape communities that depend on this resource (Stoler and Relyea 2016, Stoler et al. 2016; Migliorini et al. 2018). In our study, both detritivores and filter feeders abundance decreased with decreasing litter quality, as represented by high lignin contents. It is well documented in the literature that lignin hinders litter processing by invertebrates and decomposers (Gessner et al. 2010 and citations therein). High lignin contents could inhibit the direct litter consumption of specific taxa, or by hindering the action of microorganisms that condition the litter for detritivores consumption, increasing their mortality (Hättenschwiller and Bretscher 2001). Moreover, increasing litter dissimilarities of C, N and C:N ratio increased the abundance of detritivores and filter feeders. Such effect is probably related to increased variation of resource availability and reduced niche overlap (Tilman 1999, Grime 2006, Barantal et al. 2014), even though litter functional diversity did not affect the richness of detritivores and filter feeders. Our results show that increasing litter lignin (i.e., reducing litter quality) may indirectly decrease predator abundance by reducing the abundance of prey. The negative effects of lignin in suppressing the activity of decomposers and detritivores are well documented (Hättenschwiller and Bretscher 2001; Ríncon and Martinez 2006), but the indirect effect on predators has never been demonstrated. Moreover, our results shown that increasing litter dissimilarities in C, N and C:N ratios may indirectly increase predator abundance by increasing detritivores abundance. The mechanism behind the litter functional diversity effect on detritivores is described above. The predicted temperature increase for 2100 and that was used in our experiment (+ 4 ºC; IPCC 2013) represents a variation that is typical in the annual temperature range at our study site. Therefore, warming is unlikely to exceed organisms' physiological thresholds and such effects on species richness are more likely to be associated to changes in species interactions, such as predator-prey interactions (Blois et al. 2013, Barton and Schmitz 2009).

Warming differently affected the aquatic communities in our study. While it reduced filter feeders richness and evenness, the abundance of detritivores increased. This results contradicts a recent meta-analysis where authors found no overall effect of warming (according to future projections) on freshwater species richness and evenness (Gruner et al. 2017). Gruner et al. (2017) analysed data from 187 experiments worldwide looking for patterns in the effects of warming on species diversity across terrestrial, freshwater and marine ecosystems. They suggest that freshwater communities may be resistant or resilient to changes in temperature. The same explanation was used by Antiqueira et al (2018), who manipulated warming and predator diversity to evaluate the effects on bromeliad aquatic communities but did not detect an effect of warming on invertebrate communities. Both decreasing in filter feeders richness and evenness indicate that dominant species were more impacted by warming, as the loss of rare species should increase the evenness (Gruner et al. 2017). This is particularly relevant since the loss of rare species may increase the risks of local extinctions (Hillebrand et al. 2008). Moreover, decreasing species evenness may have negative effects on ecosystem functioning when it is controlled by synergistic interactions, because such interactions fails if one species completely dominates the assemblage (Zimmer et al. 2005; Hillebrand et al. 2008).

Our study revealed a strong effect of warming on the composition of invertebrate communities. Such changes related to species abundances are more likely to be associate to temperature-induced shifts in species interactions, such as intensified predation (Blois et al. 2013). Warming increased the abundance of detritivores and predators and may have intensified prey consumption to supply the metabolic demands (Vusic-Pestic et al. 2011; Zarnetske et al. 2012). It has been argued that higher trophic levels may be more sensitive to climate warming, which may lead to intensified trophic cascades and stronger control by top consumers (Hoekman 2010; Harley 2011; Kratina et al. 2012; Zarnetske et al. 2012). Moreover, we found that invertebrate composition was strongly determined by litter quality, represented by a gradient of high contents of N and P, as opposed to high contents of phenolics, tannins and C:N ratio. The importance of litter nutrient contents have long been demonstrated in both aquatic and terrestrial ecosystems, and for several community responses (Dudgeon, Ma, and Lam 1990; Hättenschwiller and Bretscher 2001; Cohen et al. 2014; Tuchman et al. 2003). Secondary compounds has been shown to decrease microbial colonization (Canhoto and Graça 1999), feeding by insects (Rincón and Martínez 2006) and have substantial detrimental impacts on organismal survival and development (Maerz et al 2005; Stoler and Relyea 2016). We suggest that litter quality may affect insect composition in different ways. First, the suite of chemical traits can act as an ecological filter causing differential survival of some insect groups (Letts et al. 2015). A recent study has empirically demonstrated that while the survival of scirtid bettles and a caddisfly were unaffected by litter type and chemical composition, the survival of chironomids was (Migliorini et al. 2018). Furthermore, adults looking for the appropriate ovipositing site could anticipate litter quality effects (Reiskind et al. 2009; Riesch et al. 2007; Trexler, Apperson, and Schal, 1998).

This study demonstrates that the predicted increase in temperature may interact with changes in litter diversity to affect community structuring in freshwater ecosystems. In addition, we provide clear evidence that both litter quality and functional diversity may drive freshwater community responses. Despite the small size of bromeliad systems, they have proven to be appropriate models to investigate a wide range of ecological questions, including that of climate change and anthropogenic-induced stressors (Marino et al. 2017; Antiqueira et al. 2018; Bernabé et al. 2018; Pires et al. 2018). We emphasize that our findings should not be restricted to bromeliad systems because many other freshwater, detritus-based ecosystems, such as streams, ponds and lake, are susceptible to the same conditions and stressors. Our results highlight the importance in understanding the mechanisms behind biodiversity loss effects in order to predict the potential impacts of climate change on communities and ecosystems.

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2.6 References

Antiqueira, P. A. P., O. L. Petchey, V. P. dos Santos, V. M. de Oliveira, and G. Q. Romero. 2018. Environmental change and predator diversity drive alpha and beta diversity in freshwater macro and microorganisms. Global Change Biology 24:3715–3728.

Barantal, S., H. Schimann, N. Fromin, and S. Hattenschwiler. 2014. C, N and P fertilization in an Amazonian rainforest supports stoichiometric dissimilarity as a driver of litter diversity effects on decomposition. Proceedings of the Royal Society B: Biological Sciences 281:20141682–20141682.

Barton, B. T., and O. J. Schmitz. 2009. Experimental warming transforms multiple predator effects in a grassland food web. Ecology Letters 12:1317–1325.

Bernabé, T. N., P. M. de Omena, V. P. dos Santos, V. M. de Siqueira, V. M. de Oliveira, and G. Q. Romero. 2018. Warming weakens facilitative interactions between decomposers and detritivores, and modifies freshwater ecosystem functioning. Global Change Biology 24:3170–3186.

Blois, J. L., P. L. Zarnetske, M. C. Fitzpatrick, and S. Finnegan. 2013. Climate change and the past, present, and future of biotic interactions. Science 341:499–504.

Botta-Dukát, Z. 2005. Rao’s quadratic entropy as a measure of functional diversity based on multiple traits. Journal of Vegetation Science 16:533–540.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. Ecology 85:1771–1789.

Canhoto, C., and M. A. S. Graça. 1999. Leaf barriers to fungal colonization and shredders (Tipula lateralis) consumption of decomposing eucalyptus globulus. Microbial Ecology 37:163–172.

Cardinale, B. J., K. L. Matulich, D. U. Hooper, J. E. Byrnes, E. Duffy, L. Gamfeldt, P. Balvanera, M. I. O’Connor, and A. Gonzalez. 2011. The functional role of producer diversity in ecosystems. American Journal of Botany 98:572–592.

Cogliatti-Carvalho, L. Rocha-Pessôa, T.C., Nunes-Freitas, A.F., & Rocha, C.F.D.(2010). Volume de água armazenado no tanque de bromélias, em restingas da costa brasileira. *Acta Bot. Bras.*, 24, 84-95.

Cohen, J. S., S.-K. D. Rainford, and B. Blossey. 2014. Community-weighted mean functional effect traits determine larval amphibian responses to litter mixtures. Oecologia 174:1359–1366.

Cornwell, W. K., J. H. C. Cornelissen, K. Amatangelo, E. Dorrepaal, V. T. Eviner, O. Godoy, S. E. Hobbie, B. Hoorens, H. Kurokawa, N. Pérez-Harguindeguy, H. M. Quested, L. S. Santiago, D. A. Wardle, I. J. Wright, R. Aerts, S. D. Allison, P. van Bodegom, V. Brovkin, A. Chatain, T. V. Callaghan, S. Díaz, E. Garnier, D. E. Gurvich, E. Kazakou, J. A. Klein, J. Read, P. B. Reich, N. A. Soudzilovskaia, M. V. Vaieretti, and M. Westoby. 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecology Letters 11:1065–1071.

Cotrufo, M. F., P. Ineson, and A. Scott. 1998. Elevated CO2 reduces the nitrogen concentration of plant tissues. Global Change Biology 4:43–54.

Cummins, K. W. 1974. Structure and Function of Stream Ecosystems. BioScience 24:631–641.

Dang, C. K., M. Schindler, E. Chauvet, and M. O. Gessner. 2009. Temperature oscillation coupled with fungal community shifts can modulate warming effects on litter decomposition. Ecology 90:122–131.

Dawson, T. P., S. T. Jackson, J. I. House, I. C. Prentice, and G. M. Mace. 2011. Beyond Predictions: Biodiversity Conservation in a Changing Climate. Science 332:53–58.

Dudgeon, D., H. H. T. Ma, and P. K. S. Lam. 1990. Differential palatability of leaf litter to four sympatric isopods in a Hong Kong forest. Oecologia 84:398–403.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. E. Sinclair, M. E. Soulé, R. Virtanen, and D. A. Wardle. 2011. Trophic downgrading of planet earth. Science 333:301–306.

Frainer, A., M. S. Moretti, W. Xu, and M. O. Gessner. 2015. No evidence for leaf-trait dissimilarity effects on litter decomposition, fungal decomposers, and nutrient dynamics. Ecology 96:550–561.

Forster, J., A. G. Hirst, and D. Atkinson. 2012. Warming-induced reductions in body size are greater in aquatic than terrestrial species. Proceedings of the National Academy of Sciences 109:19310–19314.

García-Palacios, P., B. G. McKie, I. T. Handa, A. Frainer, and S. Hättenschwiler. 2016. The importance of litter traits and decomposers for litter decomposition: a comparison of aquatic and terrestrial ecosystems within and across biomes. Functional Ecology 30:819–829.

García-Palacios, P., E. A. Shaw, D. H. Wall, and S. Hättenschwiler. 2017. Contrasting mass-ratio vs. niche complementarity effects on litter C and N loss during decomposition along a regional climatic gradient. Journal of Ecology 105:968–978.

Gardner, J. L., A. Peters, M. R. Kearney, L. Joseph, and R. Heinsohn. 2011. Declining body size: a third universal response to warming? Trends in Ecology & Evolution 26:285–291.

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

Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. Journal of Ecology 86:902–910.

Grime, J. P. 2006. Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. Journal of Vegetation Science 17:255–260.

Gruner, D. S., M. E. S. Bracken, S. A. Berger, B. K. Eriksson, L. Gamfeldt, B. Matthiessen, S. Moorthi, U. Sommer, and H. Hillebrand. 2017. Effects of experimental warming on biodiversity depend on ecosystem type and local species composition. Oikos 126:8–17.

Harley, C. D. G. 2011. Climate change, keystone predation, and biodiversity loss. Science 334:1124–1127.

Hättenschwiler, S., and D. Bretscher. 2001. Isopod effects on decomposition of litter produced under elevated CO2, N deposition and different soil types. Global Change Biology 7:565–579.

Heemsbergen, D. A. 2004. Biodiversity Effects on Soil Processes Explained by Interspecific Functional Dissimilarity. Science 306:1019–1020.

Hillebrand, H., D. M. Bennett, and M. W. Cadotte. 2008. Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. Ecology 89:1510–1520.

Hoekman, D. 2010. Turning up the heat: Temperature influences the relative importance of top-down and bottom-up effects. Ecology 91:2819–2825.

Ilieva-Makulec, K., I. Olejniczak, and M. Szanser. 2006. Response of soil micro- and mesofauna to diversity and quality of plant litter. European Journal of Soil Biology 42:S244–S249.

IPCC. 2013. Climate Change 2013: The Physical Science Basis. in T. F. Stocker, editor. Contribution of Working Group I to the Fourth Assessment Report of the9 Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK

Kratina, P., H. S. Greig, P. L. Thompson, T. S. A. Carvalho-Pereira, and J. B. Shurin. 2012. Warming modifies trophic cascades and eutrophication in experimental freshwater communities. Ecology 93:1421–1430.

Lambers, H. 1993. Rising CO2, secondary plant metabolism, plant-herbivore interactions and litter decomposition. Pages 263–271 in J. Rozema, H. Lambers, S. C. Van de Geijn, and M. L. Cambridge, editors. CO2 and biosphere. Springer Netherlands, Dordrecht.

Letts, B., E. G. Lamb, J. M. Mischkolz, and J. T. Romo. 2015. Litter accumulation drives grassland plant community composition and functional diversity via leaf traits. Plant Ecology 216:357–370.

Maerz, J. C., C. J. Brown, C. T. Chapin, and B. Blossey. 2005. Can secondary compounds of an invasive plant affect larval amphibians? Functional Ecology 19:970–975.

Makkar, H.P.S., Blummel, M., Borowy, N.K. & BECKER, K. (1993). Gravimetric determination of tannins and their correlation with chemical and protein precipitation methods. Journal of the Science of Food and Agriculture, 61, 161-165.

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

Marino, N. A. C., D. S. Srivastava, A. A. M. MacDonald, J. S. Leal, A. B. A. Campos, and V. F. Farjalla. 2017. Rainfall and hydrological stability alter the impact of top predators on food web structure and function. Global Change Biology 23:673–685.

Migliorini, G. H., D. S. Srivastava, and G. Q. Romero. 2018. Leaf litter traits drive community structure and functioning in a natural aquatic microcosm. Freshwater Biology 63:341–352.

Oertli, B. 1993. Leaf litter processing and energy flow through macroinvertebrates in a woodland pond (Switzerland). Oecologia 96:466–477.

Parmesan, C. 2006. Ecological and Evolutionary Responses to Recent Climate Change. Annual Review of Ecology, Evolution, and Systematics 37:637–669.

Petchey, O. L., P. T. McPhearson, T. M. Casey, and P. J. Morin. 1999. Environmental warming alters food-web structure and ecosystem function. Nature 402:69–72.

Petchey, O. L. 2000. Prey diversity, prey composition, and predator population stability in experimental microcosms. Journal of Animal Ecology 69:874–882.

Pires, A. P. F., D. S. Srivastava, N. A. C. Marino, A. A. M. MacDonald, M. P. Figueiredo-Barros, and V. F. Farjalla. 2018. Interactive effects of climate change and biodiversity loss on ecosystem functioning. Ecology 99:1203–1213.

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics 28:289–316.

Portner, H. O., and A. P. Farrell. 2008. Physiology and Climate Change. Science 322:690–692.

R Development Core Team (2016). R: A language and environmental for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org/

Reiskind, M. H., K. L. Greene, and L. P. Lounibos. 2009. Leaf species identity and combination affect performance and oviposition choice of two container mosquito species. Ecological Entomology 34:447–456.

Riesch, R., Clifton, J., Fischer, J., Forney, A., Geurin, E., Kuzmic, A., ... Spooner, D. (2007). The role of habitat type and nutrient quality on invertebrate dispersal and diversity. Proceedings of the Oklahoma Academy of Science, 87, 89–94.

Rincón, J., and I. Martínez. 2006. Food quality and feeding preferences of Phylloicus sp. (Trichoptera:Calamoceratidae). Journal of the North American Benthological Society 25:209–215.

Robertson, J. B., & Van Soest, P. J. (1981). The analysis of dietary fibre in food. In W. P. T. James & O. Theander (Eds.), The detergent system of analysis (pp. 123–158). New York, NY: Marcel Dekker.

Rockwell, R. F., L. J. Gormezano, and D. N. Koons. 2011. Trophic matches and mismatches: can polar bears reduce the abundance of nesting snow geese in western Hudson Bay? Oikos 120:696–709.

Romero, G. Q., and D. S. Srivastava. 2010. Food-web composition affects cross-ecosystem interactions and subsidies: Cross-ecosystem interactions and subsidies. Journal of Animal Ecology 79:1122–1131.

Rubbo, M. J., and J. M. Kiesecker. 2004. Leaf litter composition and community structure: translating regional species changes into local dynamics. Ecology 85:2519–2525.

