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Functionally dissimilar neighbors accelerate litter decomposition in two grass species

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SUMMARY

- Plant litter decomposition is a key regulator of nutrient recycling. In a given environment, decomposition of litter from a focal species depends on its litter quality and on the efficiency of local decomposers. Both may be strongly modified by functional traits of neighboring species, but consequences for decomposition of litter from the focal species remain unknown.
- We tested whether decomposition of a focal plant's litter is influenced by the functional-trait dissimilarity to the neighboring plants. We cultivated two grass species (*Brachypodium pinnatum* and *Elytrigia repens*) in experimental mesocosms with functionally similar and dissimilar neighborhoods, and reciprocally transplanted litter.
- For both species, litter quality increased in functionally dissimilar neighborhoods, partly due to changes in functional traits involved in plant-plant interactions. Furthermore, functional dissimilarity increased overall decomposer efficiency in one species, probably via complementarity effects.
- Our results suggest a novel mechanism of biodiversity effects on ecosystem functioning in grasslands: interspecific functional diversity within plant communities can enhance intraspecific contributions to litter decomposition. Thus, plant species might better perform in diverse communities by benefiting from higher remineralization rates of their own litter.

Key-words: afterlife traits, biotic interactions, decomposer community, intraspecific variation, functional dissimilarity, litter quality, plant litter decomposition, plant neighborhood

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INTRODUCTION

Plant-litter decomposition is one of the largest terrestrial carbon fluxes and a key regulator of nutrient cycling in ecosystems. For instance, in grasslands ecosystems, litter decomposition is crucial to maintain or restore ecosystem services such as soil fertility and productivity. Under a given set of abiotic conditions, the decomposition of the litter produced by a given plant ("focal plant" from here on) depends on two main parameters: the litter quality of the plant (Coûteaux *et al.,* 1995; Cornelissen & Thompson, 1997; Cornelissen *et al.,* 1999; Makkonen *et al.,* 2012), and the efficiency of the surrounding decomposer community (detritivore fauna, decomposing fungi and bacteria: Petersen & Luxton, 1982; Coûteaux *et al.,* 1995; Bardgett & van der Putten, 2014). Litter quality corresponds to nutritional value and digestibility for decomposers. Litter quality is controlled by after-life traits of the focal plant, typically increasing with high specific leaf area (SLA: Santiago, 2007) or with low C:N ratio (Quested *et al.,* 2007; Bakker *et al.,* 2011). The efficiency of the decomposer community corresponds to mass loss of litter of a given quality, and reflects the abundance of decomposers and their specific capacities to handle and digest litter (Petersen & Luxton, 1982; Hättenschwiler & Gasser, 2005; Güsewell & Gessner, 2009). The focal plant influences the decomposer efficiency via its litter quality, root exudates (Paterson, 2003; Kuzyakov *et al.,* 2007), and associated microbial communities (e.g. mycorrhizal fungi: Lindahl & Tunlid, 2015; Soudzilovskaia *et al.,* 2015). But most plants do not grow in isolation, and are surrounded by plant neighbors. Interactions with plant neighbors can influence litter quality of a focal plant and its decomposer community: interactions with neighbors influence the focal plant's traits (Novoplansky, 2009; Violle *et al.,* 2009) and litter, root exudates and mycorrhizal fungi from neighboring plants control the decomposer community below the focal plant (Meier *et al.,* 2008; Butenschoen *et al.,* 2011; Fernandez & Kennedy, 2016). Neighborhoods may therefore modulate both of the major controls of litter decomposition for a focal plant.

Specifically, plant neighbors may impact afterlife traits of a focal plant, mainly through competition (Jackson & Caldwell, 1993; Violle *et al.,* 2009) and sharing of enemies (Janzen, 1970; Yguel *et al.,* 2011; neighbors' above-ground effect, Fig. 1). Such impacts may depend on the neighbors' traits and their similarity with the traits of the focal plant (McGill *et al.,* 2006). For instance, according to the *limiting similarity* theory (MacArthur & Levins, 1967; Schwilk & Ackerly, 2005), a focal plant with dissimilar neighbors will compete less for light and soil nutrients. A focal plant with dissimilar neighbors will also suffer from less enemy pressure than with similar ones, if enemies prefer high resource concentration (Janzen, 1970; Yguel *et al.,* 2011). In such dissimilar neighborhoods, a focal plant may then perform better and show changes in resource acquisition traits, specifically higher SLA, as well as lower C:N ratio and LDMC (leaf dry matter content; Violle et al., 2007, 2009). A focal

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plant may also respond to lower enemy pressure by decreasing its leaf toughness (Massey et al., 2006). All these trait changes in living plants are known to increase litter quality, since litter decomposition increases with high SLA (Santiago, 2007), low C:N ratio (Wedderburn & Carter, 1999), low LDMC (Quested *et al.,* 2007), and low leaf toughness (Pérez-Harguindeguy *et al.,* 2000). Nevertheless, to our knowledge, no study have demonstrated whether functional dissimilarity to plant neighborhood ultimately affects decomposition of a focal-plant's litter via changes in its functional traits. We hypothesize that functional dissimilarity to neighborhood increases the litter quality of a focal plant.

Plant neighbors may also affect the decomposer community below a focal plant in multiple ways (neighbors's below-ground effect, Fig. 1). Neighborhoods composed of functionally dissimilar species result in a functionally diverse litter mixture (Butenschoen *et al.,* 2011) which, according to the *resource complementarity* hypothesis (Loreau *et al.,* 2001; Gessner *et al*., 2010; Tardif & Shipley, 2014), may stimulate abundance, activity, and hence efficiency of decomposers. A dissimilar mixture may also increase nitrogen transfer between litter species (Handa *et al.*, 2014), which may increase decomposer efficiency. Alternatively, a functionally dissimilar litter mixture might result in dilution of high-quality litter sources, reducing decomposer efficiency since many decomposers may be specialist and have distinct litter preferences (home-field advantage; Ayres *et al.,* 2009; Freschet *et al.*, 2012; Austin *et al.* 2014; Pan *et al.,* 2015; Veen *et al.,* 2015). Dissimilar plant neighbors can additionally produce a wide range of root exudates, thereby increasing decomposer efficiency (Paterson, 2003, and Kuzyakov *et al.,* 2007 for root litter). Finally, dissimilar plant neighbors can increase soil resource availability and trigger less competitive interactions between mycorrhizal and decomposing fungi (Gadgil effect; Fernandez & Kennedy, 2016), increasing overall decomposer efficiency. However, it remains unknown whether functional dissimilarity to plant neighborhood finally affects the efficiency of the decomposer community to decompose a focal-plant's litter. Overall, we hypothesize that functional dissimilarity to neighborhood increases the efficiency of the decomposer community.

