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MR. LOU BARBE (Orcid ID : 0000-0003-1800-407X)

DR. MATHIEU SANTONJA (Orcid ID : 0000-0002-6322-6352)

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Functionally or phylogenetically distinct neighbors turn antagonism among decomposing litter species into synergy

Authors: Barbe L. ⁽¹⁾, Mony C. ⁽¹⁾, Jung V. ⁽¹⁾, Santonja M. ⁽¹⁾, Bartish I. ⁽²⁾ and Prinzing A. ⁽¹⁾

(1) Université de Rennes 1 – OSUR, UMR CNRS 6553 ECOBIO

Avenue du G^{al} Leclerc, 35042 Rennes Cedex, France

Emails: lou.barbe@univ-rennes1.fr; cendrine.mony@univ-rennes1.fr; vincent.jung@univ-rennes1.fr; mathieu.santonja@univ-rennes1.fr; andreas.prinzing@univ-rennes1.fr;

(2) Academy of Sciences of Czech Republic, Institute of Botany

Zámek 1, 252 43 Průhonice, Czech Republic

Email: Igor.Bartish@ibot.cas.cz

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Corresponding author: Lou Barbe (+33 6 67 44 06 56; lou.barbe@univ-rennes1.fr)

ABSTRACT

1. Plant species coexisting in direct contact produce patches of mixed litters. Mixing litter sometimes synergistically accelerates and sometimes antagonistically decelerates litter decomposition, but we insufficiently understand why.
2. Here we hypothesize that antagonism or synergy within a mixed-litter patch depends on the neighboring litter matrix. Specifically, phylogenetical or functional dissimilarity within neighboring litter, or among patch and neighboring litter, may favor complementarity and thereby within-patch synergy.
3. From a pool of 20 grassland species, we created 120 mixed-litter patches of two species, and exposed these patches to neighborhoods in long-term grassland mesocosms of different functional and phylogenetic compositions.
4. We found 60% less (antagonism) to 80% more (synergy) decomposition than expected from single-species litters. Functionally similar, and grass-dominated, mixed-litter patches decomposed most synergistically. Synergy was most strongly favored by phylogenetic distance among neighbors and functional dissimilarity between neighbors and patch.
5. *Synthesis.* Our results show that the relationship between biodiversity and ecosystem functioning was context-dependent. We suggest that the coexistence of grasses and the formation of phylogenetically diverse, functionally distinct, patchy vegetation may be reinforced by synergistic nutrient recycling.

INTRODUCTION

The relationship between species richness and ecosystem functioning has been strongly debated in ecology (Grime 1998; Cameron 2002; Reiss *et al.* 2009; Gessner *et al.* 2010; Loreau & de Mazancourt 2013). In terrestrial ecosystems, an important aspect of ecosystem functioning is plant litter decomposition, driving nutrient cycling as well as carbon storage (Swift, Heal & Anderson 1979). Many studies investigated whether multi-specific litter mixes decomposed faster or slower than the

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corresponding mono-specific litters alone, *i.e.* whether coexisting species in mixed litters exerted respectively synergistic or antagonistic effects during decomposition. These studies found opposite results (Gartner & Cardon 2004; Hättenschwiler, Tiunov & Scheu 2005; Gessner *et al.* 2010), depending on abiotic conditions (Jonsson & Wardle 2008; Santonja *et al.* 2015), composition and functional properties of mixed litter (Wardle *et al.* 2006; Chapman & Koch 2007; Pérez Harguindeguy *et al.* 2008; Barantal *et al.* 2014; Bílá *et al.* 2014), and identity or activity of decomposers (Schädler & Brandl 2005; Vos *et al.* 2011; Vos *et al.* 2013; Handa *et al.* 2014). Many of these studies showed that litter mixtures that are functionally dissimilar decompose synergistically, probably by providing complementary resources needed by generalist decomposers or by multiple specialist decomposers, which have complementary effects on decomposition (Meier & Bowman 2008; Gessner *et al.* 2010; Vos *et al.* 2013; Bílá *et al.* 2014; Tardif & Shipley 2014). But, other studies showed that trait dissimilarity might also render decomposition antagonistic as a given decomposer or detritivore might find its preferred resources diluted in unpreferred ones (Pan *et al.* 2015). However, the majority of studies were done in natural conditions, in which the ambient plant communities were not held constant or even taken into account to explain litter-mixture decomposition (Jonsson & Wardle 2008; Makkonen *et al.* 2013; Santonja *et al.* 2015). This community context may control abiotic and biotic conditions surrounding litter mixtures, and might ultimately determine synergies or antagonisms during litter-mixture decomposition.

Under natural conditions, decomposition of a patch of litter mixture may depend on the ambient community matrix. Synergy or antagonism among co-decomposing litter species is induced by small, mostly microscopic organisms interacting with litters across very short distances of some centimeters. But these minute patches of mixed litter are surrounded by larger patches formed by the neighboring vegetation, reflecting for instance the clonal growth of plant species (which often promotes an aggregated vegetative growth, rendering plants different from their larger neighboring plant matrix) or short-distance dispersal of plant species (Kershaw 1963; Herben & Hara 2003; Semchenko *et al.* 2013). Due to this plant-community heterogeneity, a patch of litter mixture may be

embedded in a plant matrix ranging from identical to very different, both in traits and phylogenetic positions. Moreover, neighborhoods as such can be homogenous or composed of functionally or phylogenetically distinct plant species. We will outline below how this variation in distinctness of neighborhoods might strongly affect the synergy or antagonism during decomposition of a litter mixture, *i.e.* how the effect of diversity on ecosystem functioning might be dependent on the community context.