Sarruge, J. R. S., & Haag, H. P. (1974). Análises químicas em plantas. Piracicaba, Brazil: USP-ESALQ.

Srivastava, D. S., J. Kolasa, J. Bengtsson, A. Gonzalez, S. P. Lawler, T. E. Miller, P. Munguia, T. Romanuk, D. C. Schneider, and M. K. Trzcinski. 2004. Are natural microcosms useful model systems for ecology? Trends in Ecology & Evolution 19:379–384.

Stoler, A. B., and R. A. Relyea. 2013. Leaf litter quality induces morphological and developmental changes in larval amphibians. Ecology 94:1594–1603.

Stoler, A. B., and R. A. Relyea. 2016. Leaf litter species identity alters the structure of pond communities. Oikos 125:179–191.

Stoler, A. B., D. J. Burke, and R. A. Relyea. 2016. Litter chemistry and chemical diversity drive ecosystem processes in forest ponds. Ecology 97:1783–1795.

Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. Ecology 80:1455.

Trexler, J. D., C. S. Apperson, and C. Schal. 1998. Laboratory and Field Evaluations of Oviposition Responses of Aedes albopictus and Aedes triseriatus (Diptera: Culicidae) to Oak Leaf Infusions. Journal of Medical Entomology 35:967–976.

Tuchman, N. C., R. G. Wetzel, S. T. Rier, K. A. Wahtera, and J. A. Teeri. 2002. Elevated atmospheric CO2 lowers leaf litter nutritional quality for stream ecosystem food webs. Global Change Biology 8:163–170.

Tuchman, N. C., K. A. Wahtera, R. G. Wetzel, N. M. Russo, G. M. Kilbane, L. M. Sasso, and J. A. Teeri. 2003. Nutritional quality of leaf detritus altered by elevated atmospheric CO2: effects on development of mosquito larvae. Freshwater Biology 48:1432–1439.

Vucic-Pestic, O., R. B. Ehnes, B. C. Rall, and U. Brose. 2011. Warming up the system: higher predator feeding rates but lower energetic efficiencies. Global Change Biology 17:1301–1310.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389–395.

Woodward, G., D. M. Perkins, and L. E. Brown. 2010. Climate change and freshwater ecosystems: impacts across multiple levels of organization. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2093–2106.

Zarnetske, P. L., D. K. Skelly, and M. C. Urban. 2012. Biotic multipliers of climate change. Science 336:1516–1518.

Zimmer, M., G. Kautz, and W. Topp. 2005. Do woodlice and earthworms interact synergistically in leaf litter decomposition? Functional Ecology 19:7–16.

2.7 Figures

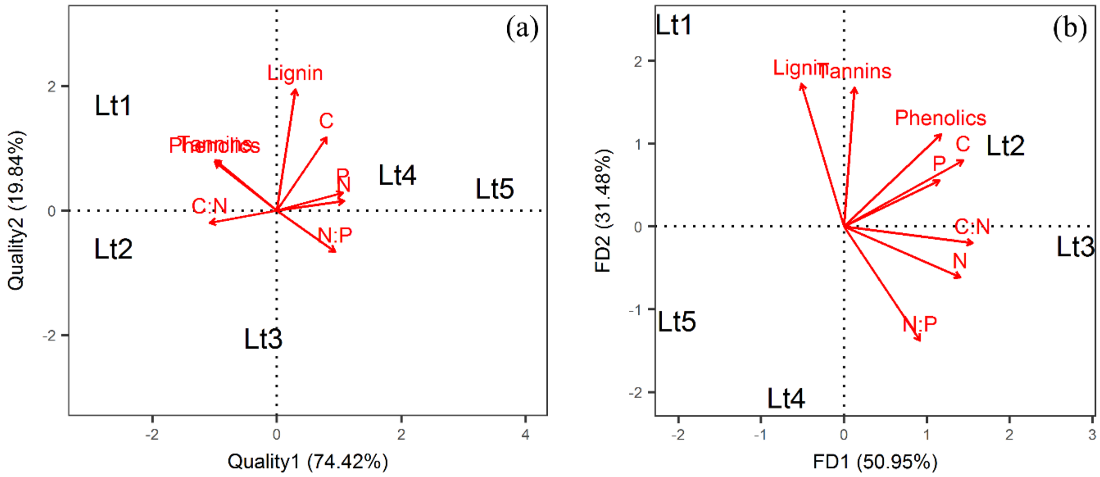


Figure 1. Principal coordinate analyses (PCA) of quality and functional diversity of the five litter treatments. Red arrows represent the loads of correlation between traits and axes. Variance explained by each principal component is shown in brackets.

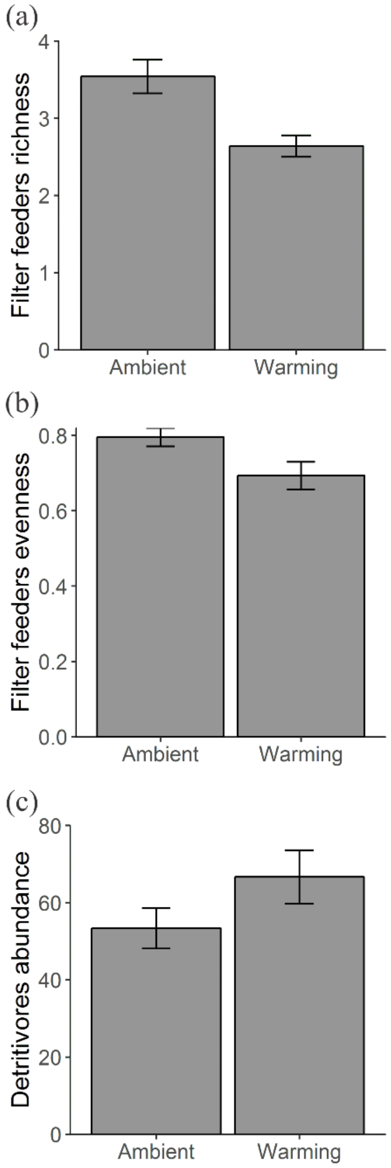


Figure 2. Effect of warming on filter feeders richness and evennes (a-b) and detritivores abundance (c). Bars indicate ±SE.

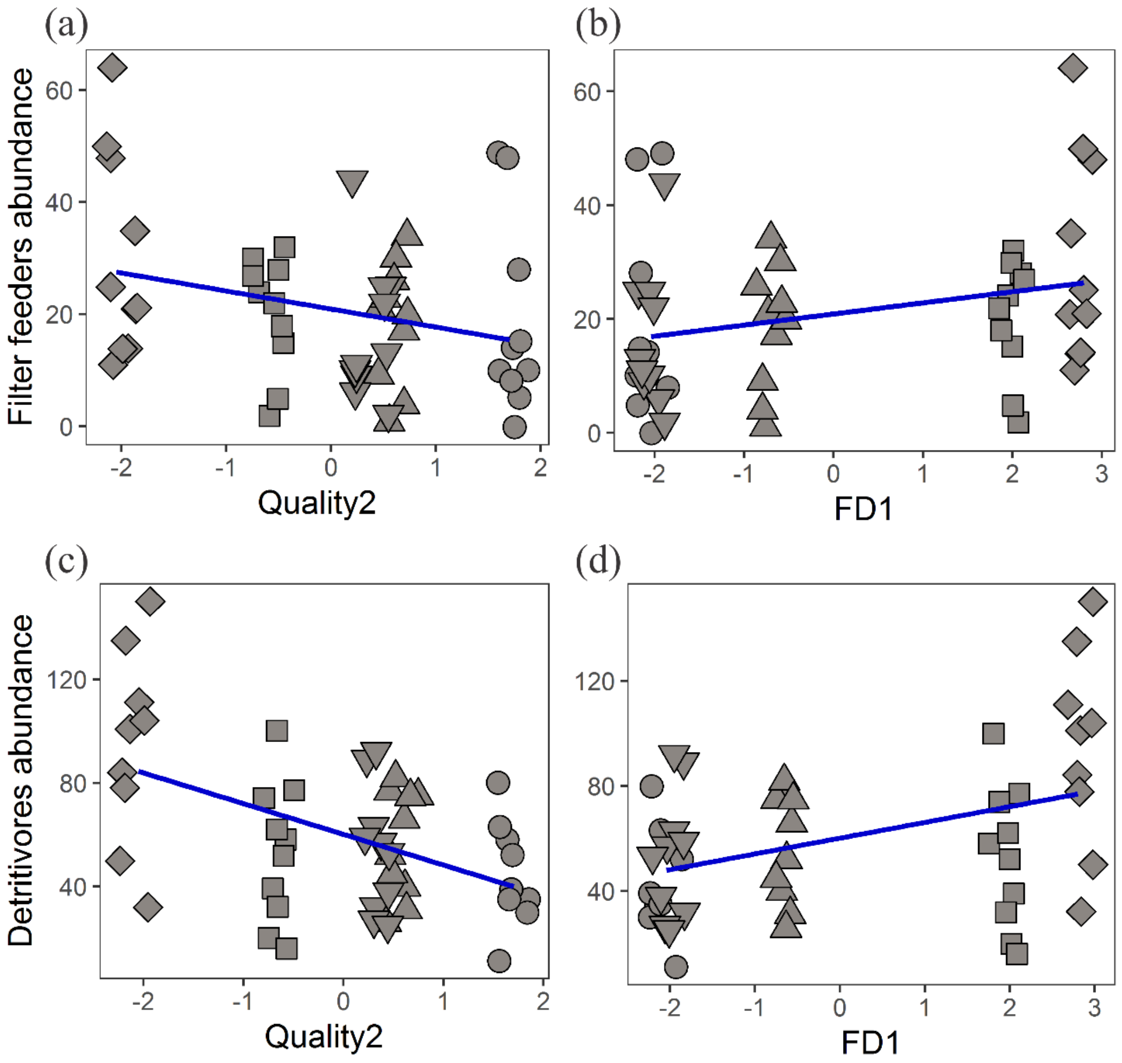


Figure 3. Relationships between (a) filter feeders abundance and the second axis of litter quality, (b) filter feeders abundance and the first axis of litter functional diversity, (c) detritivores abundance and the second axis of litter quality, (d) detritivores abundance and the first axis of litter functional diversity. Circle: LT1, square: LT2, rhombus: LT3, triangle: LT4, inverted triangle: LT5

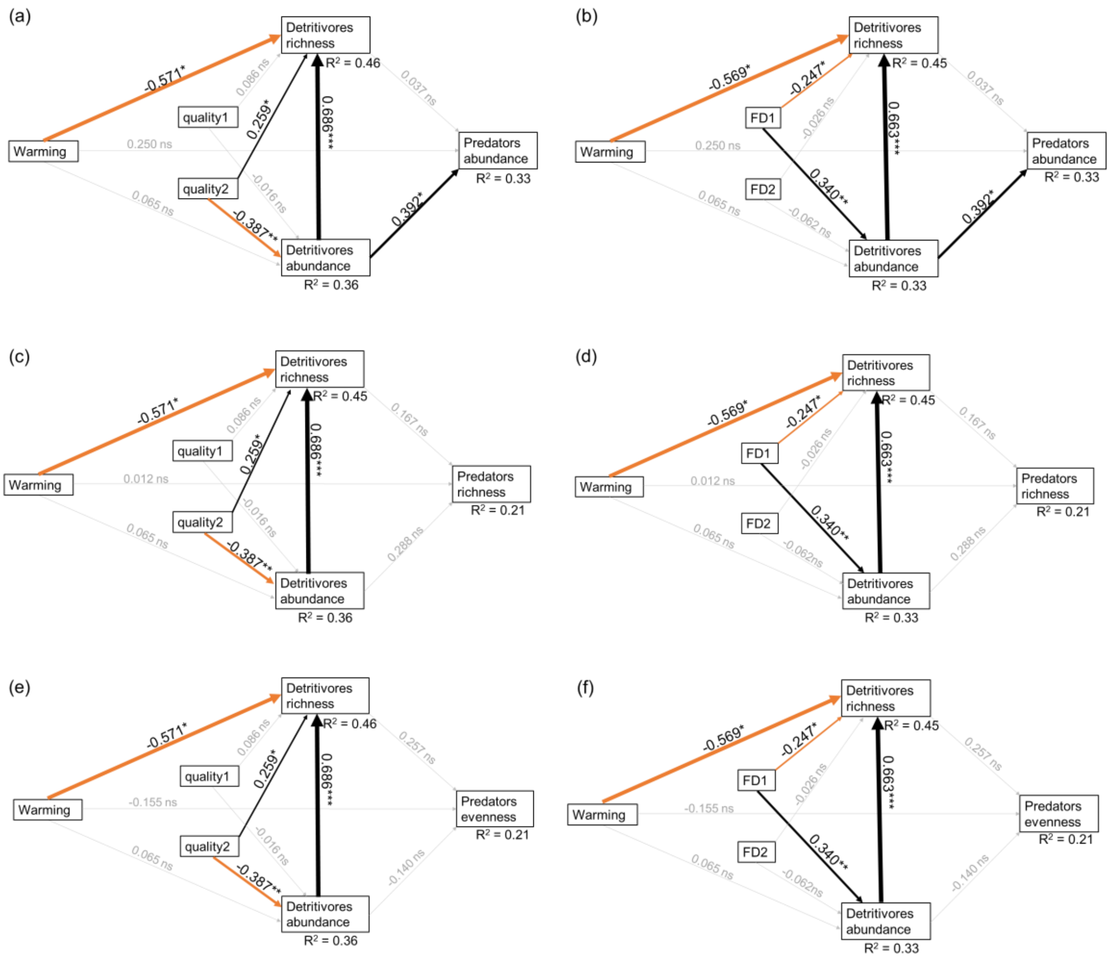


Figure 4. Structural equation models describing de influence of warming, litter quality effects (quality and functional diversity, representing the two first axes of the PCA showed in fig. 1), detritivores (detritivores + filter feeders) richness and abundance on (a-b) predators abundance, (c-d) predator richness and (e-f) predator evenness. The widths of the arrows are proportional do the strengths of the path coefficients. Solid black arrows represent significant positive paths ($P \leq 0.05$). Solid red arrows indicate negative effect. Light gray arrows represent non-significant paths. R^2 for component models are given on the boxes of endogenous variables. Goodness-of-fit tests are: (a) Fishers' C = 7.09, df = 8, $P = 0.131$, $AIC_c = 70.42$. (b) Fisher's C = 4.07, df = 8, $P = 0.396$, $AIC_c = 67.40$. (c) Fishers' C = 0.16, df = 4, $P = 0.997$, $AIC_c = 63.49$. (d) Fishers' C = 1.76, df = 4,

P = 0.781, AIC$_c$ = 65.09. (e) Fishers' C = 21.34, df = 4, *P* = 0, AIC$_c$ = 85.54. (f) Fishers' C = 14.46, df = 4, *P* = 0.006, AIC$_c$ = 78.66.