Here we tested how the functional dissimilarity between a focal plant and neighboring plants influences the litter decomposition of the focal plant. We hypothesized that (i) functional dissimilarity to plant neighborhood drives functional traits thereby increasing litter quality and (ii) functional dissimilarity to plant neighborhood increases decomposer efficiency. We considered two grassland focal species, *Elytrigia repens* (L.) and *Brachypodium pinnatum* (L.), which we cultivated in a large scale experiment including plant communities in semi-controlled mixtures along a gradient of increasing functional dissimilarity between the focal plant and its plant neighborhood. We maintained the experiment for five years, giving time for focal species to respond to their neighbors,

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and the experiment included twelve neighboring species. We performed a reciprocal litter transplant experiment to partition the effect of plant neighborhood on litter decomposition mediated only via litter quality and only via decomposer efficiency.

MATERIAL & METHODS

Studied species and neighborhood composition

We conducted this study in the experimental garden of the University of Rennes 1 (Western France, 48°06'58.6"N 1°38'15.5"W). The experiment was setup in 2009 and consisted of 120 mesocosms of 1.30 x 1.30 m containing 12 different mixtures of grassland species replicated 10 times *(see Benot et al.*, 2013 for more details on the experimental design). Mesocosms were mowed yearly, and plant material was exported, in order to mimic the classical management practice applied in semi-natural grasslands. Mixtures had four levels of species richness (1 = monoculture, 4, 8, 12) and three distinct specific compositions for each level of species richness. Functional dissimilarity of mixtures depends a lot on the moconotyledon:dicotyledon ratio, and the ratio of mixtures – 3:1, except monocultures – was very similar to the ratio that can be found in a great variety of grassland ecosystems in the study region (hayfields, pastures). Functional dissimilarity of mixtures was hence in line with functional dissimilarity that can be found in such ecosystems. Species used in mixtures were sampled from different sites around the region to maximize intraspecific variation. Among the 10 replicates of each mixture, relative abundances of species varied strongly so that local plant neighborhood was never identical, except for monocultures. Species were *Agrostis stolonifera* (L.)*, Agrostis tenuis* (L.), *Brachypodium pinnatum*, *Centaurea nigra* (L.)*, Chamaemelum nobile* (L.)*, Dactylis glomerata* (L.), *Elytrigia repens*, *Festuca rubra* (L.), *Holcus lanatus* (L.), *Holcus mollis* (L.), *Lolium perenne* (L.) and *Ranunculus repens* (L.).

We selected two Poaceae species as focal species: *Brachypodium pinnatum* and *Elytrigia repens*. These grassland species are present throughout Europe in a wide range of ecosystems and habitats. Both have a C3 photosynthetic pathway (Osborne *et al.,* 2014), and both are clonal but differ in clonal growth strategy with a Phalanx type for *B. pinnatum* and a Guerilla type for *E. repens* (*sensu* Doust, 1981). For both focal species, we selected six mixtures, one monoculture and five polycultures, with ten replicates each. We selected a single focal plant growing in the center of each of the 60 selected mixtures. Because of variation in both presence and abundance of neighboring species and variation in functional traits of neighboring species, the 60 replicate focal plants of each focal species were positioned along a continuous gradient of functional distance to their plant neighborhood.

Functional dissimilarity between focal plant and its plant neighborhood

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To characterize plant composition in the neighborhood of focal plants, we mapped plant species distribution in each mesocosm in early spring 2014 (to test for ongoing impacts of neighbors on focal plants) and in 2010 and 2012 (to test for selection of focal-plant phenotypes by past neighbors). We mapped plant species distribution with an 80 x 80 cm square grid with a 5-cm cell size (256 cells per grid) positioned in the middle of each mesocosm. The presence of all rooted species was noted for each cell. Neighborhood composition was quantified for each focal plant by georeferencing its position within the grid and then calculating the number of cells occupied per each neighboring species around the focal plant. We quantified neighborhood at three different radii (10 cm, 20 cm and 30 cm) because a focal plant may respond to its local neighborhood at different distances depending on the trait considered (Bittebière & Mony, 2014). These calculations were carried out with GIS (ArcGIS 10.1, ESRI).

We quantified the functional dissimilarity between each of the two focal species and their neighboring species using trait measurements done on individuals grown in controlled pots in isolation, to obtain basal trait values independent of neighborhood composition. On ten individuals of each species in the experiment, we measured eight functional traits which are important drivers of plant-plant interactions and represent above-ground and below-ground strategies of species to respond to abiotic and biotic conditions: specific leaf area (SLA), leaf dry matter content (LDMC), mass allocation to ramets, mass allocation to flowers, mass allocation to roots (in percentage of total dry mass), total dry mass, ramet height and spacer length. We also included the duration of flowering in our data, obtained from the BiolFlor database (Kühn *et al.,* 2004). All these traits mainly illustrate how neighbors allocate resources and hence compete for light and soil resources with the focal plant (Violle *et al.* 2007, 2009). For instance, a neighboring plant allocating more resources than the focal plant to sexual reproduction (production of flowers and duration of flowering) hence allocates less resources to growth of vegetative organs (production of roots and ramets, ramet height, spacer lenght, SLA) and may then less compete for light and soil resources with the focal plant. SLA and LDMC of plant neighbors also determine the dissimilarity between neighbors' litter and litter from the focal plant, which may drive the complementarity of litter-mixture resources (Loreau *et al.,* 2001; Gessner *et al*., 2010). All traits were measured following the protocols of Pérez-Harguindeguy *et al.* (2013). We averaged the ten replicates for each species and each trait.

For each focal plant, we quantified the functional dissimilarity to its plant neighborhood as the mean Euclidian distance between the focal plant and each neighboring species in 9-dimensional space with an axis for each trait (Villéger *et al.,* 2008). Traits data were standardized to give similar weight to each trait in the multi-dimensional space. This approach has the advantage of not reducing information by an initial ordination, which was unnecessary since traits were not overly correlated

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(the range of correlation were from -0.71 to 0.51, with an absolute value mean and median of respectively 0.35 and 0.32). We calculated the abundance-weighted mean functional dissimilarity between each focal plant and its plant neighborhood as:

$$D = \frac{\sum(\alpha_i \times \beta_i)}{\sum(\alpha_i)}$$

Where α_i is the abundance of the neighboring species *i*, and β_i is the Euclidian distance between the species *i* and the focal plant in the multi-dimensional space. This mean functional dissimilarity was calculated for the three different radii of neighborhood around each focal plant, at the three dates (2010, 2012 and 2014).

