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REBECA LEME OLIVA

Home field advantage effects on decomposition of leaf litter in tropical riparian forests: effects of restoration age, litter quality, and soil nutrients

São Carlos -SP
2020

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Dissertação apresentada ao Programa de Pós-Graduação em Ciências Ambientais da Universidade Federal de São Carlos, como parte dos requisitos para a obtenção do título de Mestre em Ciências Ambientais¹.

Orientador: Prof. Dr Marcel Okamoto Tanaka
Coorientadora: Dr. Ciska Veen

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Oliva, Rebeca Leme

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Prof. Dr. Marcel Okamoto Tanaka (UFSCar)

Profa. Dra. Ciska Veen (NIOO-KNAW)

Prof. Dr. Victor Satoru Saito (UFSCar)

Prof. Dr. Jonathan R. de Long (WUR)

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RESUMO

Citação: Oliva, R.L., Veen, G.F. and Tanaka, M.O. Home Field Advantage on decomposition of leaf litter in tropical riparian forests: effects of restoration age, litter quality and soil nutrients (2020). 40p. Dissertação (Mestrado) – Universidade Federal de São Carlos, Centro de Ciências Biológicas e da Saúde, Programa de Pós-Graduação em Ciências Ambientais, São Carlos - 2020

A decomposição da matéria orgânica é influenciada por vários fatores bióticos e abióticos. A qualidade da serapilheira, a concentração de nutrientes no solo e as interações planta-solo são os principais fatores que influenciam esse processo ecossistêmico nas florestas em escalas locais. Foi comprovado que a ocorrência do fenômeno de Home Field Advantage (HFA), caracterizado pela acelerada taxa de decomposição da serapilheira em sua própria casa, quando comparado a outros locais, está diretamente relacionado aos fatores mencionados anteriormente. Os efeitos do HFA podem ocorrer em florestas naturais, mas ainda não se sabe se podem ser detectados em zonas ripárias em restauração. Aqui, testamos se a qualidade da serapilheira, as concentrações de nutrientes no solo e o estágio de restauração (idade) influenciavam a HFA. Realizamos experimentos de translocação recíproca para testar as seguintes hipóteses: (1) áreas em restauração da mesma idade, mas com diferenças na concentração de nutrientes do solo e na qualidade da serapilheira, mostrarão HFA em áreas com baixa qualidade da serapilheira e nutrientes do solo; (2) áreas em restauração com idades diferentes, mas com conteúdo semelhante de nutrientes do solo e qualidade da serapilheira, apresentarão HFA em áreas mais antigas, uma vez que os decompositores e as plantas tiveram mais tempo para desenvolver relações estreitas; (3) áreas remanescentes intactas da floresta ripária (isto é, áreas que não estão em recuperação) que diferem nas concentrações de nutrientes do solo e na qualidade da serapilheira apresentariam HFA em áreas com baixa qualidade da serapilheira e concentrações de nutrientes no solo; (4) diferenças nos nutrientes do solo e na qualidade da serapilheira afetariam o HFA e (5) dissimilaridades mais altas nas concentrações de nutrientes no solo e na qualidade da serapilheira resultariam em efeitos mais fortes do HFA. Nossos resultados não indicaram efeitos do HFA em nenhuma hipótese testada, embora tenhamos encontrado algum suporte para a hipótese 1, pois houve um efeito de habilidade em uma área e uma tendência para um efeito negativo de HFA em outra. A serapilheira se decompôs muito rapidamente em todas as áreas, possivelmente devido a fortes chuvas no final do experimento, de modo que a porção lábil provavelmente foi totalmente decomposta, o que poderia ocultar os efeitos do HFA. Ao analisar os resultados dos três experimentos independentes simultaneamente, descobrimos uma relação entre HFA e qualidade da serapilheira, e também uma relação entre HFA e dissimilaridade na qualidade do solo entre os locais de origem e fora, e as áreas mais diferentes foram as áreas remanescentes. Em ecossistemas naturais, como remanescentes florestais, as plantas podem ter mais tempo para desenvolver relações com a comunidade do solo, em comparação com os fragmentos de floresta ripária em restauração estudados. Essa alta dissimilaridade entre as áreas remanescentes também pode ser devida ao desenvolvimento de outras complexas relações heterogêneas planta-solo, estabelecidas ao longo do tempo. Portanto, nosso estudo indica que, embora essas áreas de floresta ripária em recuperação possam cobrir grandes áreas, o tempo após a restauração

pode não ter sido suficiente para recuperar comunidades microbianas e funções ecossistêmicas mais especializadas.

Palavras chave: Home Field Advantage; Decomposição; Restauração

ABSTRACT

Decomposition of organic matter is influenced by several biotic and abiotic factors. Litter quality, soil nutrient concentration and plant-soil interactions are major factors influencing this ecosystem process in forests at local scales. The home field advantage effect (HFA) has been proven to accelerate decomposition rates for litter at its own home when compared to away sites, and is directly related to the previously mentioned factors. HFA effects can occur in natural forests, but it is still unknown if it can be detected in riparian areas under restoration. Here, we tested if litter quality, soil nutrient concentrations and restoration stage (age) influenced HFA. We carried out three-way reciprocal litter transplant experiments to test the following hypotheses: (1) areas under restoration of the same age, but with differences in soil nutrient concentration and litter quality, will show HFA in areas with low litter quality and soil nutrient concentration; (2) areas under restoration with different ages, but with similar content of soil nutrients and litter quality, will present HFA in older areas, given that decomposers and plants had more time to develop close-knit positive relationships; (3) riparian forest intact remnant areas (i.e., areas not undergoing restoration) that differ in soil nutrient concentrations and litter quality would present HFA in areas with low litter quality and soil nutrient concentrations. Our results indicated no effects of HFA in any hypotheses tested, although we found some support for hypothesis 1 as there was an ability effect in one area and a trend for a negative HFA effect in another. Leaf litter decomposed very fast across all areas possibly due to heavy rainfall in the end of the experiment, so that labile litter was likely totally decomposed, which could obscure HFA effects. We also analyzed the results of the three independent experiments simultaneously to test the additional hypotheses: (4) soil nutrients and litter quality would affect HFA and (5) higher dissimilarities in soil nutrient concentrations and litter quality between home and away sites would result in stronger HFA effects. We found a relationship between HFA and leaf litter quality, and also a relationship between HFA and dissimilarity in soil quality between home and away sites. Also, the most dissimilar areas were the remnant areas. In natural ecosystems, such as forest remnants, plants may have more time to develop relationships with the soil community, in comparison to the riparian forest fragments under restoration studied. This high dissimilarity among remnant areas could also be due to the development of other complex heterogeneous plant-soil relationships, established throughout time. Therefore, our studies suggest that although these riparian forest areas under restoration can cover large areas, the time after restoration may not have been enough to recover microbial communities and more specialized ecosystem functions.

Key words: Home Field Advantage, HFA, Decomposition, Restoration

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INTRODUÇÃO GERAL

A produtividade primária nos ecossistemas terrestres está diretamente ligada à ciclagem de nutrientes e, portanto, à produção de serapilheira, uma das principais fontes de carbono (C) orgânico em ecossistemas terrestres (Gessner *et. al.*, 2010). A decomposição da matéria orgânica fornece nutrientes e energia para as cadeias alimentares terrestres, influenciando a produção primária e a ciclagem de nutrientes, bem como o ciclo global do carbono (Gessner *et al.*, 2010, Lin *et al.*, 2019). Em escala global, as taxas de decomposição de matéria orgânica são influenciadas por: (1) qualidade da serapilheira (representada pela composição química da mesma, variando de lábil - decomposição mais rápida - a recalcitrante - decomposição mais lenta -), (2) fatores climáticos (como temperatura, precipitação e evapotranspiração) e (3) variações geográficas (por exemplo, latitude, altitude e domínios fitogeográficos) (Perez *et al.*, 2013, Keiser e Bradford, 2017). Entretanto, em escalas locais, outros fatores tendem a determinar taxas de decomposição, por exemplo, condições de microclima, a composição da biota decompositora e suas interações com as espécies de plantas presentes no ecossistema (Bezemer *et al.*, 2010, Austin *et al.*, 2014, Bradford *et al.*, 2016, Lin *et al.*, 2019). Nos ecossistemas florestais, fatores bióticos e abióticos influenciam as taxas de decomposição, incluindo a qualidade da serapilheira e a fertilidade do solo (Gessner *et al.*, 2010, Berg e McLaugherty, 2014). Tanto a qualidade da serapilheira quanto a composição da comunidade vegetal e a fertilidade do solo podem interagir para determinar a atividade microbiana e a decomposição da serapilheira em um processo de retro-alimentação (Veen *et al.* 2018, Soares *et al.* 2020). Os recursos fornecidos pelo solo e pela matéria orgânica influenciam a atividade microbiana e podem também influenciar a composição microbiana (Bhatnagar *et al.* 2018). Portanto, plantas e microrganismos podem estar altamente relacionados por meio de mecanismos de feedback (Mori *et. al.*, 2018).

Dessa forma, as taxas de decomposição podem ser mais altas quando a serapilheira se decompõe sob a comunidade vegetal da qual é derivada (em casa) e não abaixo das áreas dominadas por diferentes comunidades vegetais (fora de casa) (Gholz *et. al.*, 2000; Ayres *et. al.*, 2009; Keiser *et. al.*, 2014). Esse efeito é chamado de "Home Field Advantage" (HFA) e foi usado pela primeira vez em ecologia por Gholz *et. al.* (2000). Essa teoria é amplamente utilizada no mundo do esporte, para explicar o desempenho esperado de uma certa equipe quando se joga em casa (Clarke e Norman, 1995). Embora o HFA tenha sido exaustivamente estudado na última década, ainda há muito a ser entendido. Além disso, os efeitos da HFA demonstraram ser variáveis, e a sua força e direção podem, em certa medida, ser explicadas por vários fatores.

Ainda é incerto quais componentes ambientais interagem com a HFA e como eles podem influenciar esse efeito ecológico (Perez *et. al.*, 2013, Veen *et. al.*, 2018). Por exemplo, diferenças no estágio sucessional das florestas podem influenciar as comunidades de decompositores ao longo do tempo, alterando os padrões de decomposição (Veen *et. Al.*, 2018). Desta forma, este estudo avaliou se a quantidade de nutrientes do solo, qualidade da serapilheira, e tempo após o início da restauração florestal na decomposição podem influenciar

os efeitos de HFA na decomposição da serapilheira. Para tanto, foram feitos experimentos de translocação da serapilheira entre áreas em diferentes estágios de restauração florestal, assim como remanescentes de florestas ripárias, para avaliar os processos de decomposição. Como as interações entre planta e solo devem levar um tempo para se desenvolver e, da mesma forma, o desenvolvimento das comunidades microbianas envolvidas na decomposição não deve ser imediato, este pode dar subsídios para novos indicadores de recuperação de processos ecossistêmicos em florestas ripárias em restauração.