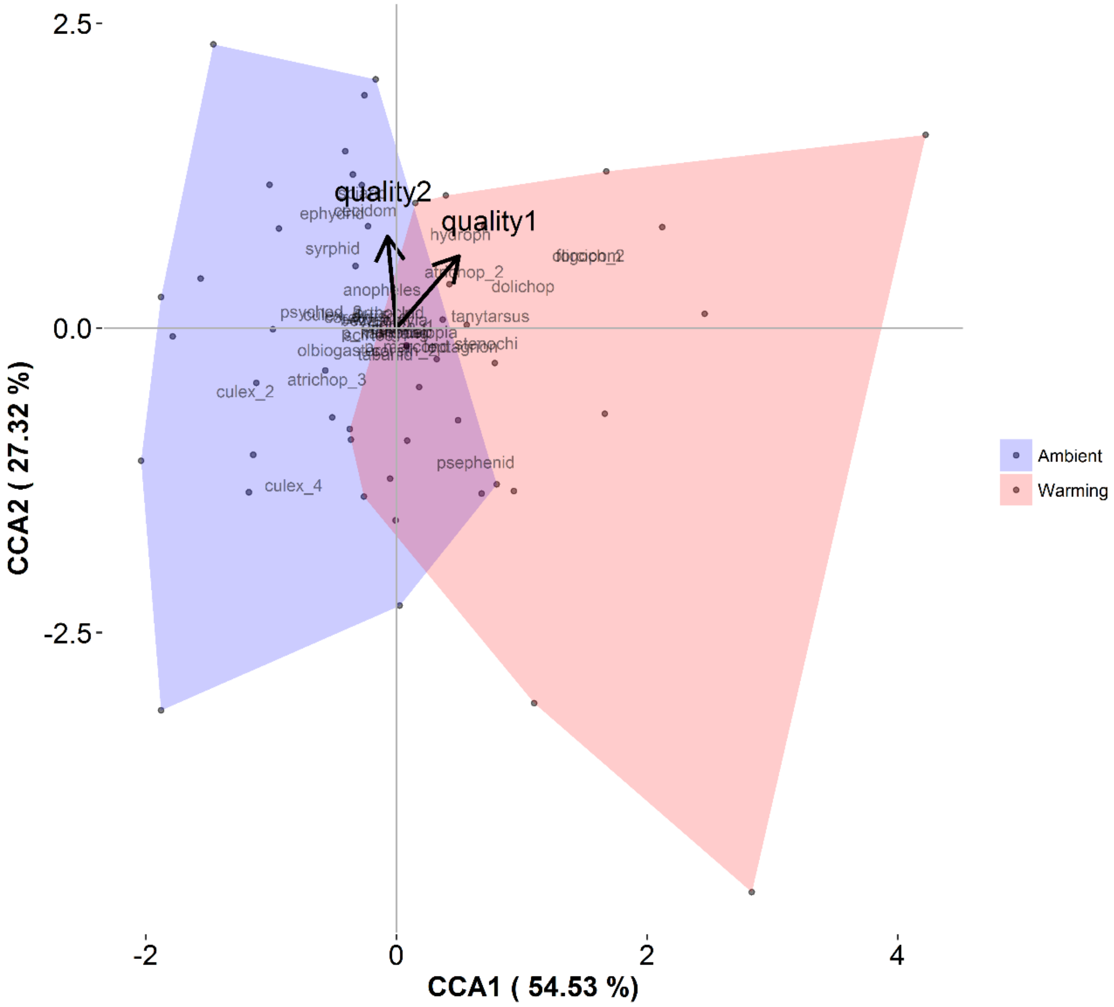


Figure 5. Canonical Correspondence Analysis (CCA) of aquatic insect communities in relation to litter quality. Litter quality is represented by two principal components of a principal component analysis on mean trait values. Increasing quality1 refers to increasing contents of N and P, and decreasing C:N ratios and secondary compounds. Increasing quality2 refers to increasing contents of lignin and decreasing N:P ratios.

2.8 Tables

Table 1. Summary of the principal component analyses for quality and functional diversity of the litter treatments. Values correspond to loadings of traits on the first two axes. Traits that significantly correlate with each axis are shown in bold.

trait	quality1	quality2	FD1	FD2
C	0.30	0.44	**0.45**	0.25
N	**0.41**	0.06	**0.44**	-0.19
P	**0.40**	0.11	0.36	0.17
Lignin	0.11	**0.73**	**-0.16**	**0.54**
Phenolics	**-0.38**	0.30	0.36	0.35
Tannins	**-0.37**	0.30	0.04	**0.52**
C:N	**-0.41**	-0.07	**0.48**	-0.06
N:P	0.35	**-0.25**	0.29	**-0.43**

Table 2. Effects of warming, quality and functional diversity of leaf litter on richness, abundance, and evenness of filter feeders and detritivores. Statistical significance in $p < 0.05$.

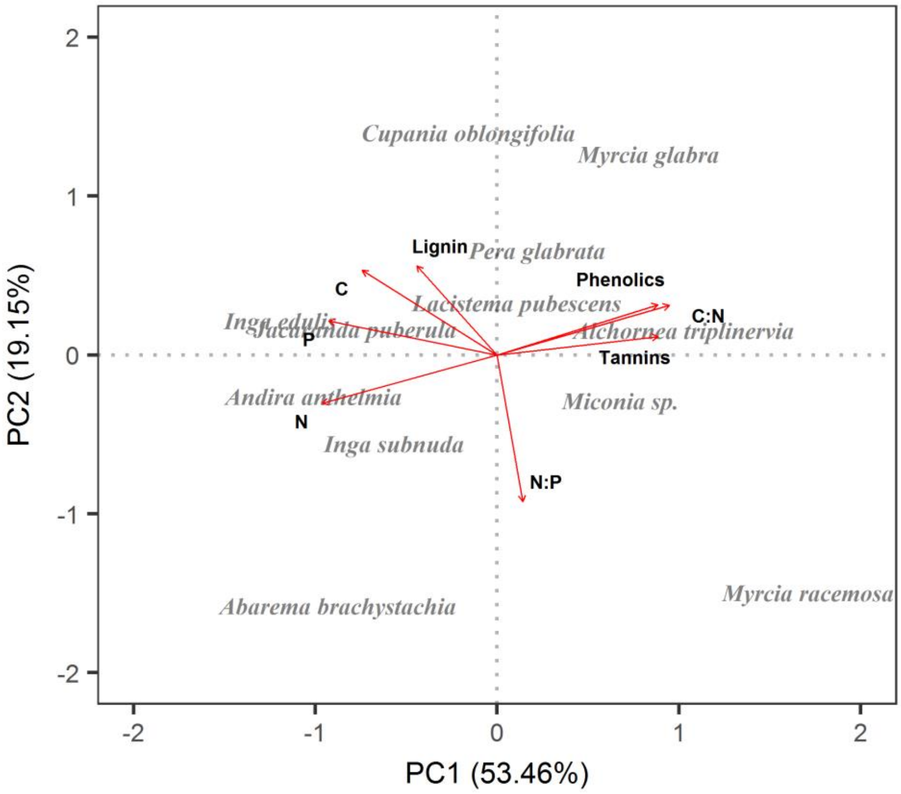
	Fixed effects	**Responses**								
Filter feeders		**Abundance**			**Richness**			**Evenness**		
		Chisq	df	P	Chisq	df	P	Chisq	df	P
Quality model	(Intercept)	46.31	1	<0.001	523.3	1	<0.001	374.5	1	<0.001
	Quality1	1.90	1	0.168	0.001	1	0.976	0.005	1	0.943
	Quality2	4.65	1	**0.031**	1.55	1	0.213	1.46	1	0.226
	Temperature	3.06	1	0.080	9.04	1	**0.003**	6.82	1	**0.009**
	Quality1:temperature	1.73	1	0.188	0.06	1	0.809	1.48	1	0.224
	Quality2:temperature	0.66	1	0.416	0.85	1	0.358	0.000	1	0.992
FD model	(Intercept)	46.07	1	<0.001	526.1	1	<0.001	371.1	1	<0.001
	FD1	5.47	1	**0.019**	1.12	1	0.291	2.28	1	0.130
	FD2	0.55	1	0.458	0.06	1	0.805	0.95	1	0.329
	Temperature	2.99	1	0.083	9.02	1	**0.003**	7.56	1	**0.006**
	FD1:temperature	1.35	1	0.245	0.56	1	0.454	0.45	1	0.502
	FD2:temperature	0.89	1	0.346	0.27	1	0.601	0.58	1	0.447
Detritivores										
Quality model	(Intercept)	49.32	1	<0.001	315.0	1	<0.001	695.1	1	<0.001
	Quality1	0.44	1	0.508	0.10	1	0.753	0.06	1	0.811
	Quality2	7.45	1	**0.006**	0.18	1	0.676	0.71	1	0.399
	Temperature	4.63	1	**0.031**	0.99	1	0.318	1.45	1	0.229
	Quality1:temperature	0.09	1	0.759	0.00	1	0.987	0.27	1	0.602
	Quality2:temperature	0.18	1	0.674.	1.60	1	0.206	0.62	1	0.430
FD model	(Intercept)	46.58	1	<0.001	320.6	1	<0.001	691.9	1	<0.001
	FD1	5.27	1	**0.022**	0.37	1	0.543	0.56	1	0.456
	FD2	2.08	1	0.150	1.05	1	0.307	0.03	1	0.856
	Temperature	4.06	1	**0.044**	1.04	1	0.307	1.44	1	0.230
	FD1:temperature	0.03	1	0.872	2.49	1	0.115	0.77	1	0.379
	FD2:temperature	0.39	1	0.531	1.17	1	0.280	0.08	1	0.779

2.9 Appendices

Appendix S1

Figure S1. Principal component analysis (PCA) summarizing the correlations between the eight functional traits measured for all litter species. Variance explained by each principal component is shown in brackets.

Figure S1



Appendix S2

Table S1. Leaf litter traits (mean ±SD, n=3) of the 12 species used in the experiment

	C % dry mass	N % dry mass	P g/kg dry mass	Lignin g/kg dry mass	Total phenolics g/kg dry mass	Total tannins g/kg dry mass	C:N ratio	N:P ratio
Jacaranda puberula	48.8 (± 0.93)	2.6 (± 0.38)	1.4 (± 0.30)	201.5 (± 8.10)	41.7 (± 4.27)	34.3 (± 4.50)	19.2(± 2.44)	1.93 (± 0.25)
Inga sbnuda	47.2 (± 0.18)	3.3 (± 0.16)	1.3 (± 0.14)	325.3 (± 2.04)	100.9 (± 5.38)	81.9 (± 4.44)	18.0 (± 0.67)	2.53 (± 0.17)
Alchornea triplinervia	45.4 (± 0.15)	2.1 (± 0.10)	1.0 (± 0.04)	151.2 (± 5.81)	175.9 (± 8.31)	169.1 (± 8.26)	21.9 (± 1.13)	2.02 (± 0.07)
Pera glabrata	47.4 (± 0.43)	1.8 (± 0.11)	0.8 (± 0.18)	498.0 (± 22.04)	94.7 (± 6.29)	56.6 (± 3.10)	26.6 (± 1.58)	2.66 (± 0.65)
Myrcia glabra	47.7 (± 0.18)	1.6 (± 0.07)	0.9 (± 0.02)	309.5 (± 4.09)	161.3 (± 4.61)	100.5 (± 7.20)	29.5 (± 1.16)	1.86 (± 0.11)
Myrcia racemosa	41.6 (± 0.37)	1.4 (± 0.04)	0.5 (± 0.07)	96.9 (± 8.74)	124.1 (± 6.19)	115.0 (± 6.30)	30.2 (± 0.71)	2.79 (± 0.33)
Andira anthelmia	48.2 (± 0.20)	3.1 (± 0.10)	1.4 (± 0.12)	338.1 (± 3.74)	43.1 (± 2.58)	37.0 (± 2.33)	15.5 (± 0.51)	2.30 (± 0.17)
Abarema brachystachia	47.2 (± 0.07)	3.1 (± 0.10)	1.1 (± 0.09)	238.8 (± 2.12)	21.7 (± 1.29)	14.7 (± 0.94)	15.2 (± 0.49)	2.82 (± 0.17)
Cupania oblongifolia	48.2 (± 0.75)	2.0 (± 0.10)	1.3 (± 0.26)	362.3 (± 5.59)	84.0 (± 10.77)	69.7 (± 8.46)	24.3 (± 1.35)	1.67 (± 0.30)
Miconia sp.	44.3 (± 0.57)	1.8 (± 0.06)	0.8 (± 0.06)	308.1 (± 3.51)	101.1 (± 6.59)	91.5 (± 6.72)	24.4 (± 0.95)	2.33 (± 0.14)
Inga edulis	46.3 (± 0.35)	2.0 (± 0.10)	1.9 (± 0.20)	350.7 (± 0.88)	59.4 (± 8.71)	41.6 (± 6.48)	13.9 (± 0.50)	1.84 (± 0.19)
Lacistema pubescens	45.1 (± 0.15)	3.3 (± 0.08)	1.2 (± 0.02)	256.1 (± 18.07)	77.2 (± 5.83)	61.5 (± 4.67)	22.6 (± 0.80)	1.71 (± 0.04)

Table S2. List of aquatic insect morphospecies collected from bromeliads in the end of the experiment.

Order	Family	Morphospecie	Abundance
Coleoptera	Dytiscidae	Dytiscidae sp.	50
	Hydrophilidae	Hydrophilidae sp.	7
	Psephenidae	Psephenidae sp.	4
	Scirtidae	*Scirtes* sp.	201
Diptera	Anisopodidae	*Olbiogaster* sp.	6
	Cecidomidae	Cecidomidae sp.	10
	Ceratopogonidae	*Bezzia* sp.	11
	Ceratopogonidae	*Atrichopogon* sp.2	20
	Ceratopogonidae	*Atrichopogon* sp.3	22
	Ceratopogonidae	*Forcipomyia* (*Phytohelea*) sp.	2
	Chironomidae	*Monopelopia* sp.	948
	Chironomidae	*Polypedilum kaingang*	647
	Chironomidae	*Polypedilum marcondesi*	1496
	Chironomidae	Orthocladinae sp.	230
	Chironomidae	*Tanytarsus* sp.	47
	Chironomidae	*Stenochironomus* sp.	25
	Corethrellidae	*Corethrella* sp.2	182
	Corethrellidae	Corethrella sp.5	84
	Culicidae	*Culex* sp.1	658
	Culicidae	*Culex* sp.2	6
	Culicidae	*Culex* sp.4	4
	Culicidae	*Culex* sp.5	126
	Culicidae	*Anopheles* sp.	87
	Culicidae	*Wyeomyia* sp.	164
	Dolichopodidae	Dolichopodidae sp.	3
	Ephydridae	Ephydridae sp.	5
	Limoniidae	*Trentepohlia* sp.	123
	Psychodidae	Psychodidae sp.	18
	Sciaridae	Sciaridae sp.	6
	Syrphidae	Syrphidae sp.	8
	Tabanidae	Tabanidae sp.	12
Haplotaxida	Tubificidae	Tubificidae sp.1	151
	Tubificidae	Tubificidae sp.2	43
Zygoptera	Coenagrionidae	*Leptagrion* sp.	56

3. CAPÍTULO 2

WARMING, QUALITY AND FUNCTIONAL DIVERSITY OF LITTER DRIVE DECOMPOSITION IN A FRESHWATER ECOSYSTEM

Warming, quality and functional diversity of litter drive decomposition in a freshwater ecosystem

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3.1 Abstract

Warming, litter quality and litter functional diversity have profound impacts on decomposition processes in both terrestrial and aquatic ecosystems. However, it remains unclear whether litter quality or functional diversity prevails under warming. Using an aquatic microecosystem, we evaluated the interactive effect of warming, litter quality and litter functional diversity on decomposition rates. We also assessed the contribution of macro and microorganisms in explaining breakdown patterns. Our models showed that decomposition was driven by both the litter trait aspects. Both litter quality and functional diversity had similar power in explaining decomposition mediated by microorganisms and detritivores together and by microorganisms alone. However, litter quality aroused as the main driver of detritivore-mediated decomposition. Warming interacted with litter quality exacerbating the effects of litter nutrient contents, secondary compounds and C:N ratio on microbial decomposition. Litter quality effects were mainly explained by lignin contents, which decreased decomposition, whereas litter with higher dissimilarity in C, N and C:N ratios, increased breakdown rates. Our results highlight the importance in considering different aspects of litter traits in order to predict decomposition in aquatic systems under climate warming. Considering the jointly effect of warming and litter traits aspects allows a more refined understanding on the underlying mechanisms of climate change and biodiversity shifts effects on ecosystem functioning.

Keywords: tank bromeliads, climate change, complementarity, litter trait effects, microcosms, litter quality, ecosystem functioning

3.2 Introduction

Warming is expected to profoundly impact biodiversity and ecosystem functioning in all biomes on Earth (Walther 2010). Rising temperatures can alter the phenology and distribution of species (Parmesan 2006), the structure of communities (Gruner et al. 2017), species interactions (Thakur et al. 2017), and ecosystem functioning (Petchey et al. 1999; Dossena et al. 2012; Williamson et al. 2016). Concomitantly, changes in biodiversity are occurring at unprecedented rates (Chapin et al. 2000). Thus, understanding the effects of global warming and biodiversity shifts should be a priority issue, since these two threats are predicted to simultaneously impact communities and ecosystems (Hooper et al. 2012).

Although species richness and identity directly influence ecosystem processes and food web structure (Hooper et al. 2005), it has been argued that the species functional traits are stronger predictors of ecosystem functioning (Díaz and Cabido 2001). Recent studies suggest that the trait composition, i.e., the distribution of species functional traits within communities plays a key role in driving ecosystem processes (Díaz et al. 2007; Barantal et al. 2014). Functional differences may lead to a variety of interactions among species, and because of the complexity of these interactions it may be difficult to predict the effects of losses or introductions of species in the communities (Heemsbergen et al. 2004).