Focal-plant trait measurements

We evaluated trait responses of the two focal species to their different plant neighborhoods by measuring four green-leaf traits and two dead-leaf traits well known to impact litter quality (Quested *et al.,* 2007; Santiago, 2007) and being potentially responsive to resource competition and enemy pressure (Novoplansky *et al.,* 2009; Violle *et al.,* 2009). On green leaves, we measured SLA, LDMC, percentage of surface attacked by fungi and percentage of senescent area, following the protocols of Pérez-Harguindeguy *et al.* (2013). SLA, LDMC and percentage of fungal attacked surface were measured on the youngest fully expanded leaf of focal plants, in order to standardize measures across individuals. The percentage of senescent area was measured on the three youngest leaves.

On air-dried dead leaves we measured C:N ratio and leaf toughness. We considered entirely senesced leaves from the focal plant as dead leaves. C:N ratio was measured using an elemental analyzer (FLASH EA 1112 Thermo Finnigan). Leaf toughness was measured following the protocol of Foucreau *et al.* (2013). We selected leaves of similar size for all focal plants and used a penetrometer applying a thrust of 3 $mm.min^{-1}$ on a flat head drill positioned on the leaf. Leaf toughness was calculated as the average maximum effort (in Newton) necessary to pierce the leaf (three points per leaf).

Litter decomposition

The decomposition of a focal-plant's litter right underneath this focal plant results from the effect of plant neighborhood on (1) litter quality and (2) decomposer efficiency. In order to disentangle the two effects, we used a litter transplant experiment. We assumed that the litter quality of focal plants grown in monocultures (*i.e.* with conspecific neighbors) was not affected by any effect of functional dissimilarity to neighborhood, as functional dissimilarity was there strictly equal to zero. Similarly, we assumed that the decomposer community located in monocultures was not affected by any effect of

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functional dissimilarity to neighborhood. Therefore, by transplanting litter from focal plants grown in polycultures (*i.e.* neighborhoods not restricted to conspecifics) to monocultures, we were able to evaluate how functional dissimilarity to neighborhood affects litter decomposition via litter quality alone. Reciprocally, by transplanting litter from focal plants grown in monocultures to polycultures, we were able to evaluate how functional dissimilarity to neighborhood affects litter decomposition via the decomposer community alone. The assigning of a litterbag originating from a monoculture to a particular polyculture was made at random, as was the assigning of a litterbag originating from a polyculture to a particular monoculture. We also placed below each focal plant a litterbag filled with its own litter, combining the two effects of neighborhood on litter decomposition. Thus, we placed six litterbags below each focal plant grown in monoculture treatments: one from the focal plant and five from each of the five polyculture treatments. We placed two litterbags below each focal plant grown in polyculture treatments: one from the focal plant and one from a monoculture treatment.

We used naturally-senesced litter collected from one to several ramets of the focal plant. As ramets are plastic and are the focal-plant organs that might respond to neighborhood, we collected litter from on to several very close ramets of focal plant, all sharing the same plant neighborhood. Thereby, we avoided confounding different levels of phenotypic responses to plant neighborhood. Litter was air-dried, and placed into 8 x 8 cm mesh bags. Litterbags had 2 mm mesh on their lower side to avoid losing small fragments of litter, and 5 mm mesh on their upper side to allow decomposers to freely access the litter. Each litterbag contained 1g of litter, oven-dry equivalent (air-dry/oven-dry ratio calculated from subsamples exposed to oven-dried but not exposed to decomposition).

We started the decomposition experiment in December, 2013 and litterbags were collected when they reached 30-60% mass loss – four months later for *E. repens* and five months later for *B. pinnatum*. High decomposition during this period of exposure results from the humid and relatively warm climate in winter, leading to high decomposer activity. We measured litter mass loss after the time of exposure as a proxy of litter decomposition. Mass loss was measured on all samples after cleaning the litter, oven-dried at 65°C for three days. Mass loss (%) was calculated as $(m_1/m_0)*100$, where m_0 is the initial oven-dry equivalent dry weight and m_1 the oven-dry weight at collection.

We also measured litter microbial biomass for a subset of 45 litter samples at the end of time of exposure to quantify colonization of litter by microorganisms. Because we could not analyze all litters, we selected this subset to be representative of the range of litter quality of all samples (mainly the range of SLA, LDMC and C:N ratio). The litter samples were incubated at 22°C for one day in polyethylene bags with gas exchange filled with moist filter paper to standardized water content.

The litter was cleaned and then cut into pieces. Microbial biomass C of approximately 0.15g litter (fresh weight) was measured using an O_2 micro compensation apparatus (Scheu, 1992). Substrate induced respiration was calculated from the respiratory response to D-glucose for 10h at 22°C to measure total microbial biomass colonizing the litter, including microbes that are inactive at the time of sampling (Anderson & Domsch, 1978). Glucose was added to saturate the catabolic enzymes of microorganisms (80mg.g^{-1} litter dry weight dissolved in 2ml deionised water). The mean of the lowest three readings within the first 6h was taken as maximum initial respiration (MIRR: ml O_2.g^{-1} litter dry weight h^{-1}) and microbial biomass (µg C_{mic}.g^{-1} litter dry weight) was calculated as 38×MIRR (Beck *et al*., 1997). We note that glucose addition over a short period might weakly stimulate arbuscular mycorrhizal fungi, but they are likely absent or rare in above-ground litter. Microbial activity (basal respiration; mg O_2.h^{-1}.g^{-1} litter dry weight) was determined without glucose addition as the mean respiration rate after 15 to 24h. Glucose addition increased respiration by a factor 50 or more, and hence stimulated many decomposer organisms. Microbial biomass correlated positively to litter mass loss (P=0.009 and r^2=0.13 for *B. pinnatum*, and P=0.003 and r^2=0.16 for *E. repens*).