INTRODUCTION

Decomposition of organic matter supplies nutrients and energy for terrestrial food webs, influencing primary production and nutrient cycling, as well as the global carbon cycle (Gessner *et al.*, 2010, Lin *et al.*, 2019). In forest ecosystems, both biotic and abiotic factors are known to influence decomposition rates, including litter quality and soil fertility (Gessner *et al.*, 2010, Berg and McLaugherty, 2014). Litter quality has a major influence on decomposition rates because some chemical attributes can facilitate or inhibit the decomposition process by decomposer microorganisms (Cornwell *et al.*, 2008, Bradford *et al.*, 2016, Joly *et al.*, 2017, Lin *et al.*, 2019). Litter quality varies according to the proportion of labile and recalcitrant compounds in the organic matter. Labile compounds, such as proteins are easier to decompose whereas recalcitrant compounds, like cell-wall components (e.g. lignin) are harder to decompose (Chapin *et al.*, 2011). Therefore, litter with higher C:N ratios has a higher proportion of recalcitrant compounds and is harder to decompose and litter with lower C:N ratios has a higher proportion of labile compounds, being easier to decompose (Lin *et al.*, 2019).

Microbial activity that is responsible for litter decomposition is also affected by soil nutrient limitation. Nitrogen (N), for example, can stimulate microbial activity and increase decomposition rates, in the early stages of the process because it is limiting to the activity of the enzymes amylase and cellulase, which are vital to decomposition (Lin *et al.*, 2017). However, in later stages of decomposition, when the recalcitrant portion is left, N can inhibit the production of ligninolytic enzymes and, as a consequence, decrease decomposition rates (Xiaogai *et al.*, 2013). Phosphorus (P) also influences decomposition, since phosphatases present increased activity (yielding higher decomposition rates) in environments with low P availability (Hoyos-Santillan *et al.*, 2018). On the other hand, P addition reduces decomposition rates, as it makes it easier for microorganisms to absorb inorganic P, instead of mineralizing P from litter (Chen *et al.*, 2013, Hicks *et al.*, 2019). Carbon (C) can also limit microbial activity because most microorganisms are heterotrophs and obtain energy from organic C in the soil. If C is in short supply, microbial activity decreases.

Both litter quality, as determined by plant community composition, and soil fertility can interact to determine microbial activity and litter decomposition (Veen *et al.* 2018, Soares *et al.* 2020). Resources provided by soil and litter influence microbial activity, and may also influence microbial composition (Bhatnagar *et al.* 2018). Therefore, plant and microbial communities can be highly related through feedback mechanisms, because changes in the microbial community may occur faster than in the plant community (Mori *et al.*, 2018). These feedback mechanisms can be complex and influence both plant community composition and ecosystem functions, and can be modulated by environmental changes (van der Putten *et al.* 2016, Chung *et al.*, 2019). Bezemer *et al.*, (2010) found that both soil food webs and mineralization processes can be related with individual plant identity and neighborhood plant composition, so that differences in plant communities can influence organic matter decomposition. These differences at small spatial scales could potentially have impacts on large-scale decomposition processes (Bradford *et al.*, 2014, 2016).

Accordingly, various studies have indicated that decomposition rates tend to be higher when litter decomposes underneath the plant community from which it is derived (at home) rather than below areas dominated by different plant communities (away) (Ayres *et. al.*, 2009, Veen *et.al.*, 2015-a). This effect is called ‘Home-Field Advantage’ (HFA) and it was first used in ecology by Gholz *et. al.* (2000), who proposed that decomposer communities adapted to leaf litter inputs from their home site, accelerating the decomposition of this litter compared to litter from ‘away’ plant species. The HFA theory is derived from the sports world, to explain a team’s improved performance when playing at home (Clarke and Norman, 1995).

Many reciprocal transplant studies have contrasted decomposition rates of leaf litter at home and away to evaluate HFA patterns (Chapman and Koch 2007, Vivanco and Austin, 2008, Strickland *et. al.*, 2009). Studies have focused on the interactive effects between site and litter origin on litter mass loss to determine the presence of HFA. However, this interaction does not necessarily indicate the presence of HFA, because HFA effects should consider whether decomposition at home is accelerated when compared to decomposition of the same litter at away sites and not simply if there is any interaction between litter origin and mass loss (Ayres *et al.* 2009).

Therefore, Ayres *et. al.* (2009) adapted the model from Clarke and Norman (1995) to calculate HFA in reciprocal translocation experiments. This new model considered the additional mass loss at home and away for each litter ‘team’ to estimate HFA values. Since then, other researchers found HFA effects in different systems. For example, Jacob *et. al.* (2010) found HFA in Central European temperate deciduous forests related to an 8% increase in decomposition rates at home rather than away, due to the interaction between the moisture regime in the litter layer and decomposer preferences. Also, higher decomposition rates were detected in litter collected after 22 months (more than double the time recommended by Ayres’ methodology), suggesting that HFA can occur over longer time spans (Jacob *et. al.*, 2010). Additionally, Lin *et. al.* (2017) found HFA effects in coniferous forests after N addition to the soil, which resulted in a more abundant soil microbiota, supporting that HFA is strongly linked to the decomposer biota because microbial respiration was limited by N concentration. Although the Ayres *et. al.* (2009) model identified HFA patterns in the field, Keiser *et al.* (2011) considered that this model led to ambiguous results because the community at home could be more adapted to the litter produced there (HFA effect), but it could also have a greater ability to decompose this litter, which could be related to the litter characteristics.

Therefore, ability should be evaluated separately from HFA, as each of these effects results from different processes. HFA occurs when decomposers adapt to their home environment, as opposed to ability, which is due to an inherent capacity for a decomposer community to break down litter faster than another. The ability of a decomposer community to break down all types of litter (regardless of how recalcitrant they are) differs from the HFA, which results from the local adaptation of a particular decomposer community (or decomposer organisms) to degrade litter species that occur at the home site (Keiser *et al.* 2014). Different abilities for decomposer communities can be explained by the Functional Breadth Hypothesis, which proposes that decomposer organisms from recalcitrant litter environments have a broader functional capacity

and hence, can degrade several litter types more efficiently, independent of the physical and chemical composition of the litter (Keiser *et. al.*, 2014, Fanin *et. al.*, 2016). In contrast, functionally limited communities occur in richer habitats with higher nutrient concentration and, as a result, do not need to invest energy in specialized enzymes to degrade recalcitrant litter, hence they decompose this litter at lower rates when compared to labile litter (Keiser *et. al.*, 2014). With these considerations, Keiser *et. al.* (2014) proposed a different model that was able to simultaneously evaluate the influence of litter quality, soil community ability and HFA on decomposition rates.

Further, HFA effects have been shown to be variable, and the strength and direction can, to some extent, be explained by a number of factors. For example, addition of N, when matched with a significantly high microbial abundance in the soil, can enhance the HFA effect in subtropical coniferous forests because it increases microbial activity of species with different litter preferences (Yu *et. al.*, 2015, Lin *et. al.*, 2017). Also, litter quality can influence HFA patterns when litter quality at “home” and “away” differ (Freschet *et. al.*, 2012, Veen *et. al.*, 2015-a) suggesting that finding HFA is context-dependent. This means that differences between environments at home and away such as vegetation types, species composition, dominance, and other environmental differences may contribute to HFA effects. Finally, the HFA effect seems to be stronger earlier in the decomposition process, suggesting positive effects of labile compounds (Jacob *et. al.*, 2010). Labile compounds can be better indicators of HFA than recalcitrant ones because they are more easily decomposed and do not require communities with high ability to degrade, contrary to recalcitrant compounds.

Even though HFA has been thoroughly studied over the last decade, there are still many knowledge gaps. For instance, most studies were carried out in temperate ecosystems, like Europe (Perez *et. al.*, 2013, Veen *et. al.*, 2015, di Leonardo *et. al.*, 2018, Purahong *et. al.*, 2019), North America (Ayres *et. al.*, 2009, Kominoski *et. al.*, 2011, Jackrel *et. al.*, 2014, Keiser and Bradford, 2017, Jackrel *et. al.*, 2019, Simon *et. al.*, 2019) and even in South America (Vivanco and Austin, 2008), with few studies in tropical environments. Climate has a dominant effect on litter decomposition rates at a global scale, since differences in temperature and humidity directly influence microbial activity, plant community composition and decomposition (Berg and McClaugherty, 2014). Further, most studies carried out in tropical ecosystems did not find HFA effects and took place in natural ecosystems (Giesselmann *et. al.*, 2011, Bacheaga *et. al.*, 2016, Both *et. al.*, 2017, Kerdraon *et. al.*, 2019). There are no studies on HFA carried out in tropical forests under restoration, which highlights the importance of our study.

In addition, it is still uncertain which environmental components interact with HFA and how they might influence this ecological effect (Perez *et. al.*, 2013, Veen *et. al.*, 2018). For example, differences in the successional stage of forests can influence decomposer communities throughout time, changing decomposition patterns (Veen *et. al.*, 2018). Forests in late successional stages are expected to have stronger interactions between decomposers and the plant community, given that they had more time to interact than forests in earlier stages of succession (Veen *et. al.*, 2018). Therefore, plants in late successional stages have had a longer time to select for decomposer communities that are specialized in breaking down the litter

characteristic of that stage (Morriën *et al.*, 2017). Further, the inverse is also true: as soil microbiota from late successional stages have decomposed different qualities of litter throughout time, they must have a broader functional capacity, and hence a higher ability to decompose diverse litter (Keiser *et al.*, 2014). Therefore, each particular phase of succession will implicate in different forest structures, contrasting litter composition and distinct soil microbiota (Hilmers *et al.*, 2018), meaning that HFA may vary according to the successional stage of the forest (Veen *et al.*, 2018).