Most of the knowledge on diversity-function relationships come from plant productivity systems, while other fundamental processes such as decomposition are less studied (Tilman, Isbell and Cowles 2014; but see Hättenschwiler, Tiunov and Scheu 2005; Gessner et al. 2010). The decomposition of plant organic matter is one of the most important ecosystem processes since it regulates the cycling of carbon and nutrients, and the efflux of greenhouse gasses such as carbon dioxide (CO_2) and methane (CH_4), which can have positive feedbacks to climate change (Davidson and Janssens 2006; Heimann and Reichstein 2008). Dead leaves that fall from trees provide energy and substrate to a wide variety of organisms both in terrestrial and aquatic ecosystems (Gessner et al. 2010). Leaf chemical and physical traits determine the nutritional value, as well as the lability and toxicity of the litter for detritivores and decomposers (e.g., invertebrates, fungi and bacteria; Gessner et al. 2010). This suite of characteristics defines the litter quality and has been shown to be the major determinant of litter decomposition at different environments and latitudes (Cornwell et al. 2008). While some litter species are nutrient-rich and composed by labile carbon, others have few nutrients or contain high concentrations of recalcitrant carbon such as lignin and secondary compounds, which inhibit the activity of microorganisms and detritivores (Gessner et al. 2010 and citations therein). On the other hand, litter functional diversity, that is, the variation in litter species trait values, has been shown to control litter decomposition through synergistic mechanisms (complementarity or facilitation), leading to a more efficient utilization of resources among litter consumers (Vos et al. 2013; Barantal et al. 2014), and thus, affecting the process of matter transformation and nutrient cycling (Heemsbergen et al. 2004). Nutrient transfer, via fungal hyphae or passive leaching, among different litter types may improve the resource availability for consumers leading to accelerated decomposition (Schimel and Hättenschwiler 2007; Handa et al. 2014). However, there is still lacking information on the importance of each litter trait aspect (quality or functional diversity) in driving decomposition, as the control of this process encompasses complex interactions between abiotic and biotic factors (Boyero et al. 2016; Garcia-Palácios 2013; Garcia-Palacios 2016). Understanding the mechanisms that cause the effects of litter diversity may help ecologists to predict the impacts of losses and shifts in plant communities and the consequent effects on terrestrial and aquatic ecosystems. This is particularly relevant in a context of environmental change, where shifts in plant species composition or even on its characteristics (chemical and physical) can result in changes in quality and functional diversity of litter and, hence, affect communities and ecosystems that depends on this resource (Cotrufo et al. 2005).

Decomposition depends strongly on temperature (Davidson and Janssens 2006) and it is expected to be particularly sensitive to climate warming, since increased temperature accelerate litter mass loss directly by leaching and indirectly by increasing the energy intake and litter consumption by detritivores and decomposers (Chergui and Pattee 1990; González and Graça 2003). However, the magnitude of temperature impacts on litter breakdown rates may not be as simple to predict because other factors, such as microbial activity, detritivore density and litter quality (Cornwell et al. 2008; Boyero et al. 2011), which can influence how the process will respond to such environmental change. A recent global experiment suggest that warming should increase microbial decomposition but also decrease decomposition mediated by detritivores, which would result in unchanged overall decomposition in response to climate warming (Boyero et al. 2011). However, the authors suggest that warming could substantially impact food webs and ecosystems because microbial decomposers and detritivores drive decomposition in different ways. Microbial decomposition converts a greater proportion of organic compounds to CO_2 (Seastedt 1984; Baldy et al. 2007), whereas detritivores transform coarse particulate litter to fine particulate and dissolved organic matter (Wallace and Webster 1996). Litter quality, as represented by chemical constituents, have been shown to influence how temperature affect decomposition, being low quality litter more sensitive to temperature compared with high quality litter (Follstad Shah et al. 2017). Therefore, knowing how temperature interacts with other drivers is of crucial importance in order to predict the consequences of climate warming on decomposition.

Here, we investigated the individual and interactive effects of warming and shifts in litter composition on decomposition in a freshwater ecosystem. We conducted an experiment using natural microcosms (phytotelm bromeliads) to manipulate litter mixtures differing in quality and functional diversity, and increasing water temperature according to future projections of global warming. Natural microcosms, such as tank bromeliads, are excellent study models because they are real ecosystems with complex food webs, but the small size allows high replicability and manipulation (Srivastava et al. 2004). We evaluated the importance of quality and functional diversity of litter, and how they interact with increased temperature to affect decomposition. We expected that both quality and functional diversity would control decomposition. Decomposition should increase with litter quality as it provides more nutritive resources for microorganisms and detritivores (fig. 1c; Gessner et al. 2010). On the other hand, decomposition would increase in mixtures with high litter functional diversity, as increasing trait dissimilarity provides complementary resources for consumers (fig. 1d; Heemsbergen et al. 2004; Vos et al. 2013; Barantal et al. 2014). Also, warming would accelerate breakdown rates through its effects on metabolic rates of microorganisms and detritivores (fig. 1c and d, Brown et al. 2004)

3.3 Methods

Study area and organisms

We conducted this study in a closed *restinga* (i.e., coastal sand-based) forest within Parque Estadual Serra do Mar - Núcleo Picinguaba (23°21’27” S, 44°51’01” W), an Atlantic forest conservation area situated in the north coast of São Paulo state, Brazil. The closed *restinga* forest is characterized by the presence of trees approximately 15 m tall with a heavy growth of epiphytes, mainly bromeliads. *Neoregelia johannis* (Carriére) L. B. Smith. (Bromeliaceae) is one of the most abundant bromeliad species in the area with leaves that can reach more than 1 m long and hold more than two liters of water in the tanks formed by their leaves (Cogliatti-Carvalho et al. 2010). Phytotelm bromeliads can and house a wide diversity of arthropod fauna, mainly insects in their larval stages, including predators (Tabanidae, Tanypodinae, Zygoptera, Dytiscidae, Corethrellidae), detritivores (Trichoptera, Limoniidae, Scirtidae, Syrphidae, Psychodidae, Chironomidae) and filter feeders (Culicidae). In addition, a diverse terrestrial fauna inhabits the non-submerged parts of bromeliad leaves, including spiders, mites, harvestmen and collembolas (Romero and Srivastava 2010; Migliorini, Srivastava and Romero 2018).

Leaf litter sampling and chemical analysis

We chose 12 native tree species from closed restinga that are abundant at the field site. The included species were *Jacaranda puberula* (Cham.), *Inga subnuda* (Salzm.), *Alchornea triplinervia* (Spreng.), *Pera glabrata* (Schott), *Myrcia glabra* (O. Berg), *Myrcia racemosa* (O. Berg), *Andira anthelmia* (Vell.), *Abarema brachystachia* (DC.), *Cupania oblongifolia* (Mart.), *Miconia* sp., *Lacistema pubescens* (Mart.), *Inga edulis* (Mart.). We cut branches of each species and air-dried at room temperature until the leaves fall for use in the chemical analysis and in the experiment. Carbon and nitrogen content were quantified by dry combustion in an elemental analyser (Perkin Elmer 2400 II CHN) and phosphorus content through colorimetry by vanadate-molybdate method (Sarruge and Haag 1974). Using this data we calculated C:N and N:P ratios for each litter species. Also, we quantified lignin content with the acid-detergent method (Robertson and Van Soest 1981). In addition, we quantified litter tannins and phenolics using the Folin-Ciocalteu method, as described by Makkar et al. (1993). Carbon and nitrogen analysis were performed at the Analytical Center of the Institute of Chemistry – University of Campinas. Lignin, phosphorus, tannins and phenolics were analyzed at the Center of Nuclear Energy in Agriculture (CENA) – University of São Paulo.

Leaf litter treatments and litter bags

In order to visualize the differences in terms of traits between litter species, we performed a principal components analysis (PCA; Fig. S1, Table S1), by which it was possible to determine five litter treatments (hereafter LT; each one containing four litter species) based on the position of each litter species in the trait space. The LTs represent a gradient of quality (ranging from low to high), which determines the expected rate at which they should decompose and also a gradient of functional diversity (fig. 1b). The LT1 included *C. oblongifolia*, *P. glabrata*, *A. triplinervia* and *Miconia* sp., LT2 included *L. pubescens*, *M. glabra*, *J. puberula* and *M. racemosa*. The LT3 was composed by *L. pubescens*, *J. puberula*, *A. brachystachia* and *M. racemosa*. LT4 contained *C. oblongifolia*, *J. puberula*, *I. subnuda*, *A. brachystachia*. Finally, the LT5 included *I. subnuda*, *A. anthelmia*, *A. brachystachia* and *I. edulis*.

To assess the role of litter quality, we calculated the mean trait values in each litter treatment. Since we selected our litter treatments in the PCA according to the proximity with traits, we assumed that greater trait values would characterize our litter combinations (i.e., ranging from low to high quality). After obtaining the mean value of each trait in each treatment, we standardized the values using *z*-scores. Then we conducted a principal components analysis (PCA) using our mean trait matrix (Fig. 2a). Litter quality was then assessed by retaining the first two PCA axes which captures most of the variance in mean trait values (Fig. 2a). The first axis of quality PCA (quality1) was positively loaded by higher contents of nitrogen and phosphorus, but negatively loaded by phenolics, tannins and C:N ratio. Quality2 was related to high lignin contents as opposed to high N:P ratio (Fig. 2a, Table 1). To determine the importance of litter functional diversity on decomposition, we calculated Rao’s quadratic entropy (Rao’s Q) for each trait in each litter treatment followed by a PCA and retained the first two axes (Fig. 2b). This measure can be used to assess the importance of niche complementarity and assumes that trait differences between litter species drive decomposition through resource complementarity for litter consumers (Botta-Dukat 2005; Barantal et al. 2014). FD1 axis of litter functional diversity PCA separated our litter treatments mainly by high dissimilarities in C and N contents, and in C:N ratios. FD2 axis separated litter with high dissimilarities in lignin and tannin contents from those with high dissimilarities in N:P ratios (Fig. 2b, Table 1).

For each LT, we placed 0.4 ± 0.05 g of air-dried leaves (0.1 ± 0.05 g of each species) in coarse (3mm plus six additional 10mm holes; fig. 1b) and fine-mesh litterbags (0.05 mm, fig.1b). Litter in fine-mesh bags is accessible only by microorganisms, whereas coarse-mesh bags also allow access of macroinvertebrates, like detritivorous insects. We prepared a total of 250 coarse-mesh and 250 fine-mesh litterbags. In order to verify the differences among our litter treatments and the effects of warming, we used linear mixed models for total decomposition, microbial decomposition and detritivore-mediated decomposition, with LTs and temperature as fixed predictors, time as a covariate and all possible interactions. Total decomposition differed among LTs ($F_{1,227} = 16.952$, $p < 0.0001$; Fig. S2a), but was not affect by warming ($F_{1,227} = 2.345$, $p = 0.127$). Microbial decomposition was affected by the interaction between warming and LTs ($F_{1,228} = 2.51$, $p = 0.042$; Fig S2b; Table S2). Decomposition mediated by detritivores differed among LTs ($F_{1,100} = 6.111$, $p = 0.0002$; Fig. S2c), but did not differ between temperature levels ($F_{1,100} = 0.495$, $p = 0.484$).

Experimental design

To investigate the mechanisms controlling litter decomposition and the effect of warming on this ecosystem function, we used 50 tank-bromeliads *Neoregelia johannis* acquired from a greenhouse in order to ensure all plants had similar sizes and water storage capacities and were virtually free of colonizing organisms. Prior to the experiments, we washed the bromeliads with spring water and solutions of antibiotics and 5% sodium hypochlorite to remove invertebrates and unnatural bacteria. We planted the bromeliads in the ground of the restinga following a randomized block design (n = 5 blocks with 10 bromeliads) and installed plastic roofs over each plant to prevent any input of rain and organic matter like branches and fallen leaves from trees. To keep the water level constant, we watered the bromeliads at 1-day intervals. Experimental warming was achieved by an electronic heating system (Fig. 1a) composed by pre-programmed controllers connected to a digital display for temperature monitoring. We used submersible water heaters (1W) in half of bromeliads of each block to maintain a continuous 4 °C increase above the ambient temperature of unheated bromeliads. This increase in the temperature was achieved by submersible sensors in the unheated bromeliads, which switched on and off the heaters through the controllers. The temperature difference used in this experiment followed the projections of temperature increase in the southeastern region of Brazil over the next century (IPCC 2014). We conducted our experiment from April to July 2015.

The heating equipment was composed of five boxes (containing the electronic components) connected one to another. Each component box (block) was responsible for accessing and controlling the temperature of 10 bromeliads (five with ambient temperature and five warmed; Fig. 1a). In each block, we placed one LT per bromeliad, repeating the treatment in warmed and ambient bromeliads. Each bromeliad received five coarse- and five fine-mesh litter bags in five different wells, being one litter bag of each mesh size per well. One pair of litter bags (coarse and fine) was retrieved from each bromeliad after 16, 32, 48, 64 and 80 days. The litter of each bag was taken out and cleaned under water to remove possible insects. Litter was oven-dried at 60 °C and weighed.

Data analysis

All data analyzes were carried out using R version 3.2.2 (R Core Team, 2016). We calculated decomposition rates using the decay coefficient (*k*) assuming the exponential decay model $m_f / m_i = e^{-kt}$ where m_f and m_i are the final and initial litter mass (g), respectively, *t* is time in days and *k* is the decomposition coefficient. We estimated the relative contributions of warming, quality and functional diversity of litter on decomposition rates using linear mixed models (LME, *nlme* package) following a backward selection procedure based on AIC (Table S2). . Since the metrics we chose to represent litter quality and functional diversity describe complementary aspects of trait composition, i.e., mean and dispersion, respectively, and they are mathematically related (Ricotta and Moretti 2011, Dias et al. 2013), we conducted separate analyzes to better test and explore their role in driving litter decomposition. We tested separate models for fine-mesh decomposition (microorganisms) and coarse-mesh decomposition (macroinvertebrates + microorganisms). In addition, we conducted a model for detritivore-mediated decomposition, which was calculated as the difference between the mass remaining in coarse-mesh and fine-mesh bags and then converted to decomposition coefficient. We began model selection on a full model for each response with additive terms for litter effect (quality or functional diversity component axes), temperature, and time as a covariate, and all possible interactions, except among litter effects. For total decomposition (coarse-mesh), we included richness and abundance of detritivores that were collected from inside the litter bags. We included quadratic terms for each litter effect component to account for nonlinear trends with the responses. Block was included as a random effect in all models but was not subjected to the model selection. We sequentially removed the least significant predictor (starting with the interactions, then the quadratic terms, and finally, the other variables) through backward selection until we reached a model where all predictors were significant, and then compared all models based on AIC. The smallest AIC model was selected and fitted using "lme" function and restricted maximum likelihood (REML) in the nlme R package. Final models of quality and functional diversity were contrasted (using anova function) to compare their AIC values. Parametric assumptions of linear models were verified using plots of residuals for normality and homoscedasticity. Decomposition rates were natural log-transformed to meet the assumptions of linear models and outliers were removed when needed.