Statistical analyzes

First, we used linear simple ordinary least squares (OLS) regression models to test the effect of functional dissimilarity to neighborhood on the six functional traits measured on focal plants (SLA, LDMC, fungal attack, senescent area, C:N ratio, leaf toughness). We used a simple linear model describing trait data as a function of functional dissimilarity to neighborhood, neighborhood being characterized for each of three radii (10 cm, 20 cm, 30 cm) for each of three years (2010, 2012, 2014, *i.e.* nine models in total for each trait). We used centered-reduced data, *i.e.* variables transformed by subtracting their mean and dividing by their standard deviation, as it ensures that regression coefficients are comparable among models. For each trait, we selected the most probable model based on the R^2 and Akaike's information criterion, corrected for small sample sizes (AICc: Burnham & Anderson, 2002). Here and in all further analyzes we graphically explored residuals using probability plots and predicted *vs* residual plots, to verify whether residuals approached normality and homogeneity. To fulfill the assumption of normality we log-transformed (before scaling) data of *B. pinnatum*.

Second, we used linear multiple OLS regression models to test the effect of the six functional traits of focal plants on (i) mass loss and (ii) microbial biomass. For each of these two dependent variables, the initial model included all explanatory variables (*i.e.* the six focal-plant's traits), and all variables were also centered-reduced. The model was optimized using a backward stepwise selection procedure of explanatory variables, and the best model was selected based on AIC criterion

(Burnham & Anderson, 2002). Comparing this to the previous analyzes, we identified which traits of focal plants were both, significantly influenced by functional dissimilarity to neighborhood and significantly influencing mass loss or microbial biomass. For these traits, we then performed a path analysis (Wright, 1934) to calculate how functional dissimilarity to neighborhood indirectly affected mass loss or microbial biomass via these traits. We calculated a compound path by multiplying the standardized regression coefficient of the model relating (i) functional dissimilarity to neighborhood to focal plant functional traits with that of the model relating (ii) focal plant functional trait to either mass loss or microbial biomass. Compound paths therefore indicate the trait-mediated influence (sign and magnitude) of functional dissimilarity to neighborhood on litter mass loss or microbial biomass.

Third, we used simple linear OLS regression models to test the effect of functional dissimilarity to neighborhood on litter mass loss and microbial biomass. We considered litters transplanted from heterospecific neighborhoods to monocultures and litters transplanted from monocultures to heterospecific neighborhoods (except for microbial biomass due to insufficient sample size, n=4). As explained above (see first paragraph of *Litter transplantation experiment*), the former reflects the effect of functional dissimilarity to neighborhood mediated via litter quality, and the latter reflects the effect mediated via decomposer efficiency. We also considered non-transplanted litters, reflecting the combined effects of litter quality and decomposer efficiency. Again, neighborhoods were characterized for each of the three radii for each of the three years, resulting in nine analyzes per litter type and dependent variable. All models were compared based on AICc to select the most parsimonious one.

Finally, we explored the degree to which the litter-mediated effect of functional dissimilarity to neighborhood on litter decomposition could be explained by the functional traits we measured. Litter-mediated effect was quantified as explained in the last paragraph; effects mediated by measured traits as compound paths were quantified as explained in the penultimate paragraph. For both mass loss and microbial biomass, we compared litter-mediated effect and effects mediated by measured traits.

In order to verify that the effect of functional dissimilarity was not due to a single species (Wardle *et al.,* 2006; Hoorens *et al.,* 2010), we also tested relationships between the dependent variables and abundances of each species in the experiment. We found that these relationships were rarely significant and always weaker than the relationship with functional dissimilarity. We also included the neighboring species richness in our models to explain functional traits and litter mass loss, but functional dissimilarity was always a more powerful predictor and species richness was excluded

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during variable selection. All statistical analyzes were performed in R 3.0.3 (R Development Core Team, 2014).

RESULTS

Past neighborhoods (2010, 2012) were not significant in any analyzes, except a weak increase of the SLA of *E. repens* in response to functional dissimilarity to neighborhood in a 20 cm radius in 2010 (P=0.03, r^2=0.09, F=5.07). Therefore, we only present results of models based on present neighborhoods. We also only present results of models of a single neighborhood radius, which is the radius yielding the strongest relationship. Nevertheless, note that different radii led to similar conclusions regarding relationship sign in all cases and significance in most cases (Tab. S1).

Functional dissimilarity to neighborhood affects functional traits of focal plants

In *B. pinnatum*, functional dissimilarity to neighborhood significantly increased SLA, from around 25 to 35 mm^2/mg, and also increased fungal attack, from 0 to 10% of foliar surface. Functional dissimilarity to neighborhood strongly decreased C:N ratio, from around 80 to 40, and also decreased senescent area, from 10 to 0% of foliar surface (Tab. 1, $0.11 \leq r^2 \leq 0.34$). LDMC (340 mg/g in mean) and leaf toughness (6 Newton in mean) remained unchanged. In *E. repens*, functional dissimilarity to neighborhood strongly increased C:N ratio, from 30 to 50, and decreased fungal attack from 20 to 5%, leaf toughness from around 10 to 6 Newton, and senescent area from 10 to 0% (Tab. 1, $0.21 \leq r^2 \leq 0.55$). LDMC (330 mg/g in mean) and SLA (23 mm^2/mg in mean) remained unchanged. The most pertinent neighborhood scales varied from 10 cm to 30 cm, with overall larger scales for *E. repens* than for *B. pinnatum*. We note that neighborhood might control fungal attack not only directly, but also indirectly through the effect of neighborhood on nutritional quality of focal plants for enemies (Solomon et al., 2003; Neumann et al., 2004). However, we found no relationship between fungal attack and an important indicator of nutritional quality of leaves, C:N ratio (df=47, r^2=-0.01, P=0.47 for *B. pinnatum* and df=57, r^2=-0.01, P=0.48 for *E. repens*).

Functional traits affect mass loss and microbial biomass

In *B. pinnatum*, the increase in litter C:N decreased litter mass loss (Tab. 2, Fig. 2 and Fig. S1 A, B). The corresponding compound path connecting functional dissimilarity to mass loss via litter C:N amounted to 0.22. None of the functional traits affected microbial biomass. In *E. repens*, none of the functional traits affected mass loss, while high leaf senescence and low litter C:N increased microbial biomass (Tab. 2, Fig. 2 and Fig. S1 C, D, E, F). The corresponding compound paths connecting functional dissimilarity to microbial biomass via senescence area and litter C:N respectively amounted to -0.15 and -0.16.