Understanding how HFA varies with ecological succession is important to explain changes in decomposition during the process of ecosystem recovery from deforestation. Large-scale deforestation of tropical forests has occurred globally, and forest restoration is necessary to recover ecosystem functions and processes. Restoration can be carried out through natural regeneration of the vegetation, to return to natural forest structure (Meli *et al.*, 2017), or by actively planting tree seedlings (Lamb *et al.*, 2005; Meli *et al.*, 2017). However, ecosystem restoration includes not only the recovery of vegetation structure and diversity, but also the recovery of functions such as nutrient cycling (Derhé *et al.*, 2016). Therefore, it is important to understand how ecosystem processes such as decomposition rates change along successional pathways and whether intimate relationships between litter types and decomposer communities are restored.

OBJECTIVES

In this study, our aim was to investigate if HFA is present and how much it contributes to decomposition rates in riparian areas under restoration in Southeastern Brazil. We designed a three-way reciprocal leaf litter transplant study that was performed in both remnant areas and areas under restoration. The chosen areas differed in litter input quality, successional stage (age, or time since active restoration) and soil nutrient concentrations. Therefore, we carried out three independent experiments to test the following hypotheses: (1) In areas under restoration which have roughly the same age, HFA should be present in areas with lower litter quality in comparison to areas with high quality litter (Perez *et al.*, 2013). (2) Also, given areas under restoration which had the same concentration of soil nutrients, but differed in age and litter quality, HFA should be present in older areas, given that plants and decomposers had more time to interact. (3) Furthermore, riparian forests remnant areas that differed in soil nutrient concentrations and litter quality, should present HFA in areas with lower values of litter quality and soil nutrient concentrations due to the presence of more generalist microbial communities (Veen *et al.*, 2018). Considering that the three experiments were independent evaluations of home and away litter decomposition in different riparian forest areas (remnants and under restoration), we used the combined data set from the three independent experiments to evaluate (4) whether litter and soil quality could result in higher HFA effects. And finally, considering that environmental differences between home and away sites can influence HFA (e.g., Ayres *et al.* 2009-a, Veen *et al.* 2015), (5) we asked if higher dissimilarities between “home” and “away” areas could lead to higher HFA effects (Freschet *et al.*, 2012, Veen *et al.*, 2018).

MATERIALS AND METHODS

Study Area

The experiment was conducted in riparian forest fragments undergoing restoration or remnant areas (Figure 1). These areas are within the Ribeirão do Feijão watershed (22° 04' 49" - 22° 09' 12" S, 47° 42' 59" - 47° 53' 20" W), the predominant source of drinking water in São Carlos city (São Paulo state). The Ribeirão do Feijão watershed extends through 22,864 ha and is a part of the Jacaré-Guaçu basin, an affluent of the Tietê River. The climate in the region is tropical altitude, Cwa according to Köppen's classification, with wet summers and dry winters (Rolim *et. al.*, 2007). Annual rainfall is concentrated between October and March (Sanches, 2015). Mean monthly rainfall in the austral summer between 1981 and 2010 was 254.6, 303.8, and 221.1 mm (December, January, and February, respectively; INMET, 2020-a). However, along the experiment (in 2020), the respective values were 233.8, 316.8, and 437.4 mm (INMET, 2020).

In this region, different geological formations can be found, and the areas selected for this study are located in the Serra Geral formation, with the predominance of oxisols (Cerminaro and Oliveira, 2015) mainly composed of clay, with homogeneous mineral soils, well-drained, and with little variation among horizons. Vegetation is heterogeneous, primarily as a result of human interference (Costa *et. al.*, 2019) and includes fragments of grasslands, arboreal savannas, riparian forests, and regeneration areas (Costa *et. al.*, 2019).

Between 2006 and 2014, the Non-Governmental Organization (NGO) "Iniciativa Verde" organized a project in partnership with landowners to restore riparian forests along the Ribeirão do Feijão basin using active restoration within the project "Plantando Águas" ("Planting Water"), which consists on planting seedlings of several species and direct seeding to speed up the recovery process of an ecosystem (Crouzeilles *et. al.*, 2017). In the present study, four riparian forests under restoration were used: R1 (planted in 2007), R2, R3 (both planted in 2008), and R6 (planted in 2012). Three remnant riparian forests (C1, C2 and C3) were also studied. Within each area, we delimited a 100 x 30 m plot parallel to the river, with four 10m x 10m plots, distanced 10 m from each other (Figure 2). Soil would drastically differ every 20-30 m in some remnant areas, ranging from a sandy soil, to a clay-dominated soil. To avoid compromising our experimental design, which relied on plots being replicates, that was the maximum distance we could set plots in the areas.

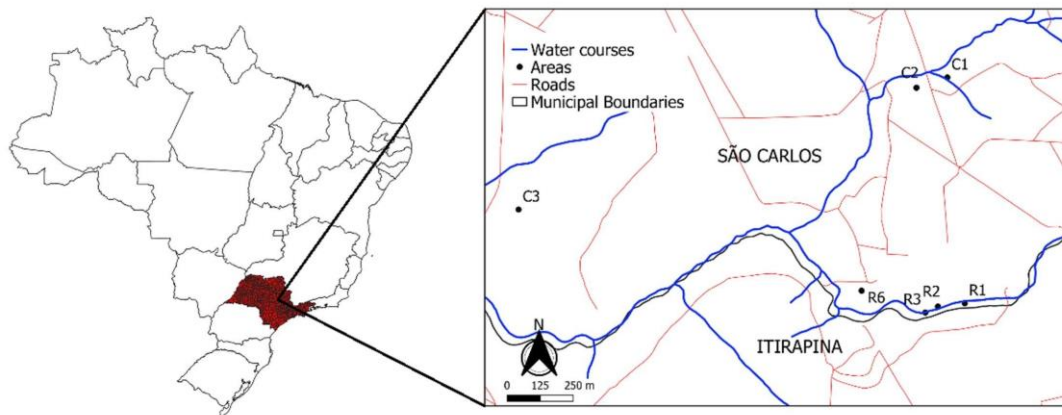


Figure 1 Location of the study areas along the Ribeirão do Feijão watershed, in São Paulo state, Brazil.

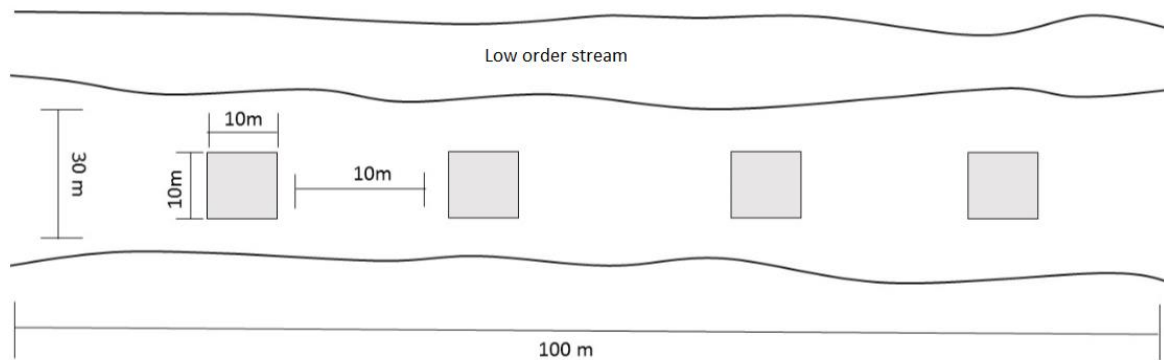


Figure 2 Representation of plot allocation within each area. Each plot was 10m x 10m and each area had 4 plots.

Soil and litter characterization

Each hypothesis assumes differences in fragment age, and litter and soil chemical characteristics. Therefore, we measured C, N and P values in litter and soil to determine which differences existed. Soil was sampled in June 17 2019 by randomly obtaining at least ten subsamples from 0 - 10 cm depth from each plot with a soil probe, avoiding the plot edges (by approximately 1m), which were grouped to form a single sample (about 300 g) per plot. Leaf litter was collected using 0.7 x 0.7 m litter traps with 2.0 mm nylon mesh (area = 0.5 m²) deployed in the center of each plot 30 cm above the ground (Figure 3). Litter traps were installed in May 2019 and recovered two months later. In the laboratory, the leaves were thoroughly mixed and about 5 g were ground with a Wiley mill for chemical analyses. Both soil and litter were analyzed for C and N by dry combustion at 1000 °C using a LECO TruSpec CHNS elemental analyzer at the Nutrient Cycling Laboratory from the Center of Nuclear Energy in

Agriculture of the University of São Paulo. Soil available P was determined by anion exchange resin (Olsen et al. 1954), and litter P was determined using colorimetric methods (Malavolta et al. 1997) in the Soil Fertility Laboratory of the Federal University of São Carlos.



Figure 3 Litter trap in the field. The image on the left shows the litter trap before while the image on the right shows it after eight weeks of collection.

Experimental design

For each hypothesis, we evaluated the effect of HFA (Home Field Advantage) adopting litter translocation experiments using three areas, following Keiser et al. (2014). For Hypothesis 1, we used areas R1, R2, and R3, which have roughly the same age (10-11 years), but differed in soil nutrient concentration and litter input quality. Hypothesis 2 included areas R1, R3 and R6, which had the same concentration of soil nutrients, but differed in age and litter input quality. Hypothesis 3 included the remnant areas C1, C2 and C3, that differed in soil nutrient concentration and litter input quality. Further, using data from the three previous hypotheses combined, we assessed how soil and litter nutrients could affect HFA (hypothesis 4) and how dissimilarities among “home” and “away” areas could lead to higher HFA effects (hypothesis 5).

The three hypotheses were tested at the same time, but with independent data. To test each hypothesis, we assembled 12 litter bags, summing 24 litter bags for areas R1 and R3 (used in two hypothesis) and 12 litterbags for each remaining area. Unfortunately, several plots presented low amounts of leaf litter, so we had to mix the leaves from the four plots to obtain enough material to construct the litterbags (Figure 4). Figure 4 is a representation of this process of litter bag assembly. The leaves from hypothetical areas A1, A2 and A3, which represent the

real areas used in each hypothesis, were collected from each of the four plots (P1, P2, P3 and P4) and then they were mixed and assembled into 12 individual litter bags.