3.4 Results

We found that both mechanisms of litter traits effects (i.e., quality and functional diversity) explained patterns of litter decomposition. In total decomposition (detritivores + microorganisms), richness and abundance of detritivores were not retained in the final model for litter quality, but abundance was retained in the final FD model (Table S3). Warming and quality1 axis did not affect decomposition (Fig. 3a, Table 2). However, decomposition rates negatively correlated with increasing lignin contents, as represented by quality2 (*r* = -0.25; Fig. 3b, Table 2). The FD model showed that decomposition positively correlated with increasing dissimilarities in C and N contents, and C:N ratios (FD1: *r* = 0.30; Fig. 3c, Table 3). A weak negative effect of FD2 indicated decreased total decomposition with increasing variability of lignin and secondary compounds (*r* = 0.05; Fig. 3d, Table 3). In microbial decomposition, warming interacted with quality 1 and negatively affected litter breakdown (Fig. 3e, Table 2) indicating low decomposition in litters with higher phenolic and tannin contents, and C:N ratios (e.g., LT1 and LT2), but also low decomposition in litters with higher contents of N and P (e.g., LT4 and LT5). Nevertheless, the negative effect of quality2 axis indicated lower decomposition in litters with higher lignin contents as opposed to higher decomposition in high N:P ratio litters (*r* = -0.29; Fig. 3f, Table 2). FD1 positively affected microbial litter breakdown, indicating that this process increased with increasing dissimilarity in C and N contents, and C:N ratios (*r* = 0.32; Fig. 3g, Table 3). Although weak, we found an interactive effect of FD2 and warming on microbial decomposition, suggesting lower decomposition rates with increasing variability of tannins and lignin (Fig. 3h, Table 3). The positive effect of quality1 on detritivores-mediated decomposition indicated higher consuming on litter with higher N and P contents and low contents of phenolics, tannins and C:N ratios (*r* = 0.22; Fig. 3i, Table 2). The second quality axis did not affect detritivore decomposition. None of functional diversity axes explained insect breakdown (Figs. 3k and 3l, Table 3). By contrasting quality and FD models we observed that quality and functional diversity similarly explained total decomposition (AIC quality: 163.14;

AIC FD: 161.43) and microbial decomposition (AIC quality: 59.54; AIC FD: 60.64). However, detritivore-mediated decomposition was better explained by litter quality (AIC quality: 111.52; AIC FD: 116.32).

3.5 Discussion

Although the effects of litter diversity and their traits on decomposition are well documented in both terrestrial and aquatic ecosystems (García-Palacios et al. 2016), the mechanisms that control litter effects are still poorly understood. Also, little is known on how decomposition will respond to climate changes and its combined effect with shifts in plant composition. As far as we know, this is the first decomposition study that investigated the interactive effects of predicted global warming and litter composition, by partitioning litter effects in quality and functional diversity. Here we show that both, litter quality and functional diversity explained decomposition in aquatic systems, but which one predominates depends on the organisms involved. Moreover, warming may interact with litter effects to affect litter breakdown.

Litter quality was characterized along two PCA axes on the trait mean values. The first axis separated nutrient-rich treatments from others with heavy investment in defense compounds, traits often shown to accelerate and slow decomposition, respectively (Gessner et al. 2010). The second quality axis distinguished those treatments with higher contents of structural compounds (i.e., lignin) from those with high nutrient ratios. Litter functional diversity was assessed with the first two PCA axes on single-trait Rao's Q. The first axis separated those treatments with greater variation in carbon, nutrients and their ratios, from others with higher variation of structural compounds such as lignin.

The second functional diversity axis distinguished litter treatments with high variation in secondary compounds from those with high variation in nutrient ratios.

Both litter quality and functional diversity were important to predict decomposition in our aquatic microcosms. The pattern found for microbial decomposition were, in part, surprising because decomposition tended to decrease with increasing litter quality (high N and P contents; quality1), contrary to expected and to previous studies (Cornwell et al. 2008; Garcia-Palacios et al. 2017; Migliorini, Srivastava and Romero 2018). Moreover, warming exacerbated this relationship. A possible explanation to this result is the fact that higher contents of nitrogen may suppress lignin degradation, reducing litter decomposition in the late stages (Berg and Ekbohm 1991, Aponte, García and Marañón 2012). On the other hand, lower litter quality, as indicated by high lignin contents (quality2), decreased decomposition both in total and microbial, agreeing with previous studies (Schindler and Gessner 2009; Frainer et al. 2015; Migliorini et al. 2018). In contrast, detritivore-mediated decomposition was positively associated with increasing litter quality, as indicated by high N and P contents and low phenolics and tannins contents. This result is in agreement with other studies that evaluated detritivore effects on litter breakdown (Santoja et al. 2017) and feeding preferences (Canhoto and Graça 1995; Rincón and Martínez 2006).

Despite litter quality was the key driver of detritivore-mediated decomposition, microbial decomposition was similarly explained by both quality and functional diversity. This result indicates that both the amount of specific compounds and their variability are important for decomposers. Interestingly, functional diversity arose as the main driver of decomposition when both microorganisms and detritivores were present. Litter functional diversity predicts that higher trait dissimilarity increases decomposition through resource complementarity for microorganisms and detritivores (Barantal et al. 2014; Coulis et al. 2015; Stoler, Burke and Relyea 2016, García-Palacios et al. 2017). In our study, decomposition was enhanced by increasing dissimilarity in C, N and C:N, in both microbial and total decomposition, supporting recent studies (Barantal et al. 2014; García-Palacios et al. 2017). Among the mechanisms of litter functional diversity effects on decomposition, nitrogen transfer between litter species has been pointed out as the main mechanism in several studies (Gessner et al. 2010; Handa et al. 2014; García-Palacios et al. 2017). N transfer among litter species, via passive leaching or active microbial transfer (fungal hyphae), is related to niche complementarity effects, where a nutrient-rich litter enhance the nutritional values of a nutrient-poor litter, increasing the resource availability for microbial decomposer and detritivores, and hence increase the overall decomposition (Hättenschwiler, Tiunov and Scheu 2005; Handa et al. 2014).

Our results provide novel evidence on the combined effects of climate change and litter diversity on decomposition in aquatic systems. The most striking result was the interactive effect of warming and litter quality for microbial decomposers. This is particularly relevant for bromeliad ecosystems where microorganisms have a similar impact to detritivores on decomposition (Figure S3; see Migliorini, Srivastava and Romero 2008; Bernabé et al. 2018). Litter decomposition rates are expected to increase with temperature because elevated temperature accelerates biochemical reactions and metabolism of litter consumers (Brown et al. 2004; Boyero et al. 2011). However, the magnitude of warming impact on litter breakdown should vary according to litter quality (Conant et al. 2008). Decomposition of low quality litter is expected to be more sensitive to changes in temperature, according to the rationale that microbial enzymatic reactions that metabolize complex macromolecules are more sensitive to temperature than enzymatic reactions that metabolize high quality litter constituents (Conant et al. 2008; Wagai et al. 2013). In our study, we found evidence that warming increases microbial decomposition of low quality litter (Fig. S2b). A recent study demonstrated that warming accelerated microbial decomposition of recalciltrant substrate by shifting the functional gene structure of microbial communities (Cheng et al. 2017). Litter quality varies strongly between tropical and temperate regions (Hättenschwiller et al. 2011), and also the environmental conditions (Boyero et al. 2011) and the importance of detritivores (Irons et al. 1994), which probably makes it difficult to find global patterns for the responses of litter decomposition to temperature changes. Further studies manipulating litter composition and temperature in aquatic systems are needed to better predict the impacts of climate warming on decomposition.

Predictive studies combining the joint evaluation of future temperature changes and litter diversity on decomposition are rare. This study demonstrates that the two main aspects (quality and functional diversity) of litter traits effects are important to control litter decomposition, but its importance may depend on the interactions between the organisms involved in the process. Moreover, global warming may interact with changes in litter diversity impacting decomposition rates. Our results highlight the importance in considering litter trait aspects in order to predict the interactive effects of biodiversity shifts and global warming on the functioning of aquatic ecosystems.

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3.6 References

Baldy, V., Gobert, V., Guerold, F., Chauvet, E., Lambrigot, D. & Charcosset, J.-Y. (2007). Leaf litter breakdown budgets in streams of various trophic status: effects of dissolved inorganic nutrients on microorganisms and invertebrates. *Freshwater Biology*, 52, 1322–1335.

Barantal, S., Schimann, H., Fromin, N. & Hattenschwiler, S. (2014). C, N and P fertilization in an Amazonian rainforest supports stoichiometric dissimilarity as a driver of litter diversity effects on decomposition. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20141682.

Bernabé, T.N., de Omena, P.M., Santos, V.P. dos, de Siqueira, V.M., de Oliveira, V.M. & Romero, G.Q. (2018). Warming weakens facilitative interactions between decomposers and detritivores, and modifies freshwater ecosystem functioning. *Global Change Biology*. 24: 3170-3186.

Botta-Dukát, Z. (2005). Rao’s quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science*, 16, 533–540.

Boyero, L., Pearson, R.G., Gessner, M.O., Barmuta, L.A., Ferreira, V., Graça, M.A.S., *et al.* (2011). A global experiment suggests climate warming will not accelerate litter decomposition in streams but might reduce carbon sequestration: Global patterns of decomposition in streams. *Ecology Letters*, 14, 289–294.

Boyero, L., Pearson, R.G., Hui, C., Gessner, M.O., Pérez, J., Alexandrou, M.A., *et al.* (2016). Biotic and abiotic variables influencing plant litter breakdown in streams: a global study. *Proceedings of the Royal Society B: Biological Sciences*, 283, 20152664.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85, 1771–1789.

Canhoto, C. & GraçA, M.A.S. (1995). Food value of introduced eucalypt leaves for a Mediterranean stream detritivore: Tipula lateralis. *Freshwater Biology*, 34, 209–214.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., *et al.* (2012). Biodiversity loss and its impact on humanity. *Nature*, 486, 59–67.

Chapin III, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., *et al.* (2000). Consequences of changing biodiversity. *Nature*, 405, 234–242.

Cheng, L., Zhang, N., Yuan, M., Xiao, J., Qin, Y., Deng, Y., et al. (2017).

Warming enhances old organic carbon decomposition through altering functional microbial communities. The ISME Journal, 11, 1825–1835.

Chergui, H. & Pattee, E. (1990). The influence of season on the breakdown of submerged leaves. *Archiv für Hydrobiologie*, 120, 1–12.

Cogliatti-Carvalho, L. Rocha-Pessôa, T.C., Nunes-Freitas, A.F., & Rocha, C.F.D.(2010). Volume de água armazenado no tanque de bromélias, em restingas da costa brasileira. *Acta Bot. Bras.*, 24, 84-95.

Conant, R.T., Drijber, R.A., Haddix, M.L., Parton, W.J., Paul, E.A., Plante, A.F., *et al.* (2008). Sensitivity of organic matter decomposition to warming varies with its quality. *Global Change Biology*, 14, 868–877.

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

Cotrufo, M.F., De Angelis, P. & Polle, A. (2005). Leaf litter production and decomposition in a poplar short-rotation coppice exposed to free air CO2 enrichment (POPFACE). *Global Change Biology*, 11, 971–982.

Coulis, M., Fromin, N., David, J.-F., Gavinet, J., Clet, A., Devidal, S., *et al.* (2015). Functional dissimilarity across trophic levels as a driver of soil processes in a Mediterranean decomposer system exposed to two moisture levels. *Oikos*, 124, 1304–1316.

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

Diaz, S., Lavorel, S., de Bello, F., Quetier, F., Grigulis, K. & Robson, T.M. (2007). Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences*, 104, 20684–20689.

Díaz, S. & Cabido, M. (2001). Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, 16, 646–655.

Dossena, M., Yvon-Durocher, G., Grey, J., Montoya, J.M., Perkins, D.M., Trimmer, M., *et al.* (2012). Warming alters community size structure and ecosystem functioning. *Proceedings of the Royal Society B: Biological Sciences*, 279, 3011–3019.

Follstad Shah, J.J., Kominoski, J.S., Ardón, M., Dodds, W.K., Gessner, M.O., Griffiths, N.A., *et al.* (2017). Global synthesis of the temperature sensitivity of leaf litter breakdown in streams and rivers. *Global Change Biology*, 23, 3064–3075.

Frainer, A., Moretti, M.S., Xu, W. & Gessner, M.O. (2015). No evidence for leaf-trait dissimilarity effects on litter decomposition, fungal decomposers, and nutrient dynamics. *Ecology*, 96, 550–561.

García-Palacios, P., Maestre, F.T., Kattge, J. & Wall, D.H. (2013). Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. *Ecology Letters*, 16, 1045–1053.

García-Palacios, P., McKie, B.G., Handa, I.T., Frainer, A. & Hättenschwiler, S. (2016a). The importance of litter traits and decomposers for litter decomposition: a comparison of aquatic and terrestrial ecosystems within and across biomes. *Functional Ecology*, 30, 819–829.

García-Palacios, P., Shaw, E.A., Wall, D.H. & Hättenschwiler, S. (2016b). Temporal dynamics of biotic and abiotic drivers of litter decomposition.

Ecology Letters, 19, 554–563.

García-Palacios, P., Shaw, E.A., Wall, D.H. & Hättenschwiler, S. (2017). Contrasting mass-ratio vs. niche complementarity effects on litter C and N loss during decomposition along a regional climatic gradient. *Journal of Ecology*, 105, 968–978.

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

Gonzalez, J.M. & Graca, M.A.S. (2003). Conversion of leaf litter to secondary production by a shredding caddis-fly. *Freshwater Biology*, 48, 1578–1592.

Gruner, D.S., Bracken, M.E.S., Berger, S.A., Eriksson, B.K., Gamfeldt, L., Matthiessen, B., *et al.* (2017). Effects of experimental warming on biodiversity depend on ecosystem type and local species composition. *Oikos*, 126, 8–17.

Hättenschwiler, S., Coq, S., Barantal, S. & Handa, I.T. (2011). Leaf traits and decomposition in tropical rainforests: revisiting some commonly held views and towards a new hypothesis. *New Phytologist*, 189, 950–965.

Hättenschwiler, S., Tiunov, A.V. & Scheu, S. (2005). Biodiversity and Litter Decomposition in Terrestrial Ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 36, 191–218.

Heemsbergen, D.A. (2004). Biodiversity Effects on Soil Processes Explained by Interspecific Functional Dissimilarity. *Science*, 306, 1019–1020.

Heimann, M. & Reichstein, M. (2008). Terrestrial ecosystem carbon dynamics and climate feedbacks. *Nature*, 451, 289–292.

Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulich, K.L., *et al.* (2012). A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature*, 486, 105–108.

IPCC (2014). Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (eds Core Writing Team, Pachauri, R.K., Meyer, L.A.). IPCC, Geneva, Switzerland, pp. 151.

Irons, J.G., Oswood, M.W., Stout, R.J. & Pringle, C.M. (1994). Latitudinal patterns in leaf litter breakdown: is temperature really important? *Freshwater Biology*, 32, 401–411.

Makkar, H.P.S., Blummel, M., Borowy, N.K. & BECKER, K. (1993). Gravimetric determination of tannins and their correlation with chemical and protein precipitation methods. Journal of the Science of Food and Agriculture, 61, 161-165.

Migliorini, G.H., Srivastava, D.S. & Romero, G.Q. (2018). Leaf litter traits drive community structure and functioning in a natural aquatic microcosm. *Freshwater Biology*, 63, 341–352.

Montoya, J.M. & Raffaelli, D. (2010). Climate change, biotic interactions and ecosystem services. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 2013–2018.

Parmesan, C. (2006). Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology, Evolution, and Systematics*, 37, 637–669.

Petchey, O.L., McPhearson, P.T., Casey, T.M. & Morin, P.J. (1999). Environmental warming alters food-web structure and ecosystem function. *Nature*, 402, 69–72.

R Development Core Team (2016). R: A language and environmental for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org/

Ricotta, C. & Moretti, M. (2011). CWM and Rao’s quadratic diversity: a unified framework for functional ecology. *Oecologia*, 167, 181–188.

Rincón, J. & Martínez, I. (2006). Food quality and feeding preferences of *Phylloicus* sp. (Trichoptera:Calamoceratidae). *Journal of the North American Benthological Society*, 25, 209–215.

Robertson, J. B., & Van Soest, P. J. (1981). The analysis of dietary fibre in food. In W. P. T. James & O. Theander (Eds.), The detergent system of analysis (pp. 123–158). New York, NY: Marcel Dekker.

Romero, G.Q. & Srivastava, D.S. (2010). Food-web composition affects cross-ecosystem interactions and subsidies: Cross-ecosystem interactions and subsidies. *Journal of Animal Ecology*, 79, 1122–1131.

Santonja, M., Pellan, L. & Piscart, C. (2018). Macroinvertebrate identity mediates the effects of litter quality and microbial conditioning on leaf litter recycling in temperate streams. *Ecology and Evolution*, 8, 2542–2553.

Sarruge, J. R. S., & Haag, H. P. (1974). Análises químicas em plantas. Piracicaba, Brazil: USP-ESALQ.

Schimel, J.P. & Hättenschwiler, S. (2007). Nitrogen transfer between decomposing leaves of different N status. *Soil Biology and Biochemistry*, 39, 1428–1436.

Schindler, M.H. & Gessner, M.O. (2009). Functional leaf traits and biodiversity effects on litter decomposition in a stream. *Ecology*, 90, 1641–1649.