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Functional dissimilarity to neighborhood accelerates litter-mass loss via both improved litter quality and improved decomposer efficiency

In both species, functional dissimilarity to neighborhood significantly increased litter-mass loss, by more than 100% ("overall effect", r^2=0.47 and 0.13, Fig. 3 A, D and Tab. 3). This increase was continuous and did not depend only on the difference between monocultures and polycultures (removing monocultures from the models did not impact significance nor magnitude of the results). In *B. pinnatum*, this increase in litter-mass loss was mediated by both litter quality (r^2=0.15, Fig. 3 B and Tab. 3) and decomposer efficiency (r^2=0.15, Fig. 3 C and Tab. 3). The litter-quality effect in *B. pinnatum* amounted to a standardized regression coefficient of 0.44, so it was only partly explained by the measured functional traits, notably by a decrease in litter C:N (standardized compound path coefficient of 0.22, see above). In *E. repens,* the increase of litter mass loss in functionally dissimilar neighborhoods was weaker than in *B. pinnatum* and was only mediated by litter quality (r^2=0.11, Fig. 3 E, F and Tab. 3). None of the measured traits could explain this litter-quality effect (see above). In both focal species, microbial biomass did not respond to any effect of functional dissimilarity to neighborhood, which is consistent with the absence of effects of neighborhood on functional traits driving microbial biomass in *B. pinnatum*, but inconsistent with the existence of such effects in *E. repens*.

DISCUSSION

We demonstrated that a functionally dissimilar neighborhood strongly increased litter decomposition for both *B. pinnatum* and *E. repens*. Notably, the litter produced in functionally dissimilar neighborhoods lost mass faster than litter produced in functionally similar neighborhoods. In *B. pinnatum*, this increase of litter quality was partly explained by a decrease of litter C:N ratio in response to functional dissimilarity to neighborhood. In *E. repens*, none of the measured functional traits could explain the increase of litter quality. In addition to this above-ground effect via litter quality, we found, in *B. pinnatum,* a below-ground effect: decomposers were more efficient in functionally dissimilar neighborhoods.

Functional dissimilarity to neighborhood affects plant functional traits

The functional traits of both focal species responded to functional dissimilarity to neighborhood. In *B. pinnatum*, litter C:N ratio decreased in functionally dissimilar neighborhoods. This decrease could be explained by a decrease of soil C:N ratio in such neighborhoods (see Fig. S2) since our plots were yearly mowed and soil conditions were hence the cause rather than the consequence of litter traits. One possible explanation is that in such dissimilar neighborhoods, *B. pinnatum* may have been competitively superior to its neighbors, as indicated by increased SLA. Competitive superiority likely

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permits increased nitrogen uptake compared to neighbors, specifically in *B. pinnatum* which is a species that takes up nitrogen more efficiently than many other species in our experiment (Bonanomi *et al*., 2006; Holub *et al.,* 2012). Then, in such neighborhoods, mowing decreased nitrogen export in comparison to similar neighborhoods. However, only a small part of the decrease of litter C:N ratio could be explained by this decrease of soil C:N ratio. An additional mechanism might be a decline in competitive pressure in dissimilar neighborhoods that in turn decreased nitrogen resorption during senescence. Overall, *B. pinnatum* may have suffered less from competition in functionally dissimilar neighborhoods. Conversely, litter C:N ratio of *E. repens* increased in functionally dissimilar neighborhoods. In such dissimilar neighborhoods, soil C:N ratio did not change (see Fig. S2). The increase of litter C:N ratio might instead be due to increased nitrogen resorption during senescence, because focal plants used nitrogen more efficiently to respond to a stronger competitive situation. Overall, *E. repens* might have suffered more from competition in dissimilar neighborhoods. Moreover, the focal species showed opposite responses also concerning fungal attack and leaf toughness. In *B. pinnatum,* leaves were more attacked in functionally dissimilar neighborhoods, suggesting enemies were probably generalists taking advantage of complementary resources (see Wahl & Hay, 1995; Barbosa *et al.,* 2009). In contrast, leaves of *E. repens* were less attacked in functionally dissimilar neighborhoods, and their toughness decreased. This result suggests that this species might face mainly specialist enemies suffering from preferential resource dilution. Therefore, the two focal species responded in opposite ways for traits involved in competition and defense.

Plant traits in functionally dissimilar neighborhoods make litter more decomposable

Despite opposite trait responses to neighbors, litter quality of both species strongly increased in functionally dissimilar neighborhoods. This result show that similar effects of plant species on litter decomposition can result from different trait-mediated mechanisms. In *B. pinnatum*, the increase of litter quality was partly explained by a decrease of litter C:N ratio. This result is consistent with previous studies assessing the positive role of low C:N in the litter decomposition process, because litter decomposition is often nitrogen limited (Wedderburn & Carter, 1999; Quested et al., 2007). In *E. repens*, none of the measured functional traits could explain the increase of litter quality. This increase might therefore be entirely due to non-measured traits. We may hypothesize that functionally dissimilar neighbors competed less with focal plants and improved nutrient status of litter from focal plants, as well as tissue quality. Specifically, functionally dissimilar neighbors might have increased focal-plant litter nutrient concentration, for example [K], [Mg] or [P] (Santiago, 2007; Makkonen *et al.,* 2012). They might also have decreased the ratio between recalcitrant C and nutrients, such as lignin:P and lignin:N ratios (Wedderburn & Carter, 1999; Güsewell & Gessner,

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2009). Overall, in both focal species, litter quality increased in functionally dissimilar neighborhoods due to different changes in afterlife traits. However, the afterlife traits we measured only partly explained the increase in litter quality.

In neither of the focal species did microbial biomass respond to functional dissimilarity to neighborhood. This lack of effect might simply be a consequence of insufficient statistical power of our approach, given the somewhat limited subsample. However, the lack of effect might also be real. In particular, for *B. pinnatum*, neighborhoods did not affect afterlife traits that affected microbial biomass. In contrast, *in E. repens,* the lack of effect of functional dissimilarity to neighborhood on microbial biomass remains surprising. We expected a strong effect, since functionally dissimilar neighbors increased litter C:N and decreased senescence, both of which decreased microbial biomass (consistent with Eiland *et al.,* 2001; Güsewell & Gessner, 2009 and Chapman *et al.,* 2003). We can only speculate that other non-measured traits compensated the effects of C:N ratio and senescent area. Finally, we note that dissimilar neighborhoods affected mass loss and that, in our experiment, mass loss was primarily driven by microbes. It is therefore possible that a functionally dissimilar neighborhood increased microbial capacities rather than sheer biomass.