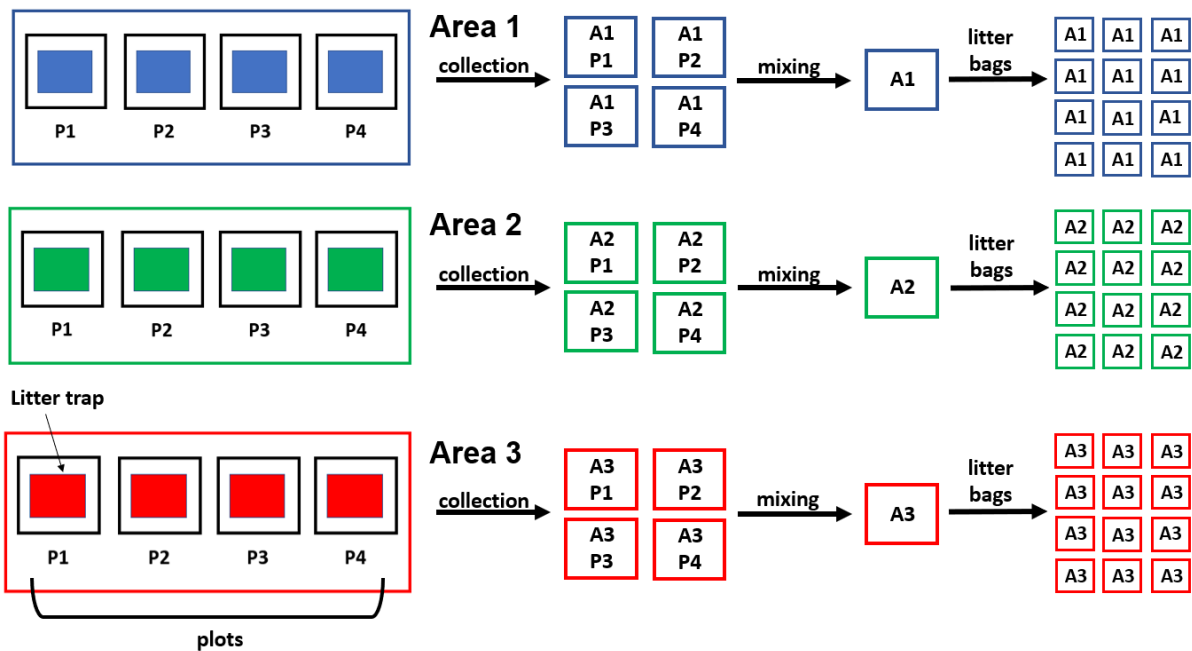


Figure 4 Collection of leaves and assemblage of litter bags (from left to right). Leaves were collected from all four plots (P1, P2, P3, P4) in each area (A1, A2, A3), then they were mixed together and assembled into 12 litter bags per area.

Three litter bags were tied together with nylon threads to allow them to be buried in a row to make them easier to find when collected (Figure 5). Each group was composed of one litter bag containing leaves from the home area, and two litter bags each containing leaves from one of the other two areas from each hypothesis. The areas involved in more than one hypothesis had two rows of litterbags buried in separate places, to maintain independence of the hypotheses. For example, plot 1 from area R1 had two rows of buried litter bags, one with leaves collected from areas R1, R2 and R3 (hypothesis 1) and another with leaves collected from R1, R3 and R6 (hypothesis 2). On the other hand, plot 1 from area C1 had only one row of litter bags buried, containing bags with leaves from areas C1, C2 and C3 (hypothesis 3). Using the combined data set from the three experiments, we tested hypothesis 4 and 5. This constituted the reciprocal translocation part of the experiment, as it guaranteed that areas tested in each of the hypotheses had litter bags from all the other areas involved in the hypothesis being tested, as well as litter collected locally.

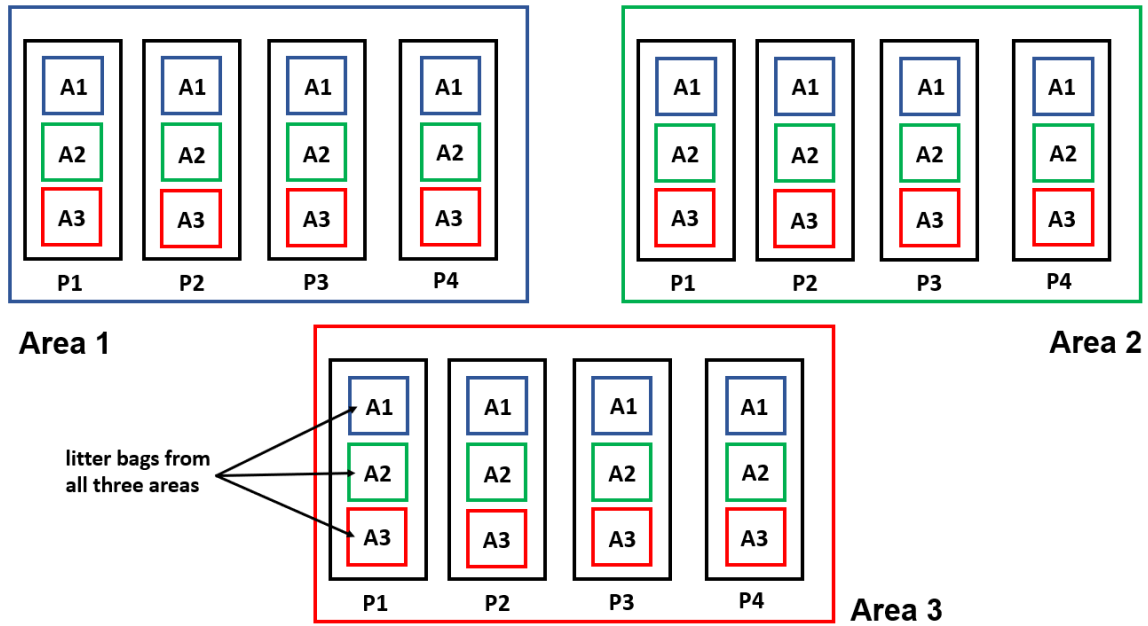


Figure 5 Experimental design of the litter translocation experiment. Blue squares represent litter bags assembled with leaves from Area 1, green squares are litter bags with leaves from Area 2 and red squares symbolize litter bags from Area 3. Every plot (P1, P2, P3, P4) was a replicate for each area and litter bags from every area (A1, A2, A3) were planted in every plot, qualifying this as a three-way reciprocal translocation experiment.

Litterbags were constructed with 2.0 mm nylon mesh, with 20 X 20 cm dimensions, sewed with a nylon line (Figure 6). Each litterbag was filled with 5 g of mixed leaf litter (which was air-dried for at least 48h) and buried at 8 cm depth on August 9 2019 (Figure 6).



Figure 6 (On the left) Example of litter bag assembled with leaves mixed from all four plots of area R1. (On the right) Row of litter bags from areas R1, R2 and R3 getting buried underground.

After approximately six months (193 days), litter bags were retrieved on February 18 2020 from the field. Leaves were carefully removed from the bags and dried at 65 °C for 72 h in an oven and then weighed to obtain remaining dry mass. The leaves were then ground in the Wiley mill

and burnt at 450 °C in a muffle furnace for 4 h to determine ash free dry mass. During retrieval of the litterbags, our team suffered a bee attack in the field and had to leave the area. This resulted in nine litter bags from three plots located in area R3 (Hypothesis 2) being retrieved almost a month later due to heavy rains during this period (March 13 2020, 217 days after the start of the experiment). We used the Olson exponential model to estimate the decomposition rate $k = (-\ln(X_t/X_0))/t$, and used this value to estimate mass loss after 193 days (Olson 1963).

Data Analysis

We evaluated each hypothesis regarding differences in soil and litter nutrients with a 1-way PERMANOVA (Permutational Multivariate Analysis of Variance) on the Euclidean distances matrix, with unrestricted permutation of the raw data and 9999 permutations (Anderson, 2001). Data (C, N, P, C:N, N:P) were transformed using the Box-Cox transformation to obtain normal distributions, and then standardized for zero means and unity variances (Legendre & Legendre, 2012). We evaluated differences among areas for each hypothesis using multiple comparisons tests. Distribution of areas and variables in the multivariate space were visualized using Principal Components Analysis (PCA) using the same distance matrix.

We evaluated mass loss from each hypothesis with a 3-factor mixed model ANOVA, considering Area and Leaf origin as fixed factors, and Plots nested in Areas as a random factor. Therefore, we used Plot(Area) as the denominator to test the effect of Area, and the interaction Leaf origin x Plot(Area) (identified as “Error” in the ANOVA tables) to test the remaining factors. When significant effects were found, differences between areas were determined with Tukey’s HSD multiple comparisons test.

For hypothesis 1, 2 and 3, the HFA effect was evaluated with the Decomposer Ability Regression Test (DART) following Keiser *et al.* (2014). This test determines simultaneously the influence of HFA, ability of the decomposer community and litter quality on decomposition rates, according to the following regression model:

$$Y_i = \alpha + \sum_{l=1}^N \beta_l \text{Litter}_{l_i} + \sum_{s=1}^M \gamma_s \text{Soil}_{s_i} + \sum_{h=1}^k \eta_h \text{Home}_{h_i} + \varepsilon_i$$

Where Y_i is the decomposition rate for observation i , β_l represents the influence of leaf litter l , γ_s is the ability of soil decomposer community s and η_h is the HFA effect from home combinations 1 to K . The intercept is α and represents the average decomposition after controlling for litter, soil, and home-field effects, and ε_i is the error term. Litter_{l_i} , Soil_{s_i} and Home_{h_i} are dummy variables that indicate presence (1) or absence (0) of litter source, soil community, or home combination, respectively (Keiser *et al.* 2014).

We fitted the model for each hypothesis using Proc Reg in SAS Studio 3.8. We used angular transformations to obtain normal distributions from mass loss data. Since a large variation was found among treatments within the same model, we used a heteroscedasticity-consistent covariance matrix to obtain standard errors (White 1980), following Keiser *et al.* (2014).

We also evaluated HFA considering the three hypotheses simultaneously by calculating additional decomposition at home (ADH) following the model by Ayres *et. al.* (2009) (Hypothesis 4). This model is as follows:

$$ADH_i = HDD_i - ADD_i - H \quad (1)$$

$$HDD_i = (D_{iI} - D_{jI}) + (D_{iI} - D_{kI}) \quad (2)$$

$$ADD_i = (D_{iJ} - D_{jJ}) + (D_{iK} - D_{kK}) \quad (3)$$

$$H = (HDD_i + HDD_j + HDD_k)/(N - 1) \quad (4)$$

Where i, j and k represent litter types i, j and k respectively; I, J and K are areas from which litters i, j and k are derived. ADH_i stands for additional decomposition at home for litter type i , being that decomposition (D) can be measured with litter mass loss or respiration rates. HDD and ADD represent decomposition differences at home (HDD) and away (ADD). H is the total HFA for all litter types considered and N represents the number of litter types.