Seastedt, T.R. (1984). The Role of Microarthropods in Decomposition and

Mineralization Processes. *Annual Review of Entomology*, 29, 25–46.

Srivastava, D.S., Kolasa, J., Bengtsson, J., Gonzalez, A., Lawler, S.P., Miller, T.E., *et al.* (2004). Are natural microcosms useful model systems for ecology? *Trends in Ecology & Evolution*, 19, 379–384.

Stoler, A.B., Burke, D.J. & Relyea, R.A. (2016). Litter chemistry and chemical diversity drive ecosystem processes in forest ponds. *Ecology*, 97, 1783–1795.

Thakur, M.P., Künne, T., Griffin, J.N. & Eisenhauer, N. (2017). Warming magnifies predation and reduces prey coexistence in a model litter arthropod system. *Proceedings of the Royal Society B: Biological Sciences*, 284, 20162570.

Tilman, D., Isbell, F. & Cowles, J.M. (2014). Biodiversity and Ecosystem Functioning. *Annual Review of Ecology, Evolution, and Systematics*, 45, 471–493.

Vos, V.C.A., van Ruijven, J., Berg, M.P., Peeters, E.T.H.M. & Berendse, F. (2013). Leaf litter quality drives litter mixing effects through complementary resource use among detritivores. *Oecologia*, 173, 269–280.

Wagai, R., Kishimoto-Mo, A.W., Yonemura, S., Shirato, Y., Hiradate, S. & Yagasaki, Y. (2013). Linking temperature sensitivity of soil organic matter decomposition to its molecular structure, accessibility, and microbial physiology. *Global Change Biology*, 19, 1114–1125.

Wallace, J.B. & Webster, J.R. (1996). The role of macroinvertebrate in stream ecosystem function. *Annual Review of Entomology*, 41, 115–139.

Walther, G.R. (2010). Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B: Biological*

Sciences, 365, 2019–2024.

Williamson, T.J., Cross, W.F., Benstead, J.P., Gíslason, G.M., Hood, J.M., Huryn, A.D., *et al.* (2016). Warming alters coupled carbon and nutrient cycles in experimental streams. *Global Change Biology*, 22, 2152–2164.

3.7 Figures

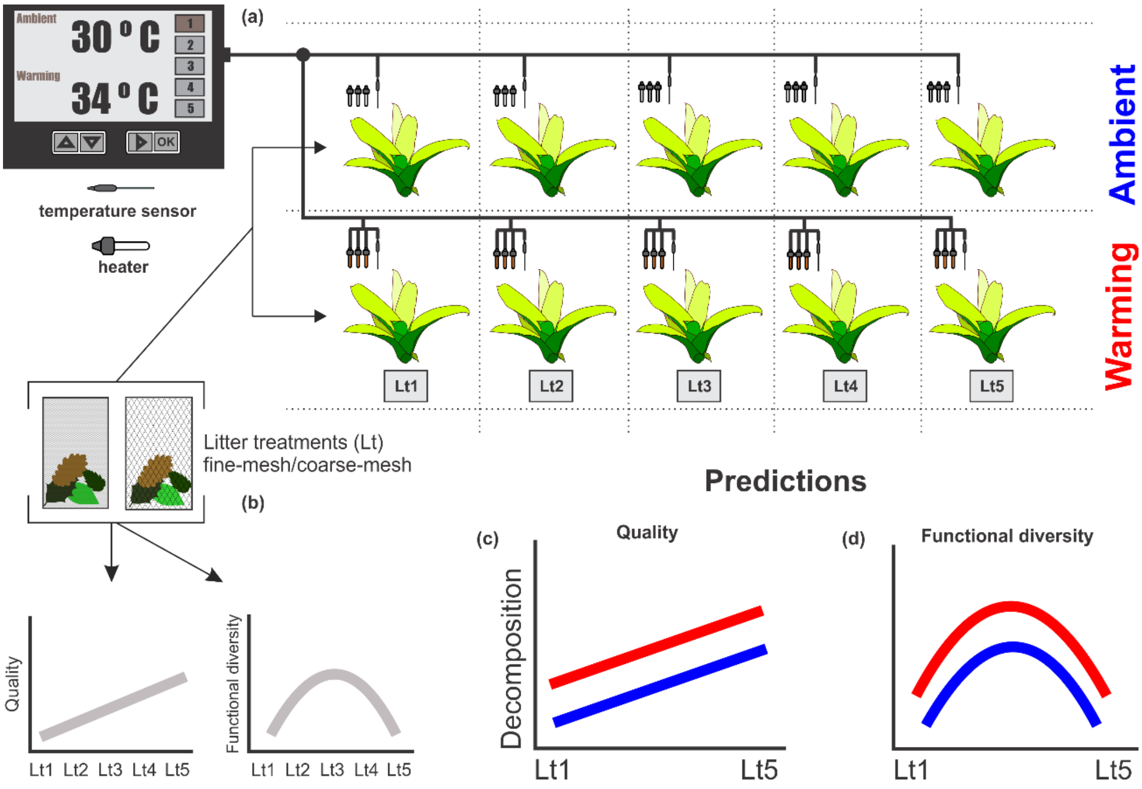

Figure 1. Schematic representation of the experimental design, temperature control system and main predictions. (a) Experimental design: ten treatment combinations per block (five blocks). Warming effect was achieved by increasing ambient temperature in 4 ºC, following the projection for the year 2100 (IPCC 2014). (b) Litter treatments (Lt) consisted of five mixtures of four litter species selected based on their chemical traits, ranging from low to high quality. In addition, these litter treatments represented a gradient of functional diversity. Based on quality hypothesis (c), decomposition should increase with litter quality; however, functional diversity hypothesis (d) assumes that breakdown increases in higher litter trait dissimilarities. Moreover, warming should exacerbate such relationships.

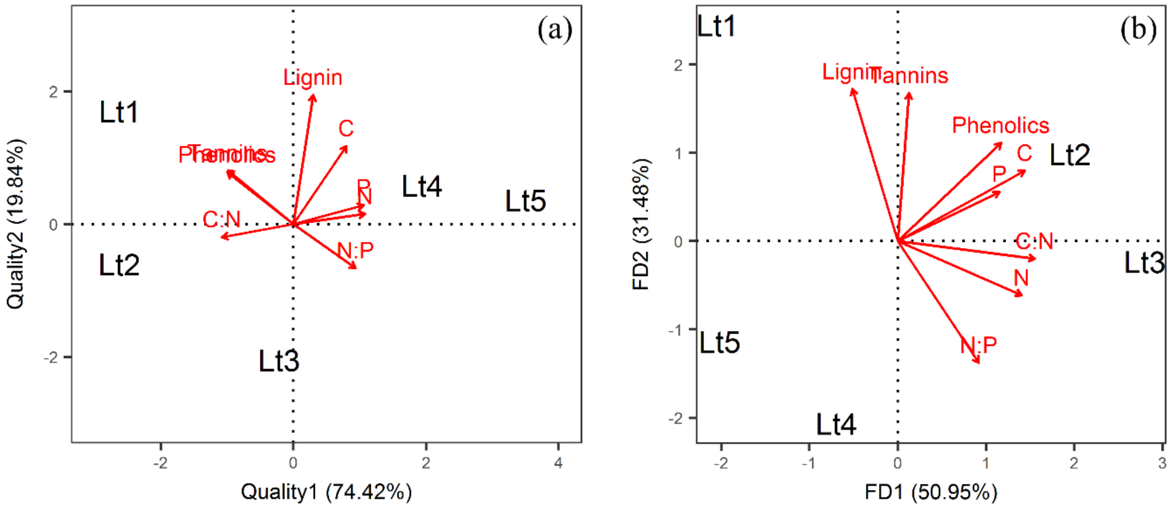

Figure 2. Principal component analyses (PCA) of quality and functional diversity of the five litter treatments. Red arrows represent the loads of correlation between traits and axes. Variance explained by each principal component is shown in brackets.

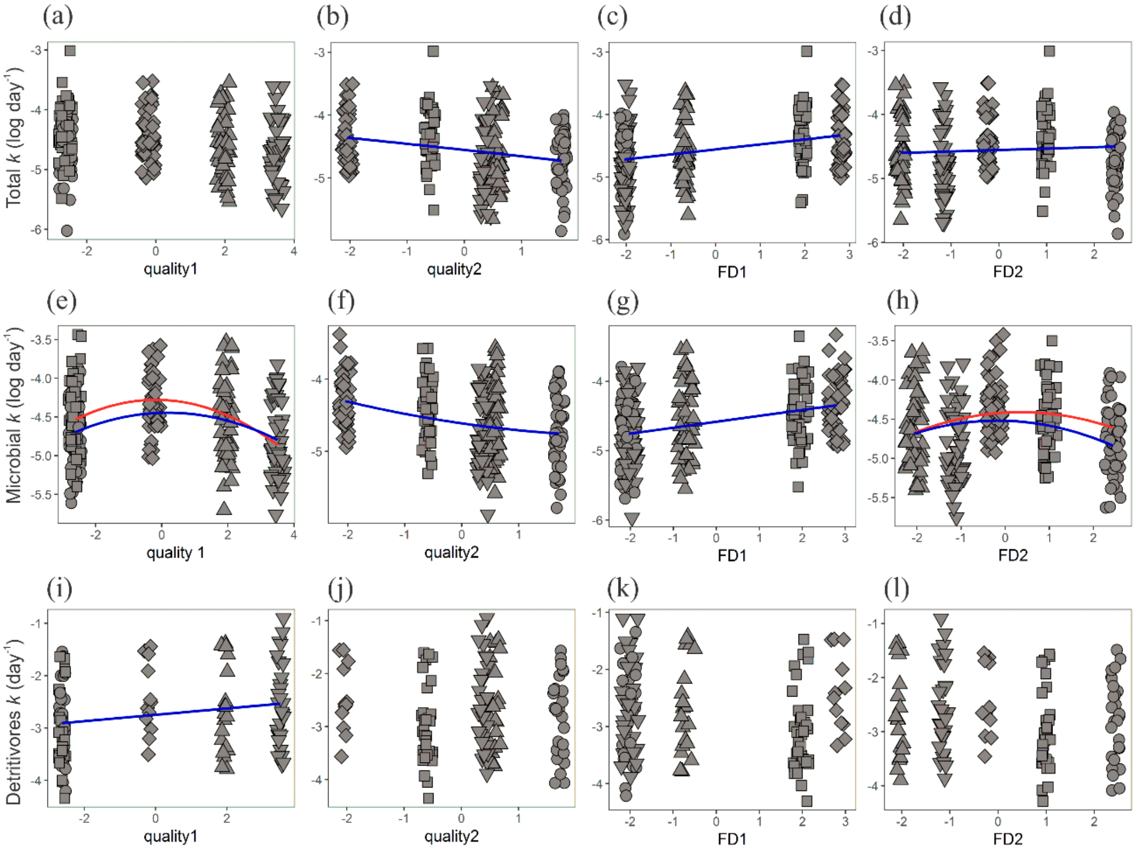

Figure 3. Relationship between the first and second axes of quality (fig. 2a) and functional diversity (fig. 2b) PCAs and (a-d) total decomposition, (e-h) microbial decomposition and (i-l) detritivore-mediated decomposition. Circle: LT1, square: LT2, rhombus: LT3, triangle: LT4, inverted triangle: LT5

3.8 Tables

Table 1. Summary of the principal component analyses for quality and functional diversity of the litter treatments. Values correspond to loadings on traits on the first two axes. Traits that significantly correlate with each axis are shown in bold.

trait	quality1	quality2	FD1	FD2
C	0.30	0.44	**0.45**	0.25
N	**0.41**	0.06	**0.44**	-0.19
P	**0.40**	0.11	0.36	0.17
Lignin	0.11	**0.73**	**-0.16**	**0.54**
Phenolics	**-0.38**	0.30	0.36	0.35
Tannins	**-0.37**	0.30	0.04	**0.52**
C:N	**-0.41**	-0.07	**0.48**	-0.06
N:P	0.35	**-0.25**	0.29	**-0.43**

Table 2. Effects of warming and litter quality on decomposition rates mediated by microorganisms and detritivores (total), microorganisms (microbial) and only by detritivores. Statistical significance in $p < 0.05$.

Quality models	Source	Estimate	SE	DF	t	p
Total						
	(intercept)	-3.862	0.065	236	-59.41	<0.001
	quality1 (qlt1)	0.014	0.021	236	0.68	0.491
	quality2 (qlt2)	-0.113	0.018	236	-6.25	<0.001
	I(qlt2^2)	-0.037	0.015	236	-2.45	0.015
	temperature (temp)	-0.060	0.042	236	-1.44	0.150
	time	-0.013	0.0009	236	-13.62	<0.001
	qlt1:time	-0.001	0.0003	236	-3.68	<0.001
Microbial						
	(intercept)	-3.582	0.085	232	-41.82	<0.001
	quality1	-0.006	0.019	232	-0.34	0.736

	quality2	-0.088	0.016	232	-5.38	<0.001
	I(qlt1^2)	-0.028	0.006	232	-4.41	<0.001
	I(qlt2^2)	-0.095	0.027	232	-3.46	<0.001
	temperature	0.023	0.079	232	0.29	0.768
	time	-0.015	0.001	232	-11.80	<0.001
	qlt1:temp	0.038	0.014	232	2.77	0.006
	qlt1:time	-0.0006	0.0003	232	-1.71	0.089
	I(qlt2^2):time	0.001	0.0004	232	2.79	0.006
	temp:time	-0.003	0.001	232	-1.91	0.058
Detritivores						
	(intercept)	-1.531	0.123	111	-12.46	<0.001
	quality1	0.080	0.032	111	2.47	0.015
	I(qlt2^2)	0.049	0.025	111	1.95	0.054
	temperature	0.375	0.165	111	2.27	0.025
	time	-0.024	0.002	111	-11.64	<0.001
	qlt1:time	-0.0005	0.0006	111	-0.88	0.382
	temp:time	-0.010	0.003	111	-3.19	0.002

Tabela 3. Effects of warming and litter functional diversity on decomposition rates mediated by microorganisms and detritivores (total), microorganisms (microbial) and only by detritivores. Statistical significance in $p < 0.05$.

FD models	Source	Estimate	SE	DF	t	p
Total						
	(intercept)	-3.887	0.064	236	-61.07	<0.001
	FD1	0.082	0.010	236	7.89	<0.001
	FD2	-0.084	0.031	236	-2.68	0.008
	temperature (temp)	-0.060	0.042	236	-1.44	0.150
	time	-0.013	0.0009	236	-13.60	<0.001
	insect abundance	-0.004	0.002	236	-1.77	0.079
	FD2:time	0.002	0.0006	236	3.80	<0.001

Microbial						
	(intercept)	-3.788	0.111	233	-34.09	<0.001
	FD1	0.105	0.012	233	8.66	<0.001
	FD2	-0.057	0.031	233	-1.85	0.066
	I(FD1^2)	-0.034	0.020	233	-1.70	0.090
	I(FD2^2)	0.039	0.015	233	2.67	0.008
	temperature (temp)	-0.112	0.034	233	-3.32	0.001
	time	-0.019	0.002	233	-12.00	<0.001
	FD2:temp	-0.053	0.021	233	-2.47	0.014
	FD2:time	0.0009	0.0005	233	1.81	0.072
	I(FD1^2):time	0.001	0.0003	233	3.13	0.002
Detritivores						
	(intercept)	-1.603	0.147	109	-10.93	<0.001
	FD1	-0.071	0.044	109	-1.62	0.109
	FD2	-0.102	0.056	109	-1.83	0.070
	I(FD1^2)	0.035	0.021	109	1.65	0.102
	temperature (temp)	0.377	0.168	109	2.24	0.027
	time	-0.024	0.002	109	-11.54	<0.001
	FD1:time	0.0005	0.0008	109	0.58	0.565
	FD2:time	0.0007	0.001	109	0.71	0.478
	temp:time	-0.010	0.003	109	-3.17	0.002

3.9 Supplementary material

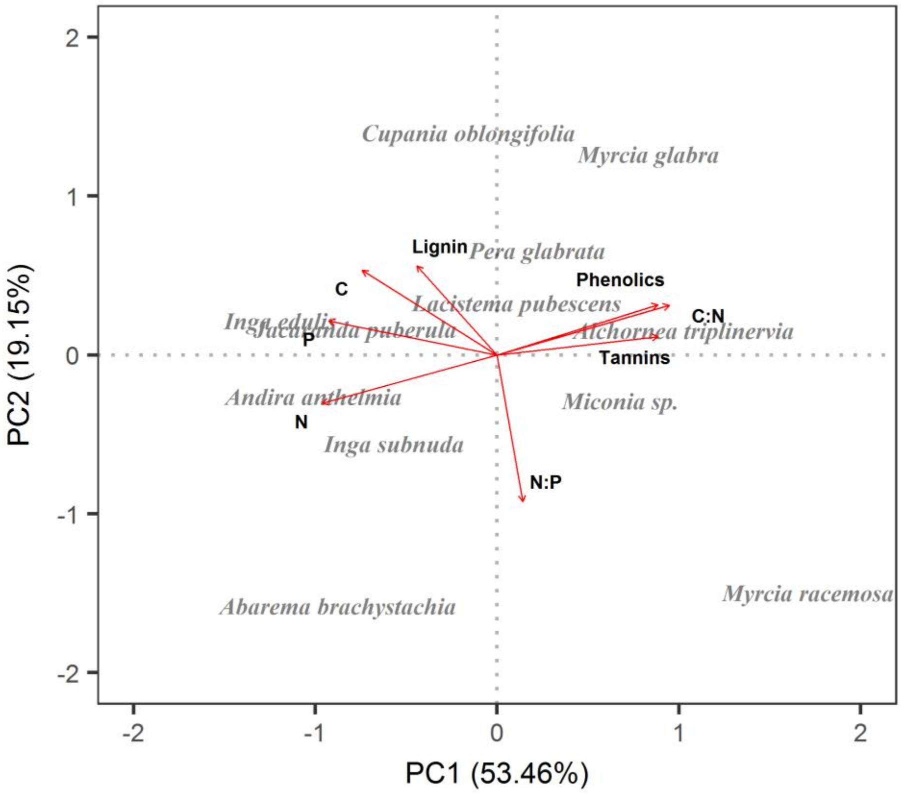

Figure S1. Principal component analysis (PCA) summarizing the correlations between the eight functional traits measured for all litter species. Variance explained by each principal component is shown in brackets.