Decomposers in functionally dissimilar neighborhoods can be more efficient

The decomposer community of *B. pinnatum* was more efficient in functionally dissimilar neighborhoods. Multiple explanations are possible and we stress from the onset that for a complete explanation we would need more below-ground traits measured on neighbors. We also note that our system was mowed yearly and plant material was exported, which reduced the thickness of the litter layer and might have lowered neighbors effects on the complementarity of litter-mixture resources. In *B. pinnatum,* decomposer efficiency did increase in functionally dissimilar neighborhoods, suggesting decomposers benefited from the availability of functionally complementary litter and that they were generalist rather than specialist (see Loreau *et al.,* 2001 and Gessner *et al*., 2010). It is also likely that in functionally dissimilar neighborhoods, soil resource availability increased, possibly reducing competition between mycorrhizal fungi and decomposing fungi then improving efficiency of the latter in litter decomposition (Gadgil effect; Fernandez & Kennedy, 2016). Root exudates might also have been more diverse, stimulating a greater range of decomposer organisms. This latter mechanism, to our knowledge, has never been tested for leaf litter and should be investigated in the future. In *E. repens*, we did not observe a response of decomposer efficiency to functional dissimilarity to neighborhood. Mowing with exportation might have removed neighbors effects on decomposer efficiency. Alternatively, litter of *E. repens*, which lost mass more rapidly than litter of *B. pinnatum,* might always be appetent or a high-quality substrate for decomposer organisms,

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regardless of soil conditions or neighborhood litter quality (see Wardle *et al.,* 2006; Hoorens *et al.,* 2010). Thus, functionally dissimilar neighbors might increase decomposer efficiency only in poorly decomposable species, probably via complementarity effects.

Functional diversity of plant communities accelerates ecosystem functioning

Our study showed that functional diversity of plant communities increased litter quality within both focal species, and also increased efficiency of the decomposer community in one species. Thus, interspecific functional diversity of plant communities accelerated the ecosystem function of litter decomposition, via plant-plant and plant-decomposer interactions. The magnitude of increase in litter decomposition (more than 100% with combined effects of litter quality and decomposer efficiency) was much higher than commonly-observed changes in litter decomposition during litter transplant experiments (see Makkonen *et al*., 2012; Veen *et al*., 2015). The mesocosm experiment was conceived to mimic semi-natural grasslands, with similar species composition, similar monocotyledon:dicotyledon ratio and similar management (yearly mowing with removal). Therefore, the strong increase of focal-plant's litter decomposition in functionally diverse plant communities might well apply to semi-natural grasslands, which are the dominant grasslands in many regions of the world. In entirely natural systems, plant material is not exported, potentially rendering neighbors effects on litter decomposition more important. Overall, in diverse communities, the increase of litter decomposition might accelerate nutrient remineralization, as well as promote higher below-ground biodiversity (Hättenschwiler *et al.*, 2005; Gessner *et al*., 2010); it could also improve microclimatic conditions for germination or establishment of propagules. These changes together increase soil fertility. Consequently, our results may provide a novel explanation for how functional diversity accelerates ecosystem functioning in grasslands, and notably ecosystem productivity (see e.g. Tilman *et al.*, 2001; Loreau *et al*., 2001): interspecific functional diversity within grassland communities can magnify intraspecific contributions to litter decomposition, which might accelerate nutrient cycling. In our study, sampling afterlife traits permitted to mechanistically understand the link between functional diversity and ecosystem functioning. We therefore believe that a trait-based ecology would be very helpful to integrate above and below-ground plant interactions during community assembly with various ecosystem processes.

CONCLUSIONS

Our study revealed that a functionally dissimilar neighborhood strongly increased litter decomposition in two Poaceae species. In both species, litter decomposition increased via improved litter quality. This was due to intraspecific afterlife trait responses resulting from interactions with plant neighbors. In one species, litter decomposition also increased via an increase of decomposer

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efficiency. Our results suggest a novel mechanism for how functional diversity may increase ecosystem functioning in grassland ecosystems: the interspecific functional diversity within plant communities can increase intraspecific litter quality and decomposer efficiency.

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AUTHOR CONTRIBUTION

C. Mony, V. Jung, A. Prinzing and A.-K. Bittebière conceived the experiment. L. Barbe, V. Jung, C. Mony, A.-K. Bittebière and O. Butenschoen performed the experiments. L. Barbe analyzed the data. L. Barbe wrote the manuscript, with the help of C. Mony, V. Jung, A. Prinzing and A.-K. Bittebière.

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SUPPORTING INFORMATION

Table 1. Summary of all models explaining functional traits of both focal plants by functional dissimilarity to neighborhood (i.e. models for each radius of neighborhood).

Figure 1. Trait-mediated influence of functional dissimilarity to neighborhood on litter mass loss or litter microbial biomass.

Figure 2. Effect of functional dissimilarity on soil C:N ratio, in *E. repens* and *B. pinnatum.*

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TABLES

Table 1. Functional dissimilarity to neighborhood affected functional traits of focal plants: summary of the best regression models explaining each functional trait of each focal species by the functional dissimilarity to present neighborhood (see Materiel and Methods section for model selection, and Tab. S1). Spatial scale is the radius (in cm) of the considered neighborhood. Other model characteristics are the standardized regression coefficient (Stand. Coeff.), the degree of freedom (Df), the value of the F-test (F), the *p-value* (*P*) and the percentage of trait variation accounted for by the neighborhood (r^2). Significant models are in bold ($P < 0.05$).

Functional trait	Species	Spatial scale	Stand. Coeff.	Df	F	*P*	r^2
SLA	*B. pinnatum*	**10**	**0.33**	**48**	**6.91**	**0.011**	**0.11**
	E. repens	30	-0.01	35	0.01	0.93	-0.03
LDMC	*B. pinnatum*	30	0.43	22	2.8	0.11	0.07
	E. repens	30	-0.03	35	0.09	0.77	-0.03
Fungal attack	*B. pinnatum*	**30**	**0.37**	**22**	**4.7**	**0.042**	**0.14**
	E. repens	**30**	**-0.32**	**35**	**8.3**	**0.007**	**0.17**
Senescent area	*B. pinnatum*	**30**	**-0.53**	**22**	**8.8**	**0.007**	**0.25**
	E. repens	**30**	**-0.42**	**30**	**11.5**	**0.002**	**0.25**
C:N ratio	*B. pinnatum*	**20**	**-0.59**	**36**	**22.2**	**3.59×10^{-5}**	**0.36**
	E. repens	**30**	**0.61**	**35**	**44.6**	**9.9×10^{-8}**	**0.55**
Leaf toughness	*B. pinnatum*	20	-0.16	20	0.8	0.40	-0.01
	E. repens	**20**	**-0.49**	**19**	**10.0**	**0.005**	**0.31**

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Table 2. Functional traits affected mass loss and microbial biomass: summary of the best models explaining mass loss and microbial biomass of each focal species by its functional traits (see Materiel and Methods section for model selection). Model characteristics are the standardized regression coefficients (with their significance: *, *** for $P < 0.05$ and $P < 0.001$), the degree of freedom (Df), the value of the F-test (F), the *p-value* (*P*) and the adjusted percentage of dependent variable variation accounted for by functional traits (adj-R^2). Significant models are in bold ($P < 0.05$).