This model states that if ADH values are zero, then there is no HFA, since there is not a significant difference in decomposition rates at home and away. When ADH values are below zero, then there is a negative HFA effect, or a home-disadvantage and litter actually decomposes faster away or, inversely, slower at home. Finally, if positive values of ADH are found, then HFA is present for the set of litter types and areas compared. We evaluated if ADH was related to soil (C:N, N:P) and litter (C:N, N:P) chemical properties using a stepwise multiple regression. Since soil and litter C:N were strongly correlated (Pearson correlation coefficient = 0.864), we used only soil C:N in the analysis.

We evaluated hypothesis 5 by calculating the Home Field Advantage Index (HFAI) as proposed by Ayres *et al.* (2009-a). For each experiment, we calculated the relative mass loss of litter decomposing at home and away sites (e.g., for Hypothesis 1 we calculated R1 vs R2, R1 vs R3, and R2 vs R3; the same approach for hypotheses 2 and 3). We estimated the dissimilarity of each pair of sites by calculating the Euclidean distance between the centroids of each site considering the multivariate space defined by litter and soil quality variables. In other words, for each area's dataset (constituted of 4 data points obtained from each plot), we calculated one "average" centroid, which was in the "center" of all four measurements. Then, we calculated the distance between centroids of each pair of areas: the more distant those centroids were, the more dissimilar the areas were. We also did this analysis using two predictive variables: distance between centroids (soil), which used data from soil chemical characteristics and distance between centroids (litter), using data from litter chemical attributes. The effects of these two variables on HFAI were evaluated with a stepwise forward multiple regression. Significance levels in this study were $P < 0.05$.

RESULTS

Site background data: Litter and Soil Nutrient Concentrations

Litter quality and soil nutrients were different between the seven study sites (PERMANOVA: $F_{6,21} = 6.66$, $P < 0.001$ for litter quality and $F_{6,21} = 4.56$, $P < 0.001$ for soil nutrients). Some of the riparian forest remnants and areas under restoration presented large variation among plots within each area, in particular C1 and R3 for both litter and soil (Figure 7).

Litter from areas R1, R2, and R3, which were of similar ages (Hypothesis 1), presented significant differences in litter quality. R3 had the lowest litter quality (C:N ratio 60% higher and N:P ratio 25% lower than R1), followed by R1 (which presented an N:P ratio 45% lower than R2) and R2 presenting the litter with highest quality. Only R2 and R3 differed according to the multiple comparisons test and the Tukey Test (Figure 7A, Table 1). There were also differences in soil nutrients, with R3 presenting higher C:N ratio (6% higher than R1 and 13% higher than R2), with large variation among plots (Figure 7B). R3 did not differ from the other two areas regarding soil nutrient concentrations, but R1 and R2 presented significant differences: R2 had the largest N:P values (50% higher than R1 and 52% higher than R3) (Table 1, Figure 7B).

Riparian forests under restoration with different ages (R1 and R3 vs R6; Hypothesis 2) did not present significant differences in either litter or soil quality (Fig. 7). Average litter C:N varied 60% between all three areas, with R1 presenting the litter with the highest quality, followed by R6 and then R3 (Table 1). Further, even though areas R3 and R6 had similar content of litter N:P, they presented values 70% lower than R1.

In the remnant areas (C1, C2, C3) C3 presented the litter with the highest quality, with litter C:N values 65% lower than C1 and 105% lower than C2; and litter N:P values 35% higher than C1 and C2. Areas C1 and C2 did not significantly differ from each other regarding litter quality (Table 1; Fig. 7A). The three areas also differed from each other in relation to soil nutrients (Table 1; Fig. 7B): regarding soil C:N, area C2 presented the highest values, 4% higher than C1 and 54% higher than C3. Area C2 also presented the soil with the lowest N:P ratio, which was 55% lower than C1 and 80% lower than C3.

Table 1 Means \pm standard errors of litter and soil variables ($n = 4$) of remnant riparian forest areas (C) and riparian forests under restoration (R). Letters on the C:N and N:P columns represent the results from the Tukey HSD Test.

	C (g/kg)	N (g/kg)	P (g/kg)	C:N	N:P
Litter					
C1	419.6 \pm 13.94	13.6 \pm 1.46 A	0.768 \pm 0.13 A	31.6 \pm 2.61 AB	19.7 \pm 4.42 AB
C2	457.7 \pm 6.80	11.7 \pm 1.00 A	0.580 \pm 0.04 A	39.9 \pm 3.22 A	20.6 \pm 2.28 AB
C3	422.9 \pm 5.81	22.0 \pm 0.46 B	0.723 \pm 0.040 A	19.3 \pm 0.33 CD	30.7 \pm 2.09 A

R1	443.5 ± 6.83	22.4 ± 1.48 B	1.313 ± 0.150 AB	20.1 ± 1.59 C	17.9 ± 2.52 AB
R2	455.3 ± 4.91	20.2 ± 1.51 BC	0.808 ± 0.110 A	23.0 ± 1.79 BCE	25.7 ± 2.39 A
R3	436.4 ± 17.08	14.0 ± 1.43 A	1.230 ± 0.246 AB	32.0 ± 2.73 AE	13.1 ± 3.46 B
R6	440.7 ± 5.73	16.3 ± 0.48 AC	1.593 ± 0.143 B	27.0 ± 0.56 BD	10.5 ± 1.12 B

Soil

C1	68.1 ± 23.99 A	4.228 ± 1.388 A	0.028 ± 0.006 A	15.6 ± 0.81 A	220.3 ± 126.66 AC
C2	15.2 ± 3.43 B	0.931 ± 0.201 B	0.013 ± 0.004 AC	16.3 ± 0.28 A	99.7 ± 30.77 B
C3	30.8 ± 2.82 AB	2.997 ± 0.257 A	0.011 ± 0.011 AC	10.3 ± 0.28 B	283.1 ± 21.13 AB
R1	26.2 ± 0.68 AB	2.323 ± 0.273 A	0.011 ± 0.001 AC	11.6 ± 1.00 B	214.6 ± 21.87 A
R2	36.5 ± 2.83 A	3.375 ± 0.240 A	0.008 ± 0.000 BC	10.9 ± 0.60 B	416.7 ± 50.72 C
R3	44.9 ± 4.61 A	3.591 ± 0.246 A	0.032 ± 0.014 AC	12.4 ± 0.51 B	202.1 ± 87.21 AB
R6	29.5 ± 3.58 AB	2.616 ± 0.245 A	0.014 ± 0.001 AC	11.2 ± 0.54 B	195.6 ± 12.91 A

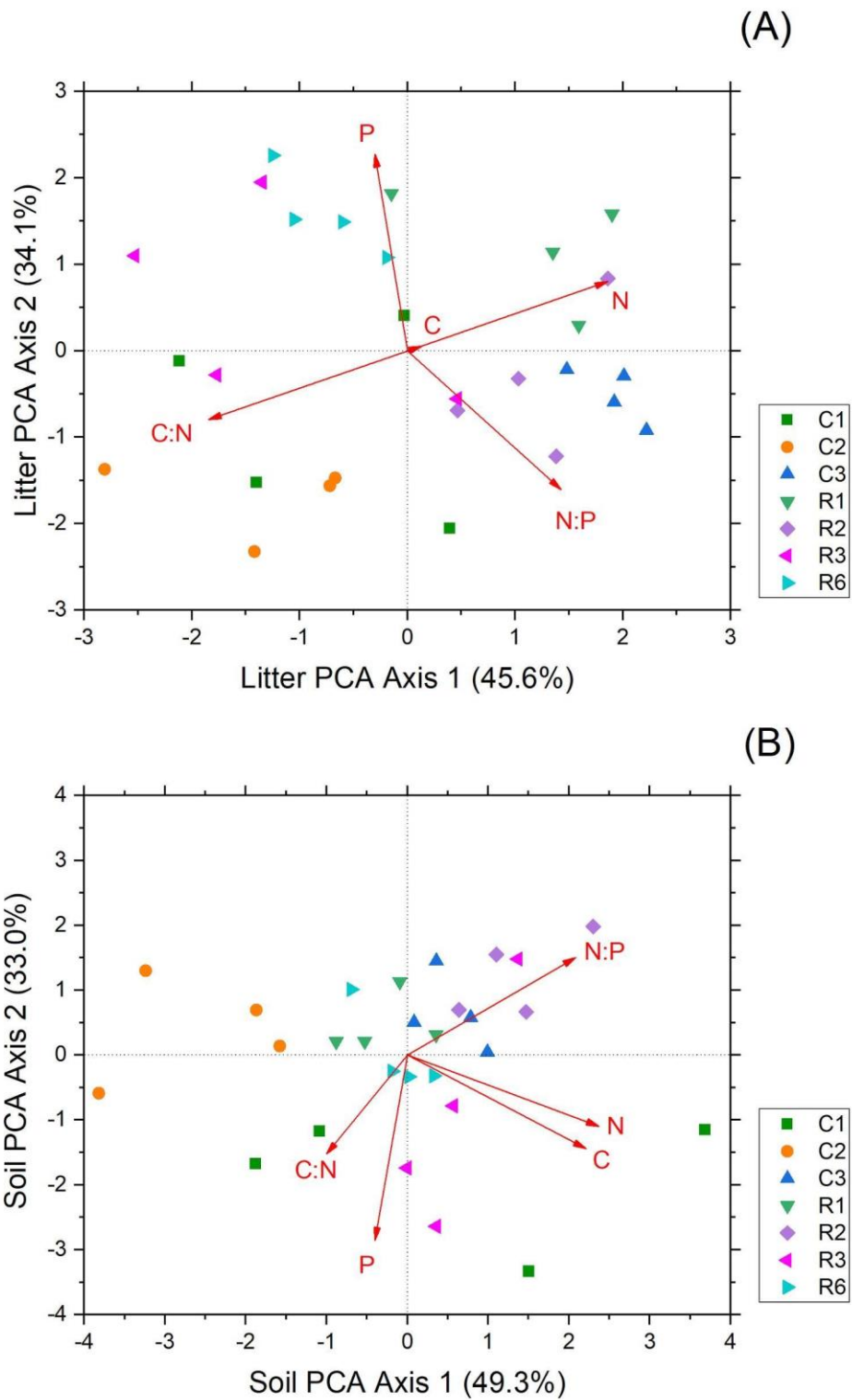


Figure 7 Results of PCA ordination of remnant riparian forests (C) and riparian forests under restoration (R) in relation to (A) litter and (B) soil nutrient variables. Symbols indicate the four plots in each studied area.