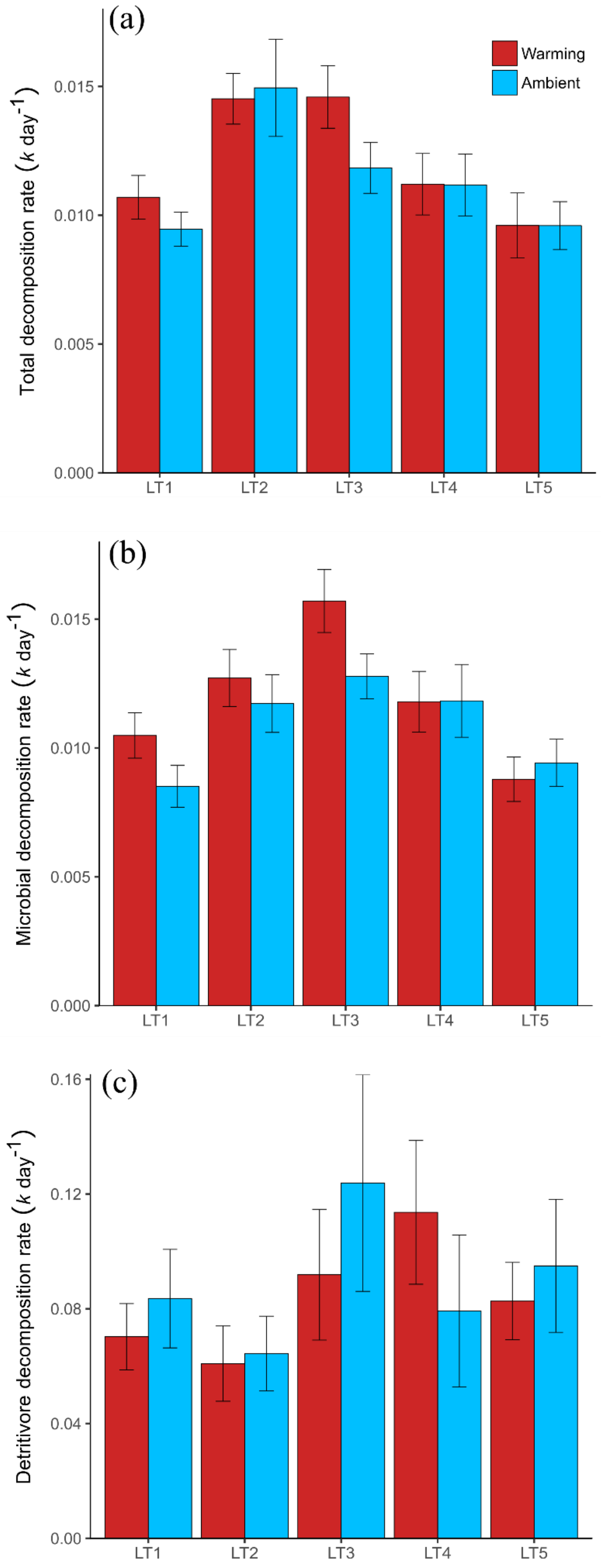
(a)
Warming
Ambient
Total decomposition rate (k day^{-1})
0.000
0.005
0.010
0.015
LT1
LT2
LT3
LT4
LT5
(b)
Microbial decomposition rate (k day^{-1})
0.000
0.005
0.010
0.015
LT1
LT2
LT3
LT4
LT5
(c)
Detritivore decomposition rate (k day^{-1})
0.00
0.04
0.08
0.12
0.16
LT1
LT2
LT3
LT4
LT5

Figure S2. Decomposition rates of the different litter treatments under ambient and warming temperature: (a) total decomposition (coarse-mesh), (b) microbial decomposition (fine-mesh) and (c) detritivore-mediated decomposition. Error bars are SE.

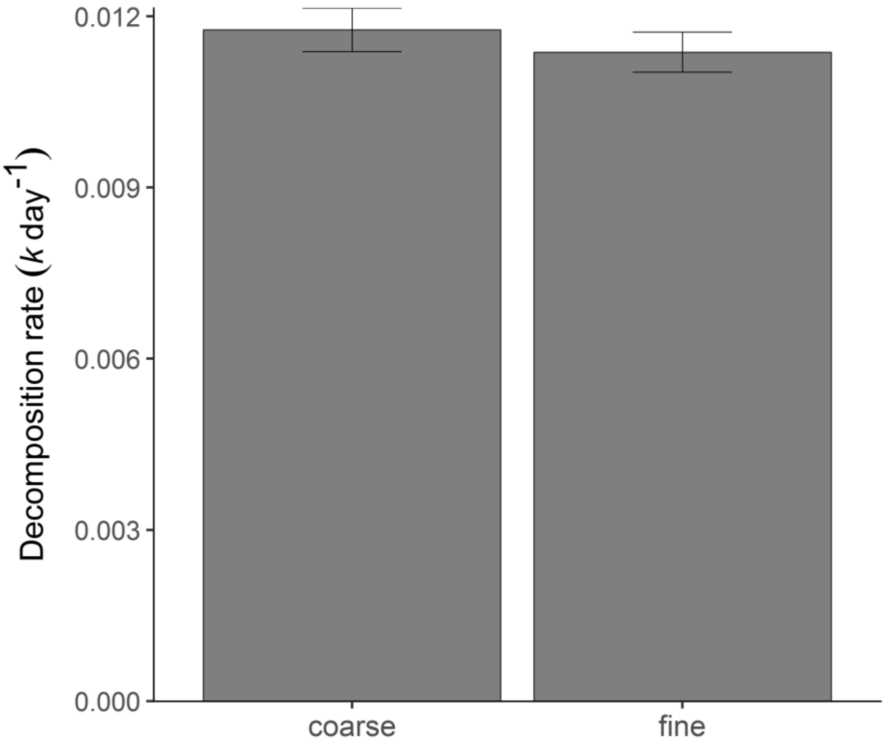

Figure S3. Decomposition rates in coarse-mesh bags (microorganisms and detritivores) and fine-mesh bags (microorganisms only). LME: $p = 0.428$. Error bars are SE.

Table S1. Leaf litter traits (mean ±SD, n=3) of the 12 species used in the experiment

	C % dry mass	N % dry mass	P g/kg dry mass	Lignin g/kg dry mass	Total phenolics g/kg dry mass	Total tannins g/kg dry mass	C:N ratio	N:P ratio
Jacaranda puberula	48.8 (± 0.93)	2.6 (± 0.38)	1.4 (± 0.30)	201.5 (± 8.10)	41.7 (± 4.27)	34.3 (± 4.50)	19.2(± 2.44)	1.93 (± 0.25)
Inga sbnuda	47.2 (± 0.18)	3.3 (± 0.16)	1.3 (± 0.14)	325.3 (± 2.04)	100.9 (± 5.38)	81.9 (± 4.44)	18.0 (± 0.67)	2.53 (± 0.17)
Alchornea triplinervia	45.4 (± 0.15)	2.1 (± 0.10)	1.0 (± 0.04)	151.2 (± 5.81)	175.9 (± 8.31)	169.1 (± 8.26)	21.9 (± 1.13)	2.02 (± 0.07)
Pera glabrata	47.4 (± 0.43)	1.8 (± 0.11)	0.8 (± 0.18)	498.0 (± 22.04)	94.7 (± 6.29)	56.6 (± 3.10)	26.6 (± 1.58)	2.66 (± 0.65)
Myrcia glabra	47.7 (± 0.18)	1.6 (± 0.07)	0.9 (± 0.02)	309.5 (± 4.09)	161.3 (± 4.61)	100.5 (± 7.20)	29.5 (± 1.16)	1.86 (± 0.11)
Myrcia racemosa	41.6 (± 0.37)	1.4 (± 0.04)	0.5 (± 0.07)	96.9 (± 8.74)	124.1 (± 6.19)	115.0 (± 6.30)	30.2 (± 0.71)	2.79 (± 0.33)
Andira anthelmia	48.2 (± 0.20)	3.1 (± 0.10)	1.4 (± 0.12)	338.1 (± 3.74)	43.1 (± 2.58)	37.0 (± 2.33)	15.5 (± 0.51)	2.30 (± 0.17)
Abarema brachystachia	47.2 (± 0.07)	3.1 (± 0.10)	1.1 (± 0.09)	238.8 (± 2.12)	21.7 (± 1.29)	14.7 (± 0.94)	15.2 (± 0.49)	2.82 (± 0.17)
Cupania oblongifolia	48.2 (± 0.75)	2.0 (± 0.10)	1.3 (± 0.26)	362.3 (± 5.59)	84.0 (± 10.77)	69.7 (± 8.46)	24.3 (± 1.35)	1.67 (± 0.30)
Miconia sp.	44.3 (± 0.57)	1.8 (± 0.06)	0.8 (± 0.06)	308.1 (± 3.51)	101.1 (± 6.59)	91.5 (± 6.72)	24.4 (± 0.95)	2.33 (± 0.14)
Inga edulis	46.3 (± 0.35)	2.0 (± 0.10)	1.9 (± 0.20)	350.7 (± 0.88)	59.4 (± 8.71)	41.6 (± 6.48)	13.9 (± 0.50)	1.84 (± 0.19)
Lacistema pubescens	45.1 (± 0.15)	3.3 (± 0.08)	1.2 (± 0.02)	256.1 (± 18.07)	77.2 (± 5.83)	61.5 (± 4.67)	22.6 (± 0.80)	1.71 (± 0.04)

Table S2. Tukey pairwise contrasts between temperature levels for each litter treatment in the microbial decomposition. Significance in $p < 0.05$ are highlighted in bold.

treatment	contrast	estimate	df	t ratio	p
LT1	ambient x warming	0.251	228	3.273	**0.001**
LT2	ambient x warming	0.095	228	1.240	0.216
LT3	ambient x warming	0.193	228	2.547	**0.011**
LT4	ambient x warming	0.042	228	0.556	0.579
LT5	ambient x warming	-0.052	228	-0.698	0.486

Table S3. Results of a backward model selection based on the Akaike information criterion, AIC, examining the influence of quality (qlt1 and qlt2), functional diversity (FD1 and FD2) and temperature (temp) on microbial, total (microorganisms and detritivores) and detritivore-mediated decomposition rates. Time was included in the models as a covariate and quadratic terms were included to account for non-linear trends. Non-signinficant p-values indicate that models are similar.

	Models	**df**	**AIC**	**p**
	total (quality)			
1	log(k) ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + richness + abundance+qlt1:temp + qlt1:time + qlt1:richness + qlt1:abundance + qlt2:temp + qlt2:time + qlt2:richness + qlt2:abundance + I(qlt1^2):temp + I(qlt1^2):time + I(qlt1^2):richness + I(qlt1^2):abundance + I(qlt2^2):temp + I(qlt2^2):time + I(qlt2^2):richness + I(qlt2^2):abundance + temp:time + temp:richness + temp:abundance + time:richness + time:abundance + richness:abundance	33	276.5	
2	log(k) ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + richness + abundance+qlt1:temp + qlt1:time + qlt1:richness + qlt1:abundance + qlt2:temp + qlt2:time + qlt2:richness + qlt2:abundance + I(qlt1^2):temp + I(qlt1^2):time + I(qlt1^2):richness + I(qlt1^2):abundance + I(qlt2^2):temp + I(qlt2^2):time + I(qlt2^2):richness + I(qlt2^2):abundance + temp:time + temp:richness + time:richness + time:abundance + richness:abundance	32	274.7	0.63
3	log(k) ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + richness + abundance+qlt1:temp + qlt1:time + qlt1:richness + qlt1:abundance + qlt2:temp + qlt2:time + qlt2:richness + qlt2:abundance + I(qlt1^2):temp + I(qlt1^2):time + I(qlt1^2):richness + I(qlt1^2):abundance + I(qlt2^2):temp + I(qlt2^2):time + I(qlt2^2):richness + I(qlt2^2):abundance + temp:time + temp:richness + time:richness + richness:abundance	31	272.9	0.65
4	log(k) ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + richness + abundance+qlt1:temp + qlt1:time + qlt1:richness + qlt1:abundance + qlt2:temp + qlt2:time + qlt2:richness + I(qlt1^2):temp + I(qlt1^2):time +	30	271	0.75

	I(qlt1^2):richness + I(qlt1^2):abundance + I(qlt2^2):temp + I(qlt2^2):time + I(qlt2^2):richness + I(qlt2^2):abundance + temp:time + temp:richness + time:richness + richness:abundance			
5	log(k) ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + richness + abundance+qlt1:temp + qlt1:time + qlt1:richness + qlt1:abundance + qlt2:temp + qlt2:time + qlt2:richness + I(qlt1^2):temp + I(qlt1^2):time + I(qlt1^2):richness + I(qlt2^2):temp + I(qlt2^2):time + I(qlt2^2):richness + I(qlt2^2):abundance + temp:time + temp:richness + time:richness + richness:abundance	29	269.3	0.61
6	log(k) ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + richness + abundance+qlt1:temp + qlt1:time + qlt1:richness + qlt1:abundance + qlt2:temp + qlt2:time + qlt2:richness + I(qlt1^2):temp + I(qlt1^2):time + I(qlt1^2):richness + I(qlt2^2):temp + I(qlt2^2):time + I(qlt2^2):richness + temp:time + temp:richness + time:richness + richness:abundance	28	267.3	0.96
7	log(k) ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + richness + abundance+qlt1:temp + qlt1:time + qlt1:richness + qlt1:abundance + qlt2:temp + qlt2:time + qlt2:richness + I(qlt1^2):temp + I(qlt1^2):time + I(qlt1^2):richness + I(qlt2^2):temp + I(qlt2^2):time + temp:time + temp:richness + time:richness + richness:abundance	27	265.5	0.63
8	log(k) ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + richness + abundance+qlt1:temp + qlt1:time + qlt1:richness + qlt1:abundance + qlt2:temp + qlt2:time + qlt2:richness + I(qlt1^2):temp + I(qlt1^2):time + I(qlt2^2):temp + I(qlt2^2):time + temp:time + temp:richness + time:richness + richness:abundance	26	263.6	0.71
9	log(k) ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + richness + abundance+qlt1:temp + qlt1:time + qlt1:richness + qlt1:abundance + qlt2:temp + qlt2:time + I(qlt1^2):temp + I(qlt1^2):time + I(qlt2^2):temp + I(qlt2^2):time + temp:time + temp:richness + time:richness + richness:abundance	25	261.7	0.76
10	log(k) ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + richness + abundance+qlt1:temp + qlt1:time + qlt1:richness + qlt2:temp + qlt2:time + I(qlt1^2):temp + I(qlt1^2):time + I(qlt2^2):temp + I(qlt2^2):time + temp:time + temp:richness + time:richness + richness:abundance	24	260.3	0.45
11	log(k) ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + richness + abundance+qlt1:temp + qlt1:time + qlt1:richness + qlt2:temp + qlt2:time + I(qlt1^2):time + I(qlt2^2):temp + I(qlt2^2):time + temp:time + temp:richness + time:richness + richness:abundance	23	258.4	0.79
12	log(k) ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + richness + abundance+qlt1:temp + qlt1:time + qlt1:richness + qlt2:temp + qlt2:time + I(qlt2^2):temp + I(qlt2^2):time + temp:time + temp:richness + time:richness + richness:abundance	22	257.4	0.31
13	log(k) ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + richness + abundance+qlt1:temp + qlt1:time + qlt1:richness + qlt2:temp + qlt2:time + I(qlt2^2):temp + temp:time + temp:richness + time:richness + richness:abundance	21	255.7	0.61
14	log(k) ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + richness + abundance+qlt1:temp + qlt1:time + qlt1:richness + qlt2:temp + I(qlt2^2):temp + temp:time + temp:richness + time:richness + richness:abundance	20	255.1	0.24
15	log(k) ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + richness + abundance+qlt1:temp + qlt1:time + qlt1:richness + qlt2:temp + I(qlt2^2):temp + temp:richness + time:richness + richness:abundance	19	253.6	0.46
16	log(k) ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + richness + abundance+qlt1:temp + qlt1:time + qlt1:richness + qlt2:temp + temp:richness + time:richness + richness:abundance	18	252.4	0.39
17	log(k) ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + richness + abundance + qlt1:temp + qlt1:time + qlt1:richness + temp:richness + time:richness + richness:abundance	17	252	0.20