		Effects of functional traits of focal species									
Effect on	Species	LDMC	SLA	C:N	Leaf toughness	Fungal attack	Senescent area	Df	F	*P*	adj-R^2
Mass loss	*B. pinnatum*			**-0.367*** **				**130**	**18.56**	**3.21 x10^{-5}**	**0.12**
	E. repens		-0.064		-0.113			76	0.47	0.624	0.01
Microbial biomass	*B. pinnatum*	0.115				-0.297		40	0.44	0.646	-0.03
	E. repens			**-0.260***			**0.360***	**42**	**6.83**	**2.71 x10^{-3}**	**0.21**

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Table 3. Functional dissimilarity to neighborhood improved focal-plant mass loss via litter quality and decomposer efficiency: summary of the best models explaining mass loss and microbial biomass by functional dissimilarity to neighborhood mediated via litter quality (Q), decomposer efficiency (D, except for microbial biomass) and both (Q + D). See Materiel & Methods section for model construction and selection, and Fig. 3 for illustration. Spatial scale is the radius (in cm) of the considered neighborhood, and Stand. Coeff is the standardized regression coefficient. Other model characteristics are the degree of freedom (Df), the value of the F-test (F), the *p-value* (*P*) and the percentage of dependent variable variation accounted for by the neighborhood (r^2). Significant models are in bold ($P < 0.05$).

Effect of functional dissimilarity to neighborhood								
Effect on	Species	Mediated by	Spatial scale	Stand. Coeff.	Df	F	*P*	r^2
Mass loss	*B. pinnatum*	**Q + D**	**10**	**0.695**	**45**	**41.11**	**7.62×10^{-8}**	**0.47**
		Q	**10**	**0.436**	**45**	**9.09**	**4.21×10^{-3}**	**0.15**
		D	**10**	**0.400**	**44**	**9.11**	**4.21×10^{-3}**	**0.15**
	E. repens	**Q + D**	**30**	**0.352**	**32**	**6.12**	**0.019**	**0.13**
		Q	**30**	**0.364**	**34**	**5.46**	**0.026**	**0.11**
Microbial biomass	*B. pinnatum*	D	30	0.019	35	0.02	0.887	-0.03
		Q + D	10	0.252	19	1.25	0.277	0.01
		Q	10	-0.028	20	0.02	0.865	-0.05
	E. repens	Q + D	30	-0.014	16	0.01	0.95	-0.06
		Q	30	0.106	9	0.12	0.731	-0.09

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FIGURE CAPTIONS

Figure 1. Hypothetical mechanisms for how functional dissimilarity to plant neighborhood may influence decomposition of focal-plant's litter: functionally dissimilar neighbors may decrease resource competition and enemy pressure, increasing focal-plant litter quality, and may also increase complementarity of litter mixture and root exudates and decrease competition between mycorrhizal fungi and decomposers, increasing decomposer efficiency.

Figure 2. Path analysis models for the effects of functional dissimilarity to neighborhood on litter mass loss or litter microbial biomass mediated by functional traits. Arrows represent significant relationships between two variables, whose standardized regression coefficients and significances are given with arrows (*: $P<0.05$, **: $P<0.01$, ***: $P<0.001$). R^2 of each model is indicated in the box of its dependent variable. See Tab. 1 and Tab. 2 for the details of models and Fig. 2 of Supporting Information for graphical results.

Figure 3. Functional dissimilarity to neighborhood improved litter mass loss in both focal species: influence of neighborhood on litter mass loss, mediated via the combined effects of litter quality and decomposer efficiency ("overall effect" A, D), via only litter quality (B, E), and via only decomposer efficiency (C, F). The r^2 and the significance are given (*: $P<0.05$, **: $P<0.01$, ***: $P<0.001$, NS: non-significant). Note logarithmic scale for mass loss in *B. pinnatum*. See Tab. 3 for model characteristics.

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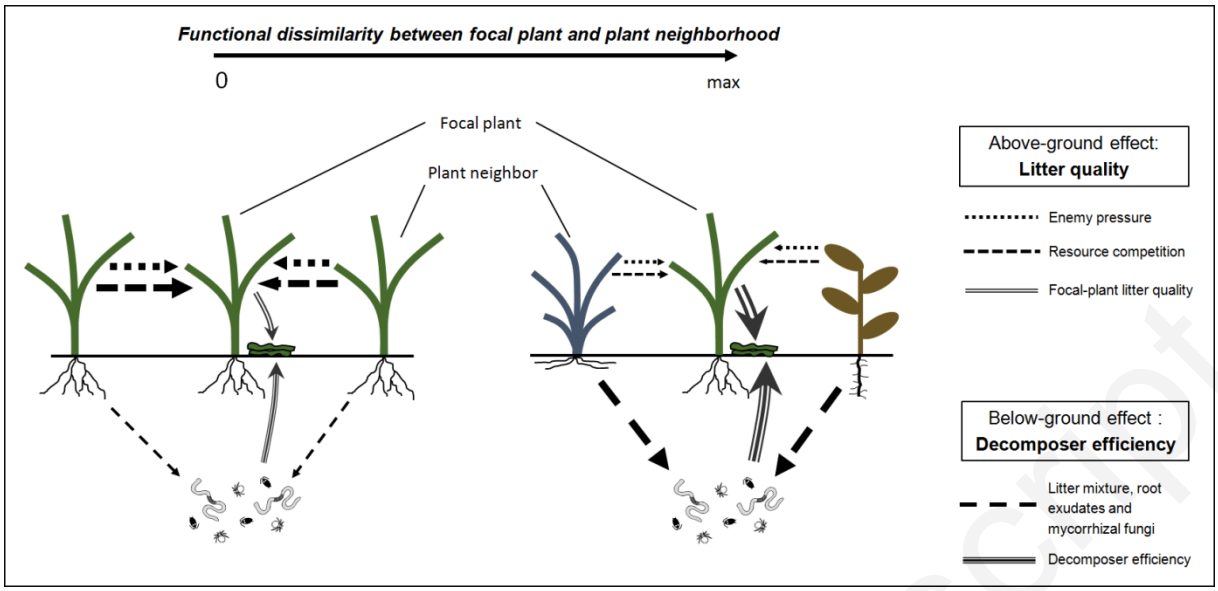