Hypothesis 1 - Do areas with the same age, but differing litter and soil quality, differ in mass loss and HFA?

Mass loss significantly differed between areas. Litter decomposing in R1 had the highest mass loss and significantly differed from the other two areas, R2 and R3, which did not differ significantly from each other. In addition, a trend for a small difference between R2 and R3 was found (Tukey's HSD test: $P = 0.081$; Figure 8).

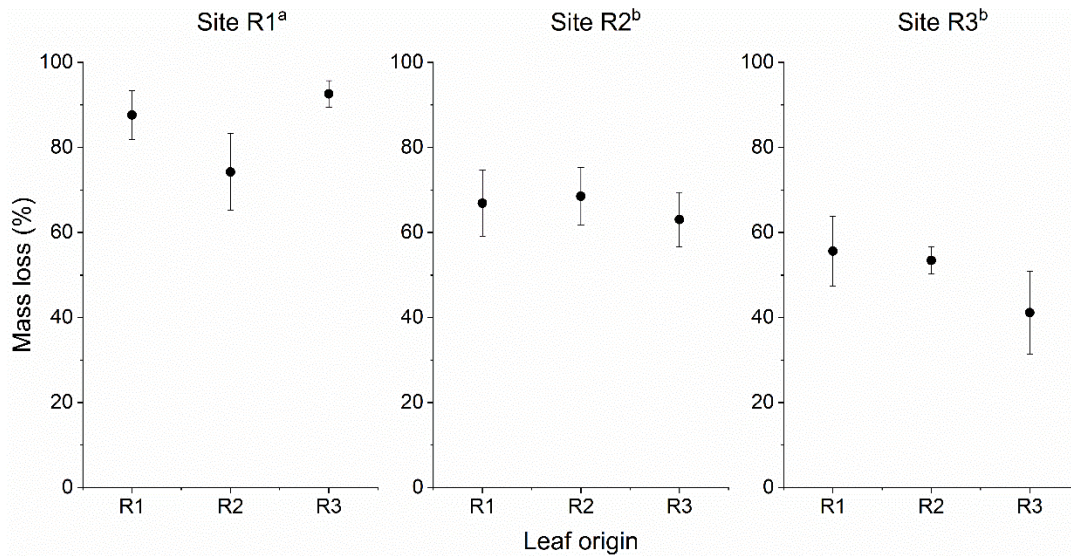


Figure 8 Mean mass loss of leaf litter from R1, R2, and R3 decomposing in each of the three areas (Hypothesis 1). Bars indicate the standard errors ($n = 4$). Letters a and b refer to the result of Tukey's HSD test.

Table 2 Results of mixed model ANOVA comparing the effects of area and leaf origin on leaf litter mass loss for hypothesis 1.

Source	Type III SS	df	Mean Squares	F-ratio	p-value
Area	7259.0	2	3629.5	14.4	0.002***
Leaf origin	167.2	2	83.6	0.495	0.618
Area x Leaf origin	1108.6	4	277.2	1.641	0.207
Plot (Area)	2266.7	9	251.9	1.491	0.225
Error	3040.2	18	168.9		

The DART model was significant for hypothesis 1 ($P < 0.001$, $\text{adj-R}^2 = 0.53$). The model indicated that leaf litter mass loss was significantly higher overall in area R1 and a trend for lower decomposition in area R3 was also detected (Table 3). A tendency for a negative effect of ability was also found in R3 (Table 3). Leaves from R3 generally decomposed slower than leaves from the other areas (Figure 8). HFA effects were not different from zero, although we found a trend for a negative effect for R3 (Table 3).

Table 3 Results of the Decomposer Ability Regression Test evaluating the effects of soil decomposer ability, leaf origin (environment), and HFA on leaf litter mass loss for Hypothesis 1. The model was significant ($P < 0.001$, $\text{adj-R}^2 = 0.53$).

Variable	df	Parameter estimate	Standard error	t	P
Intercept	1	0.987	0.0283	34.84	<.0001
Ability R1	1	0.208	0.0428	4.86	<.0001
Ability R2	1	-0.089	0.0463	-1.91	0.066
Ability R3	1	-0.119	0.0494	-2.41	0.023
Leaf origin R1	1	0.024	0.0443	0.54	0.592
Leaf origin R2	1	-0.094	0.0451	-2.09	0.046
Leaf origin R3	1	0.070	0.0491	1.43	0.163
HFA R1	1	0.018	0.1120	0.16	0.875
HFA R2	1	0.176	0.1048	1.68	0.103
HFA R3	1	-0.248	0.1228	-2.02	0.053

Hypothesis 2 - Do areas under restoration with similar soil/litter quality, but with different ages, differ in mass loss and HFA?

These areas did not differ from one another with respect to litter and soil quality. Also, there was no effect of leaf origin and area on leaf litter mass loss and a large proportion (approximately 80%) of the litter was decomposed in all areas (Table 4). Further, an outlier was verified from leaves of R3 (plot 3) decomposing at the home area (studentized residual = -4.2)(Figure 9).

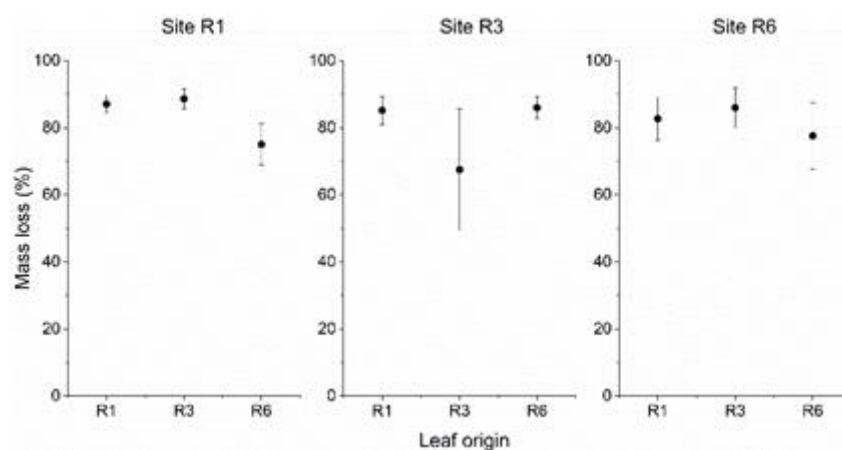


Figure 9 Mean mass loss of leaf litter from R1, R3, and R6 decomposing in each of the three areas (Hypothesis 2). Bars indicate the standard errors (n = 4).

Table 4 Results of mixed model ANOVA comparing the effects of area and leaf origin on leaf litter mass loss for hypothesis 2.

Source	Type III SS	Df	Mean Squares	F-ratio	p-value
Area	101.1	2	50.5	0.147	0.865
Leaf Origin	199.7	2	99.8	0.454	0.642
Area x Leaf Origin	1267.6	4	316.9	1.440	0.262
Plot (Area)	3084.1	9	342.7	1.557	0.202
Error	3961.4	18	220.1		

The DART model for Hypothesis 2 was not significant ($P = 0.649$). We found a trend for a positive effect of area R3 ($P = 0.072$) and litter from R3 ($P = 0.092$) on leaf litter mass loss (Table 5), but these trends are probably not reliable as we found an outlier in R3 litter decomposing in area R3 (Figure 9).

Table 5 Results of the Decomposer Ability Regression Test evaluating the effects of soil decomposer ability, leaf origin (environment), and HFA on leaf litter mass loss for Hypothesis 2. The model was not significant ($P = 0.649$).

Variable	Df	Parameter estimate	Standard error	t	P
Intercept	1	1.187	0.0260	45.61	<.0001
Ability R1	1	-0.052	0.0418	-1.24	0.225
Ability R3	1	0.076	0.0408	1.87	0.072
Ability R6	1	-0.025	0.0448	-0.55	0.589
Leaf origin R1	1	-0.022	0.0455	-0.49	0.631
Leaf origin R3	1	0.080	0.0458	1.75	0.092
Leaf origin R6	1	-0.058	0.0353	-1.64	0.113
HFA R1	1	0.097	0.0864	1.12	0.273
HFA R3	1	-0.323	0.2040	-1.59	0.124
HFA R6	1	-0.006	0.1248	-0.05	0.964

Hypothesis 3 - Do riparian forest remnant areas with differences in soil nutrient concentration and litter quality differ in mass loss and HFA?

There was a large variation among plots in mass loss (Figure 10), with no significant effects of leaf origin, area, or their interaction (Table 6).

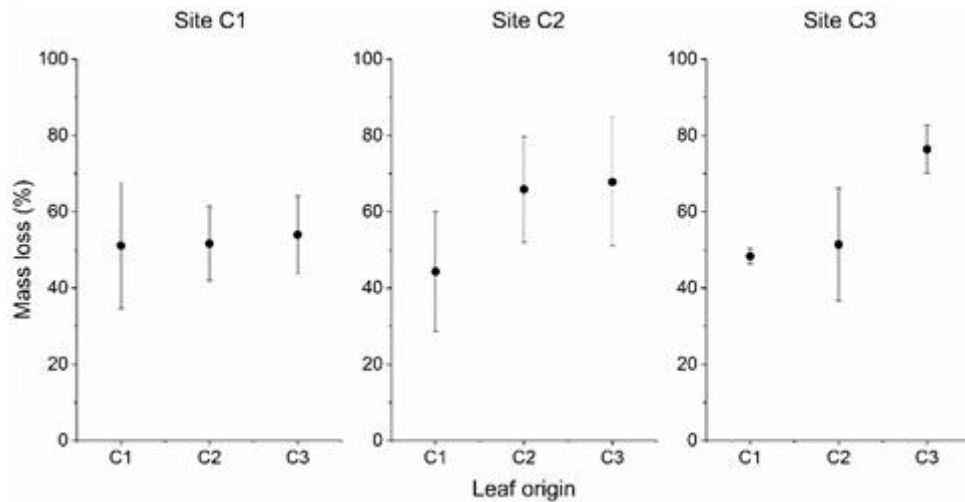


Figure 10 Mean mass loss of leaf litter from C1, C2, and C3 decomposing in each of the three areas (Hypothesis 3). Bars indicate the standard errors (n = 4).