18	log(k) ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + richness + abundance + qlt1:temp + qlt1:time + qlt1:richness + time:richness + richness:abundance	16	252.1	0.15
19	log(k) ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + richness + abundance + qlt1:temp + qlt1:time + qlt1:richness + richness:abundance	15	251.1	0.32
20	log(k) ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + richness + abundance + qlt1:temp + qlt1:time + qlt1:richness	14	250.2	0.28
21	log(k) ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + richness + abundance + qlt1:temp + qlt1:time	13	250.8	0.11
22	log(k) ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + richness + abundance + qlt1:time	12	251.6	0.10
23	log(k) ~ qlt1 + qlt2 + I(qlt2^2) + temp + time + richness + abundance + qlt1:time	11	253.1	0.06
24	log(k) ~ qlt1 + qlt2 + I(qlt2^2) + temp + time + abundance + qlt1:time	10	251.1	0.99
25	log(k) ~ qlt1 + qlt2 + I(qlt2^2) + temp + time + qlt1:time	9	249.8	0.43
	microbial (quality)			
1	log(k) ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + qlt1:temp + qlt1:time + qlt2:temp + qlt2:time + I(qlt1^2):temp + I(qlt1^2):time + I(qlt2^2):temp + I(qlt2^2):time + temp:time	18	107.1	
2	log(k) ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + qlt1:temp + qlt1:time + qlt2:temp + qlt2:time + I(qlt1^2):temp + I(qlt2^2):temp + I(qlt2^2):time + temp:time	17	107.1	0.15
3	log(k) ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + qlt1:temp + qlt1:time + qlt2:time + I(qlt1^2):temp + I(qlt2^2):temp + I(qlt2^2):time + temp:time	16	105.1	0.93
4	log(k) ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + qlt1:temp + qlt1:time + qlt2:time + I(qlt1^2):temp + I(qlt2^2):temp + I(qlt2^2):time + temp:time	15	103.6	0.49
5	log(k) ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + qlt1:temp + qlt1:time + qlt2:time + I(qlt1^2):temp + I(qlt2^2):time + temp:time	14	102.8	0.27
6	log(k) ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + qlt1:temp + qlt1:time + qlt2:time + I(qlt2^2):time + temp:time	13	100.9	0.72
	detritivores (quality)			
1	k ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + qlt1:temp + qlt1:time + qlt2:temp + qlt2:time + I(qlt1^2):temp + I(qlt1^2):time + I(qlt2^2):temp + I(qlt2^2):time + temp:time	18	-433.6	
2	k ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + qlt1:temp + qlt1:time + qlt2:time + I(qlt1^2):temp + I(qlt1^2):time + I(qlt2^2):temp + I(qlt2^2):time + temp:time	17	-435.4	0.68
3	k ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + qlt1:temp + qlt1:time + qlt2:time + I(qlt1^2):temp + I(qlt1^2):time + I(qlt2^2):temp + temp:time	16	-437.4	0.91
4	k ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + qlt1:temp + qlt1:time + I(qlt1^2):temp + I(qlt1^2):time + I(qlt2^2):temp + temp:time	15	-439.2	0.65
5	k ~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + qlt1:temp + qlt1:time + I(qlt1^2):temp + I(qlt2^2):temp + temp:time	14	-440.8	.051
6	k ~ qlt1+ qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + qlt1:temp + qlt1:time + I(qlt2^2):temp + temp:time	13	-441.4	0.23
7	k ~ qlt1+ qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + qlt1:temp + qlt1:time + temp:time	12	-443.3	0.86
8	k~ qlt1 + qlt2 + I(qlt1^2) + I(qlt2^2) + temp + time + qlt1:time + temp:time	11	-444.8	0.47
9	k ~ qlt1 + qlt2 + I(qlt2^2) + temp + time + qlt1:time + temp:time	10	-446.6	0.63
10	k ~ qlt1 + I(qlt2^2) + temp + time + qlt1:time + temp:time	9	-448	0.47
	total (FD)			
1	log(k) ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + richness + abundance + FD1:temp + FD1:time + FD1:richness + FD1:abundance + FD2:temp + FD2:time + FD2:richness + FD2:abundance + I(FD1^2):temp + I(FD1^2):time + I(FD1^2):richness + I(FD1^2):abundance + I(FD2^2):temp + I(FD2^2):time + I(FD2^2):richness + I(FD2^2):abundance + temp:time +	33	276.5	

	temp:richness + temp:abundance + time:richness + time:abundance + richness:abundance			
2	log(k) ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + richness + abundance + FD1:temp + FD1:time + FD1:abundance + FD2:temp + FD2:time + FD2:richness + FD2:abundance + I(FD1^2):temp + I(FD1^2):time + I(FD1^2):richness + I(FD1^2):abundance + I(FD2^2):temp + I(FD2^2):time + I(FD2^2):richness + I(FD2^2):abundance + temp:time + temp:richness + temp:abundance + time:richness + time:abundance + richness:abundance	32	274.5	0.85
3	log(k) ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + richness + abundance + FD1:temp + FD1:time + FD1:abundance + FD2:temp + FD2:time + FD2:richness + FD2:abundance + I(FD1^2):temp + I(FD1^2):time + I(FD1^2):richness + I(FD1^2):abundance + I(FD2^2):temp + I(FD2^2):time + I(FD2^2):richness + I(FD2^2):abundance + temp:time + temp:richness + time:richness + time:abundance + richness:abundance	31	272.7	0.64
4	log(k) ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + richness + abundance + FD1:temp + FD1:time + FD1:abundance + FD2:temp + FD2:time + FD2:richness + I(FD1^2):temp + I(FD1^2):time + I(FD1^2):richness + I(FD1^2):abundance + I(FD2^2):temp + I(FD2^2):time + I(FD2^2):richness + I(FD2^2):abundance + temp:time + temp:richness + time:richness + time:abundance + richness:abundance	30	270.9	0.67
5	log(k) ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + richness + abundance + FD1:temp + FD1:time + FD1:abundance + FD2:temp + FD2:time + FD2:richness + I(FD1^2):temp + I(FD1^2):time + I(FD1^2):richness + I(FD1^2):abundance + I(FD2^2):temp + I(FD2^2):time + I(FD2^2):richness + I(FD2^2):abundance + temp:time + temp:richness + time:richness + richness:abundance	29	269	0.74
6	log(k) ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + richness + abundance + FD1:temp + FD1:time + FD1:abundance + FD2:temp + FD2:time + FD2:richness + I(FD1^2):temp + I(FD1^2):time + I(FD1^2):richness + I(FD1^2):abundance + I(FD2^2):temp + I(FD2^2):richness + I(FD2^2):abundance + temp:time + temp:richness + time:richness + richness:abundance	28	267.2	0.69
7	log(k) ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + richness + abundance + FD1:temp + FD1:time + FD1:abundance + FD2:temp + FD2:time + FD2:richness + I(FD1^2):temp + I(FD1^2):time + I(FD1^2):richness + I(FD1^2):abundance + I(FD2^2):temp + I(FD2^2):abundance + temp:time + temp:richness + time:richness + richness:abundance	27	265.5	0.57
8	log(k) ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + richness + abundance + FD1:temp + FD1:time + FD1:abundance + FD2:temp + FD2:time + FD2:richness + I(FD1^2):time + I(FD1^2):richness + I(FD1^2):abundance + I(FD2^2):temp + I(FD2^2):abundance + temp:time + temp:richness + time:richness + richness:abundance	26	264.2	0.42
9	log(k) ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + richness + abundance + FD1:temp + FD1:time + FD1:abundance + FD2:temp + FD2:time + FD2:richness + I(FD1^2):time + I(FD1^2):richness + I(FD1^2):abundance + I(FD2^2):temp + temp:time + temp:richness + time:richness + richness:abundance	25	262.4	0.65
10	log(k) ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + richness + abundance + FD1:temp + FD1:time + FD1:abundance + FD2:temp + FD2:time + FD2:richness + I(FD1^2):time + I(FD1^2):richness + I(FD1^2):abundance + temp:time + temp:richness + time:richness + richness:abundance	24	260.7	0.57
11	log(k) ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + richness + abundance + FD1:temp + FD1:time + FD2:temp + FD2:time + FD2:richness + I(FD1^2):time + I(FD1^2):richness + I(FD1^2):abundance + temp:time + temp:richness + time:richness + richness:abundance	23	259.4	0.43
12	log(k) ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + richness + abundance + FD1:temp + FD1:time + FD2:temp + FD2:time + FD2:richness	22	257.4	0.98

	+ I(FD1^2):time + I(FD1^2):richness + temp:time + temp:richness + time:richness + richness:abundance			
13	log(k) ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + richness + abundance + FD1:temp + FD2:temp + FD2:time + FD2:richness + I(FD1^2):time + I(FD1^2):richness + temp:time + temp:richness + time:richness + richness:abundance	21	255.8	0.50
14	log(k) ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + richness + abundance + FD1:temp + FD2:temp + FD2:time + FD2:richness + I(FD1^2):richness + temp:time + temp:richness + time:richness + richness:abundance	20	254	0.62
15	log(k) ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + richness + abundance + FD1:temp + FD2:temp + FD2:time + FD2:richness + temp:time + temp:richness + time:richness + richness:abundance	19	252.4	0.53
16	log(k) ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + richness + abundance + FD1:temp + FD2:temp + FD2:time + FD2:richness + temp:richness + time:richness + richness:abundance	18	251	0.44
17	log(k) ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + richness + abundance + FD1:temp + FD2:temp + FD2:time + FD2:richness + time:richness + richness:abundance	17	251.7	0.10
18	log(k) ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + richness + abundance + FD1:temp + FD2:temp + FD2:time + FD2:richness + time:richness	16	250.8	0.30
19	log(k) ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + richness + abundance + FD1:temp + FD2:time + FD2:richness + time:richness	15	251.1	0.13
20	log(k) ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + richness + abundance + FD1:temp + FD2:time + FD2:richness	14	250.6	0.22
21	log(k) ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + richness + abundance + FD1:temp + FD2:time	13	250.2	0.20
22	log(k) ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + richness + abundance + FD2:time	12	250.3	0.15
23	log(k) ~ FD1 + FD2 + I(FD1^2) + temp + time + richness + abundance + FD2:time	11	248.5	0.63
24	log(k) ~ FD1 + FD2 + temp + time + richness + abundance + FD2:time	10	249.4	0.09
25	log(k) ~ FD1 + FD2 + temp + time + abundance + FD2:time	9	247.4	0.99
	microbial (FD)			
1	log(k) ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + FD1:temp + FD1:time + FD2:temp + FD2:time + I(FD1^2):temp +I(FD1^2):time + I(FD2^2):temp + I(FD2^2):time + temp:time	18	107.1	
2	log(k) ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + FD1:temp + FD1:time + FD2:temp + FD2:time +I(FD1^2):time + I(FD2^2):temp + I(FD2^2):time + temp:time	17	105.6	0.46
3	log(k) ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + FD1:temp + FD1:time + FD2:temp + FD2:time + I(FD1^2):time + I(FD2^2):time + temp:time	16	104.8	0.28
4	log(k) ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + FD1:temp + FD1:time + FD2:temp + FD2:time + I(FD1^2):time + temp:time	15	104.2	0.24
5	log(k) ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + FD1:time + FD2:temp + FD2:time + I(FD1^2):time + temp:time	14	104	0.17
6	log(k) ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + FD1:time + FD2:temp + FD2:time + I(FD1^2):time	13	104.5	0.11
7	log(k) ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + FD2:temp + FD2:time + I(FD1^2):time	12	102.6	0.71
	detritivores (FD)			
1	k ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + FD1:temp + FD1:time + FD2:temp + FD2:time + I(FD1^2):temp + I(FD1^2):time + I(FD2^2):temp + I(FD2^2):time + temp:time	18	-433.6	
2	k ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + FD1:temp + FD1:time + FD2:temp + FD2:time + I(FD1^2):temp + I(FD1^2):time + I(FD2^2):temp + temp:time	17	-435.5	0.72

3	k ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + FD1:temp + FD1:time + FD2:time + I(FD1^2):temp + I(FD1^2):time + I(FD2^2):temp + temp:time	16	-437.4	0.83
4	k ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + FD1:temp + FD1:time + FD2:time + I(FD1^2):temp + I(FD2^2):temp + temp:time	15	-438.7	0.39
5	k ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + FD1:time + FD2:time + I(FD1^2):temp + I(FD2^2):temp + temp:time	14	-439.1	0.21
6	k ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + FD1:time + FD2:time + I(FD1^2):temp + temp:time	13	-441.1	0.84
7	k ~ FD1 + FD2 + I(FD1^2) + I(FD2^2) + temp + time + FD1:time + FD2:time + temp:time	12	-442.7	0.56
8	k ~ FD1 + FD2 + I(FD1^2) + temp + time + FD1:time + FD2:time + temp:time	11	-444.2	0.48

4. SÍNTESE

Nesse estudo simulamos o efeito do aquecimento e de mudanças na biodiversidade através de um experimento em microcosmos aquáticos naturais. O efeito do aquecimento foi obtido com equipamento de controle de temperatura programado para aumentar em 4ºC a temperatura real do ambiente. Alterações na biodiversidade foram simuladas através da variação na qualidade e diversidade funcional de detritos. Como objetivos, investigamos os efeitos da temperatura e variações nos detritos sobre a estrutura de comunidades de insetos aquáticos e sobre o processo de decomposição. Nossos resultados mostraram que tanto o aumento da temperatura como a variação na qualidade e na diversidade funcional dos detritos afetam a abundância, a riqueza e a composição de insetos aquáticos. Interessantemente, mostramos que características específicas dos detritos (i.e., atributos funcionais) podem gerar efeitos indiretos sobre níveis tróficos mais elevados (predadores) através de seus recursos (presas). Além disso, mostramos que essas variações nos tipos de detritos combinados com a mudança na temperatura, pode afetar o funcionamento desses ecossistemas, e o efeito dessas perturbações podem variar de acordo com os organismos envolvidos. De maneira geral, podemos concluir que mudanças climáticas, como o aumento da temperatura, juntamente com alterações na biodiversidade podem gerar efeitos determinantes em alguns sistemas naturais, desde a estruturação das comunidades até o funcionamento desses ecossistemas.