Figure 1

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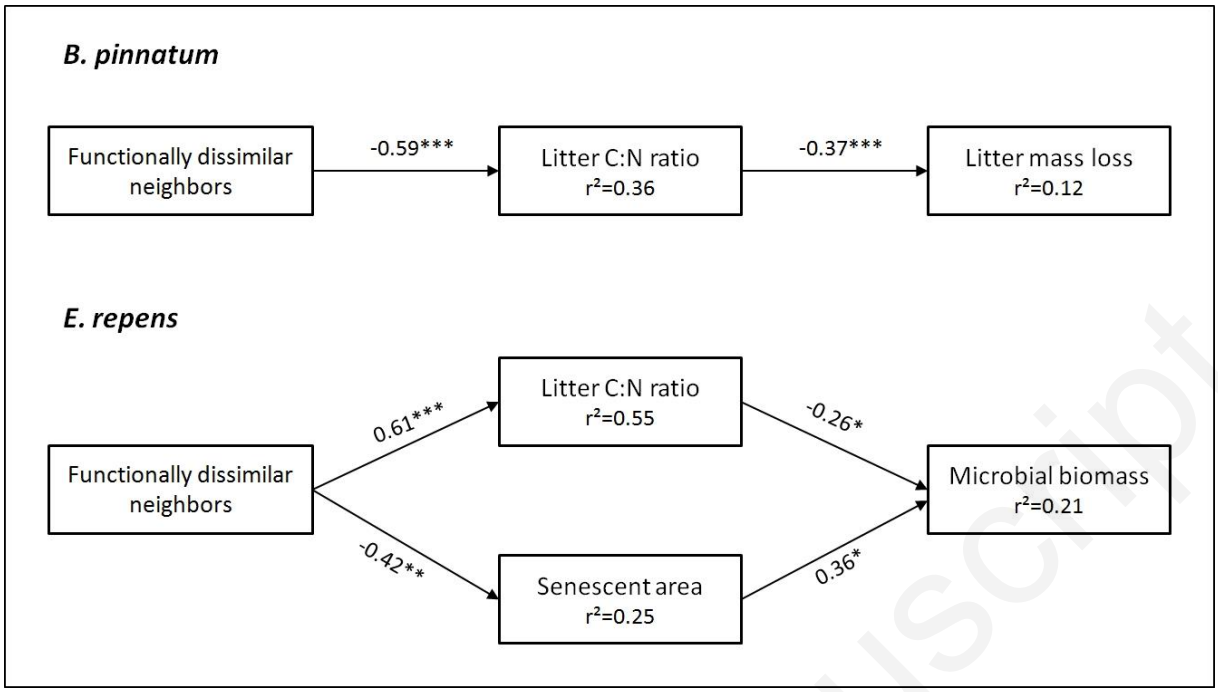

Figure 2

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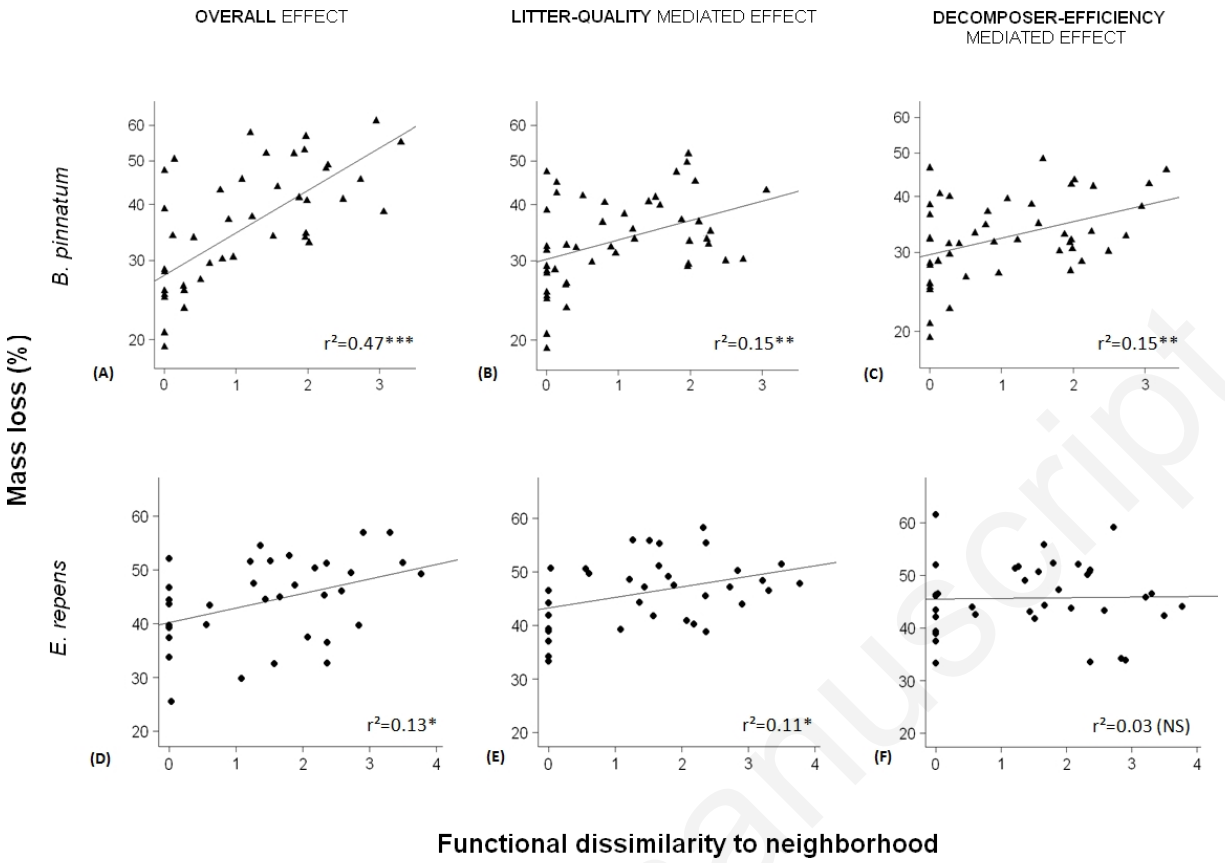

Figure 3

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