Table 6 Results of mixed model ANOVA comparing the effects of area and leaf origin on leaf litter mass loss for hypothesis 3.

Source	Type III SS	df	Mean Squares	F-ratio	p-value
Area	368.9	2	184.5	0.152	0.861
Leaf Origin	1972.9	2	986.5	2.724	0.093
Area x Leaf Origin	1296.2	4	324.0	0.895	0.487
Plot (Area)	10902.9	9	1211.4	3.345	0.014**
Error	6518.5	18	362.1		

The DART model for Hypothesis 3 was not significant ($P = 0.595$). Although there was a trend for a higher decomposition of leaf litter from C3 in its home area (Figure 10), there were no effects of either community, leaf origin, or HFA when adjusting for the heteroscedasticity observed (Table 7).

Table 7 . Results of the Decomposer Ability Regression Test evaluating the effects of soil decomposer ability, leaf origin (environment), and HFA on leaf litter mass loss for Hypothesis 3. The model was not significant ($P = 0.595$).

Variable	Df	Parameter estimate	Standard error	t	P
Intercept	1	0.820	0.0487	16.82	<.0001
Ability C1	1	-0.056	0.0840	-0.66	0.513
Ability C2	1	0.036	0.0792	0.45	0.658
Ability C3	1	0.020	0.0753	0.27	0.791
Leaf origin C1	1	-0.104	0.0876	-1.19	0.244
Leaf origin C2	1	0.008	0.0650	0.12	0.902
Leaf origin C3	1	0.096	0.0843	1.14	0.263
HFA C1	1	0.127	0.2181	0.58	0.566
HFA C2	1	0.101	0.1963	0.51	0.611

Home field advantage - general patterns (hypotheses 4 and 5)

When regressing home field advantage effects against litter and soil quality variables, we found that HFA effects (measured as additional decomposition at home - ADH) increased with litter N:P (Figure 11).

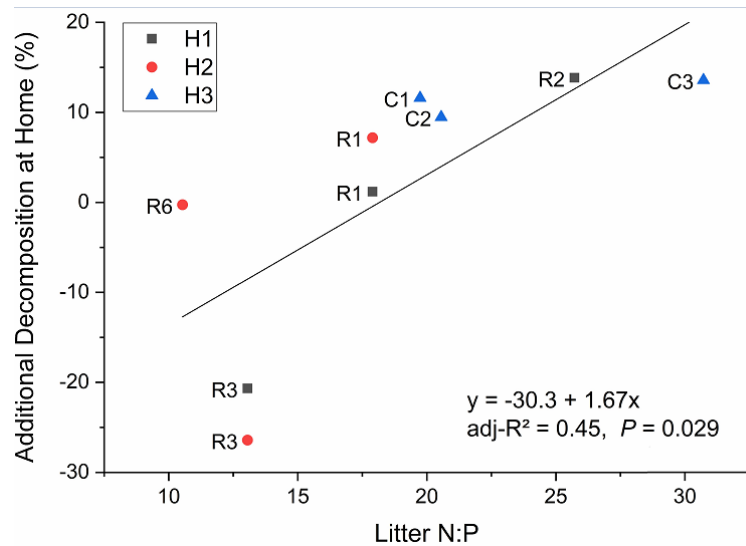


Figure 11 Relationship between additional decomposition at home (ADH) and litter N:P ratio of leaf litter decomposing in riparian forest remnants (C) and riparian forests under restoration (R). Symbols denote experimental data from the different hypotheses tested (H1, H2, H3)

The final model explaining HFAI included only the distance between centroid areas in relation to soil variables (Figure 12), so that higher chances to find HFAI were found the more dissimilar the study areas were. On the other hand, more similar areas in relation to soil variables had more chance to find lower values of HFAI, including negative values that were found when comparing areas R1, R2, and R6 to the R3 area (Figure 12).

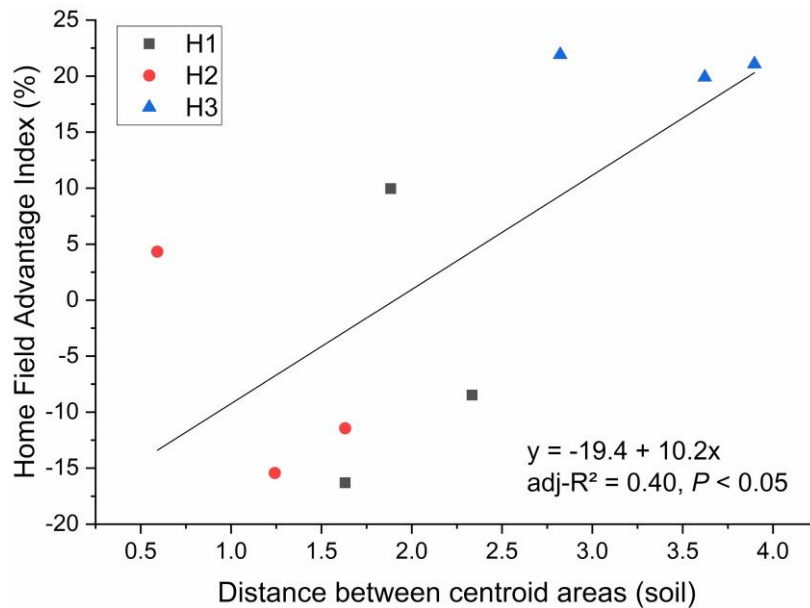


Figure 12 Relationship between Home Field Advantage Index and distance between area centroids in relation to soil nutrient concentrations of leaf litter decomposing in riparian forest remnants and riparian forests under restoration. Symbols denote experimental data from the different hypotheses tested (H1, H2, H3).

DISCUSSION

In this study, we tested five hypotheses to evaluate if forest age, litter and soil quality influenced HFA on decomposition rates in riparian forests under restoration in Southeastern Brazil. In contrast to our expectations, we did not find any HFA for any hypotheses tested. We did, however, find a significant effect of decomposer community ability in area R1 and a trend for a negative HFA effect in area R3 in the first hypothesis. Further, we found a positive correlation between litter N:P and additional decomposition at home (ADH – hypothesis 4). And finally, our findings also support previous studies which proved that increasing dissimilarities between “at home” and “away” areas result in higher HFA effects (hypothesis 5).

In hypothesis 1, we expected that considering areas under restoration with the same age, but differences in soil nutrient concentration and litter quality, HFA should be found in areas with lower litter quality and soil nutrient concentration. We predicted that HFA would be found in area R2, which had lower litter C:N (i.e., relatively higher amounts of N) and higher N:P ratios (i.e., relatively higher amounts of P), as well as higher soil N:P concentrations when compared to R3 (i.e., lowest litter quality). In addition to not finding any HFA effects for areas R1, R2 and R3, we also found a tendency for a negative HFA effect in R3. This result implies that litter quality was not a major driver of HFA effects in our experiment, meaning that communities which are used to degrading lower quality litters are not necessarily more specialized. This finding is in line with some previous studies (Giesselman *et al.*, 2011; Both *et al.*, 2017) but also, contrasts with others (Veen *et al.*, 2015-a; Cassart *et al.*, 2020). And there are several possibilities for our results contrasting with what was expected, perhaps that other factors influenced more on HFA effects. For example, this could be explained by a limiting effect of P on the soil (Kaspari *et al.*, 2008). R3 has high concentrations of P in both soil and litter (Figure

7). That could indicate that microorganisms are absorbing P found in the soil, instead of mineralizing P present in the litter (Xiaogai *et al.*, 2013). Therefore, when we introduced litter with higher concentrations of other nutrients, such as N (found in R1 and R2), litter from R3 was at a slight disadvantage decomposing at home because it did not provide microorganisms the nutrients that were necessary.

Further regarding hypothesis 1, we found a significant positive effect for decomposer community ability for R1, which cannot be explained by the Functional Breath Hypothesis (FBH) (Kaiser *et al.*, 2014; Fanin *et al.*, 2016) which depends on the adaptation of the soil biota to low quality leaf litter input, because R1 litter had high concentrations of N and low C:N ratios. Higher ability in R1 might be explained by differences in forest structure between the areas. Because, even though the areas were of similar age, previous work showed that R1 had the most established forest, while sites R2 and R3 had lower tree density and higher grass coverage (Batisteli *et al.* 2018). In this study, Batisteli *et al.* (2020) also concluded that the successional stage (age) of the riparian forest under restoration was not significantly linked with forest structure because of strong environmental interferences. This may have allowed for soil communities to develop higher ability, because more established forests offer more shade and the soil is less exposed not only to the Sun, but to other environmental interferences. So, even though R1, R2 and R3 are the same age, R1 had the most established forest, allowing the soil biota to develop a better decomposer ability.

For the second hypothesis, we expected that HFA would be higher in areas that were restored longer ago (Veen *et al.* 2018). This is because in such areas, intimate relationships between litter and decomposer communities had more time to develop. In line with that, HFA would be expected in areas R1 and R3, which are older than R6. However, in contrast to our hypothesis we did not find any significant effect of stand age on leaf litter decomposition, suggesting that other factors, such as litter quality, may have had a larger influence on decomposition rates in our experiment, which is in line with some previous work (Peres *et al.*, 2013; Cassart *et al.*, 2020). Further, HFA has been found in areas with a significant dissimilarity between their leaf litter, and higher dissimilarities tend to lead to stronger HFA effects (Veen *et al.*, 2018). The fact that the areas were restored in an active restoration project (“Plantando Águas”, see the Methodology section) means that similar tree species may have been introduced into the study areas, and maybe this resulted in leaf litters that were not significantly different enough to ensure more accelerated decomposition rates at home than away. Another possible explanation is that the disturbance that these areas suffered prior to being restored was such that they did not have enough time to re-establish plant-soil relationships yet. Vauramo and Setälä (2011) confirmed that the land-use history and frequency of disturbances of an area can influence the decomposition process, and that one of those contributions could be delaying ecosystem recovery.

Our third hypothesis was explored in remnants of riparian forests, which differed in soil nutrient concentration and litter quality, and we expected that HFA would be present in areas with low litter quality and soil nutrient concentration. However, as in our second hypothesis, none of the tested parameters had a significant effect on decomposition rates. Further, we found a

significant difference in leaf litter mass loss among plots within areas C1, C2 and C3, which means that the difference among plots of the same area was higher than among the areas themselves. Natural forests have higher structural heterogeneity than restored forests, especially when small spatial scales are considered, and this results in extensive variation in microbial processes, as a consequence of factors like tree diversity and differences in the soil (e.g. abiotic like soil structure and biotic like the composition of the soil biota) (Baldrian, 2016; McClain et al., 2003). Relating this to HFA, it is possible that this heterogeneity expands to plant-soil relationships and the remnant areas had a longer period of time to strengthen those interactions, leading to more complex plant-soil relations (other than HFA) and other factors, not tested in this study, may influence decomposition rates. One possible factor influencing this process is the decomposition stabilization factor (S) (Keuskamp, et al, 2013). It represents a portion of the litter's labile fraction which is not decomposed and therefore stabilizes adding up to the recalcitrant portion of the litter. This factor is known to vary with environmental conditions. For example, Soares *et. al.* (2020) found that the S was significantly linked to soil base saturation, but only in riparian forest remnant areas, when compared to areas with other types of land use.

We believe that this lack of HFA found in our study could be because home field advantage effects can vary at different stages of leaf litter decomposition (Ayres *et. al.*, 2009a). For example, the labile fraction gets decomposed at higher rates in earlier stages of this process when compared to later stages, when the recalcitrant fraction gets decomposed (Keuskamp *et. al.*, 2013, Berg and McClaugherty, 2014-a). This results in different decomposition rates throughout the process, and HFA (associated with accelerated decomposition at home) may vary along with them. These temporal differences in HFA have seldom been examined, as most studies, including this one, are based on single time point observations (Veen *et. al.*, 2015a). In fact, Cassart *et. al.* (2020) found a higher than expected HFA effect in earlier stages of decomposition (1 and 2 months) when compared to later stages (3 and 6 months) in old-growth tropical forests in Congo. They suggested that plant-litter relations had a stronger impact on decomposition rates than litter quality itself. This contrasts with theories that low litter quality environments have a high functional capacity to degrade all litter types (van der Heijden et al. 2008). Hence, in our study, it is possible that HFA effects could have been detected if we had sampled earlier time points.

In line with this, even though we did not find an HFA regarding any of our three hypotheses, our results concur with other HFA studies carried out in tropical climates that did not find home field advantage (Barlow *et. al.*, 2007, Giesselmann *et. al.*, 2011, Bachega *et. al.*, 2016, Both *et. al.*, 2017, Kerdraon *et. al.*, 2019). Litter decomposition in tropical ecosystems happens overall at a faster rate than in temperate ones, due to climatic conditions such as warmer temperatures and higher air humidity, which enhances microbial activity in the soil (Powers *et. al.*, 2009). Further, the protocol we followed in this study, proposed by Keiser *et. al.* (2014), recommends that litter bags are collected after 6 months, which would mean that in tropical forests, decomposition would be at a later stage than in temperate ones after the same period. Assessing HFA at this stage of decomposition could lead to unreliable results that are unable to differentiate between HFA and ability, precisely because of how recalcitrant litter would be in

this stage. Several factors may influence leaf litter decomposition rates in tropical ecosystems, so further studies are necessary to evaluate the effect of stage in leaf litter decomposition (early vs late) on HFA patterns.

The fact that few studies found HFA in tropical environments, could also mean that HFA does not exist at all in these areas, or that at least it has a very limited effect on decomposition rates. In fact, as seen in hypothesis 3, the remnant riparian areas show that HFA is very limited in general and possibly that such diverse ecosystems have high decomposer abilities overall, and relatively low HFA. Therefore, not finding any HFA effect in hypotheses 1 and 2 wouldn't be so surprising. However, further studies are needed in order to comprehend how plant-soil relationships are established in tropical environments and if HFA exists at all in those ecosystems.

In our study, environmental factors may have had strong effects on leaf litter mass loss. Due to the heavy period of rains in São Carlos prior to litter bags collection, we believe that our results may have been impacted, and rainfall must have helped to leach a percentage of litter weight out of the litter bags. Considering data from 1981-2010, the rainfall recorded in January and February 2020 was 44% higher than the historical average, and during the last two months of our experiment (between 19 December 2019 and 18 February 2020), the rainfall recorded was 627.4 mm (INMET, 2020). Considering the three experiments, average mass loss in our experiment was 82.5% per litter bag. This is more than twice that expected for these areas, considering Bachega (2019) found mean mass loss of about 42% after seven months (between November 2016 and June 2017). This means that our data reflects late stages of decomposition, with slower rates and higher concentration of recalcitrant compounds.

Even though we did not find any significant HFA effect related to the first three hypotheses tested, our analyses on compound data from the three separate experiments indicated that higher levels of litter N:P resulted in higher values for additional decomposition at home (ADH). These results support the theory, to some extent, that higher quality litter does not select generalist decomposer communities. This means that when low quality litter is introduced into rich environments, it might be decomposed at slower rates because the decomposer biota did not have to adapt in order to efficiently degrade more recalcitrant types of litter. Also, higher HFAI values were related to higher dissimilarities in soil quality between home and away sites (Figure 12). This result concurs with expected HFA differences related to dissimilarity in litter matrix quality between areas (Freschet *et. al.*, 2012; Veen *et. al.*, 2015-a). However, the most heterogeneous areas in relation to soil nutrients (which are also the ones with higher HFAI) were the forest remnant areas C1, C2 and C3 (Figure 12). These findings suggest that natural ecosystems are much more complex than areas under restoration when small scales are considered, and that possibly other factors that contribute to forest heterogeneity, such as differences in diversity and composition of decomposer communities and resource distribution, may have more influence than the factors studied in our experiments.

CONCLUSION

In this study, even though we did not find any effect of HFA in individual experiments, we conclude that HFA does not seem to change with time since restoration or litter quality, as seen in hypothesis 1 and 2. Further, HFA is not very apparent in tropical systems under study, as verified by our third hypothesis. And finally, the more dissimilar the areas, the higher the HFA (verified in our fourth and fifth hypothesis). This means that decomposition in natural (and more dissimilar) systems seems to be influenced by several factors that cause heterogeneity at small spatial scales. Hence, possibly other factors (not taken into consideration in the present study) may have had more influence on HFA effects. Also, we point to the possibility that HFA could be stronger in earlier stages of decomposition (due to the presence of more labile compounds at that stage) and, due to extraordinary weather conditions, we assessed HFA when the decomposition process was at a late stage. Our results point out the need for more HFA and decomposition studies in tropical environments, especially in restored vs. remnant ecosystems, to understand how plant-soil relations are established in disturbed ecosystems.

CONSIDERAÇÕES FINAIS

Neste estudo, embora não tenhamos encontrado nenhum efeito do HFA em experimentos individuais, concluímos que o HFA parece não mudar com o tempo desde a restauração ou a qualidade da serapilheira, como visto nas hipóteses 1 e 2. Além disso, o HFA não é muito aparente nos sistemas tropicais em estudo, conforme verificado por nossa terceira hipótese. E, por último, quanto mais diferentes as áreas, maior o HFA (verificado em nossa quarta e quinta hipótese). Isso significa que a decomposição em sistemas naturais (e mais desiguais) parece ser influenciada por vários fatores que causam heterogeneidade em pequenas escalas espaciais. Portanto, possivelmente outros fatores (não levados em consideração no presente estudo) podem ter tido mais influência nos efeitos da HFA. Além disso, apontamos para a possibilidade de o HFA ser mais forte em estágios iniciais de decomposição (devido à presença de compostos mais lábeis nesse estágio) e, devido a condições climáticas extraordinárias, avaliamos o HFA quando o processo de decomposição estava em estágio avançado. Nossos resultados apontam para a necessidade de mais estudos de HFA e decomposição em ambientes tropicais, especialmente em ecossistemas restaurados vs. remanescentes, para entender como as relações planta-solo são estabelecidas em ecossistemas perturbados.

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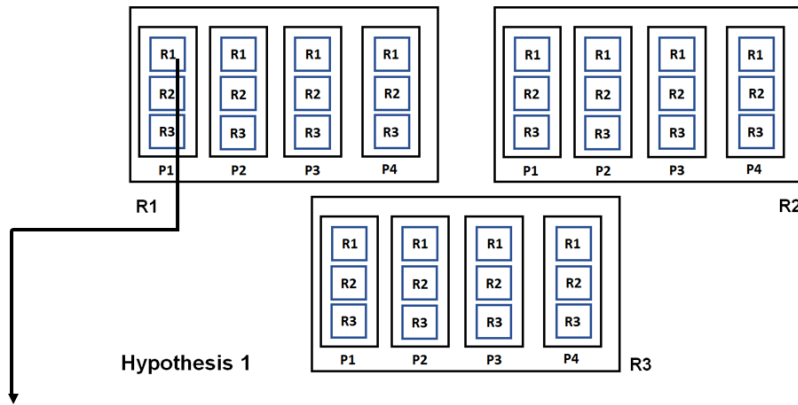
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ANNEX

In our study, hypothesis 1 comprehends the reciprocal translocation of litter from areas R1, R2 and R3 (Figure 1). Each litter bag buried in the field stands for one observation. So, for litter bag R1P1-R1 (bag buried in plot P1 from area R1 containing leaves from R1), the following equation is obtained, as shown in Figure 1:



$$Y_{R1P1-R1} = \alpha + \beta_{R1}(1) + \beta_{R2}(0) + \beta_{R3}(0) + \gamma_{R1}(1) + \gamma_{R2}(0) + \gamma_{R3}(0) + \eta_{R1}(1) + \eta_{R2}(0) + \eta_{R3}(0) + \varepsilon_{R1P1-R1}$$

$$Y_{R1P1-R1} = \alpha + \beta_{R1} + \gamma_{R1} + \eta_{R1} + \varepsilon_{R1P1-R1}$$

Figure 1: Keiser *et al.* (2014) HFA equation for litter bag R1P1-R1. β_{R2} and β_{R3} are multiplied by 0 because there is no litter from R2 or R3 in this particular litter bag, so the dummy variables $Litter_{R2}$ and $Litter_{R3}$ adopt the value zero. The same happens for γ_{R2} and γ_{R3} (with variables $Soil_{R2}$ and $Soil_{R3}$), for the reason that the bag is not buried neither in area R2 or R3. Finally, as there is a home field match with litter from R1 in its original area, dummy variable $Home_{R1}$ multiplies η_{R1} by one resulting in the final equation.

Consequently, each of the 108 litter bags (3 hypothesis x 3 areas per hypothesis x 4 plots per area x 3 litter bags per plot) had their own equation. The software SAS 9.4 calculates all variables based on the curve created from data on mass loss during the six months of the project.