First, synergy among co-decomposing litter species might be favored by a plant neighborhood composed of functionally dissimilar species. A functionally dissimilar neighborhood might provide dissimilar resources and constraints. For instance, dissimilar specific leaf areas (SLA), leaf C:N ratios or water-holding capacities (WHC), might correspond to dissimilar nutritional compositions or microclimates. Thereby, functionally dissimilar plant neighborhoods may favor resource complementarity and harbor diverse and generalist decomposers and detritivores (Wardle *et al.* 1999; Spohn *et al.* 2000; Hättenschwiler *et al.* 2005; Meier & Bowman 2008; Gessner *et al.* 2010). Diverse and generalist decomposers and detritivores might not only tolerate but require the combination of multiple litter resources to be fully performant and active, which might trigger a synergy during litter-mixture decomposition (Hedde *et al.* 2010; Vos *et al.* 2011; Handa *et al.* 2014; Coulis *et al.* 2015). Therefore, we hypothesize that functional dissimilarity within the plant neighborhood triggers synergy during decomposition of a litter mixture (Fig. 1).

Second, decomposition of a litter mixture might be synergistic if the plant neighborhood is functionally similar to the litter mixture. In such a case, ambient detritivores and decomposers might show particular adaptations for using the mixed-litter type in the local litter-mixture patch. For instance, ambient decomposers and detritivores that have been exposed to leaf dry matter contents (LDMC) or WHC similar to those in the litter mixture likely show the adaptations needed for decomposing the litters in the patch. Availability of decomposers adapted to a locally dominant litter explains why litters often decompose faster below the plants that have produced them, an effect

called "Home-Field Advantage" (Ayres *et al.* 2009; Austin *et al.* 2014; Freschet *et al.* 2012; Veen *et al.* 2015). Such adapted decomposer species might immigrate into the litter mixture and might there be capable of using both litters and profiting from their complementarity, thereby triggering synergistic decomposition. In contrast, decomposers that might colonize a litter mixture from a dissimilar neighborhood might be capable of profiting at most from a single of the litter species, and might suffer from dilution of that species among a second entirely unusable species, thereby possibly triggering antagonistic decomposition. Whether Home-Field Advantage may also foster synergy among litter mixtures is still unknown. We hypothesize that high functional similarity between plant neighborhood and litter mixture triggers Home-Field Advantage also in terms of synergy during decomposition (Fig. 1).

Third, such neighborhood dependency of synergistic effects also implies that the relationship between litter mixing and litter decomposition may change with the phylogenetic diversity of the litter mixture as well as that of the plant neighborhood. Phylogenetically distant species may have diverged in traits related to litter decomposition (Crisp & Cook 2012; Pan *et al.* 2015; but see Prinzing *et al.* 2008). Overall, phylogenetic dissimilarity between two species drawn at random from a pool can be used as a proxy for their functional dissimilarity, which may be useful if traits of interest are numerous and hard to measure (for example, concentrations in possible micronutrients for decomposers and detritivores). Phylogenetic dissimilarity within plant neighborhood and similarity between plant neighborhood and litter mixture may hence trigger synergy for the same reasons as previously listed for functional dissimilarity. Phylogenetic dissimilarity within a litter mixture may also reflect divergence of litter traits and hence complementarity in litter resources, triggering synergy as explained above. Overall, we hypothesize that decomposition of a litter mixture might be synergistic if phylogenetic dissimilarity within litter mixture and within plant neighborhood is large, or if phylogenetic dissimilarity between litter mixture and plant neighborhood is small (Fig. 1).

Fourth, and independently of the neighborhood, synergy may especially arise in poorly decomposable litter mixtures. Litter decomposition rate of any species may have a maximum, determined by the local environmental conditions, e.g. available decomposers. A highly decomposable litter species, which decomposes at this maximal rate, might not decompose even better due to synergistic effect resulting from litter mixing. Such high litter decomposability results from particular litter traits, for instance high WHC (ensuring water availability for decomposers and detritivores: Makkonen *et al.* 2013), high SLA or low LDMC (representing respectively thin leaves and leaves with few recalcitrant compounds, facilitating colonization by decomposers and consumption by detritivores: Pérez-Harguindeguy *et al.* 2000; Garnier *et al.* 2004; Santiago 2007), or low C:N ratio (ensuring nitrogen inputs for decomposers: Kazakou *et al.* 2006; Fortunel *et al.* 2009). Litter mixtures having such high quality traits will decompose rapidly but close to the maximal rate, so they might decompose less synergistically. Moreover, some of these traits may be established in some lineages more or less than in others. Grasses for instance, tend to be less decomposable than eudicots (Cornwell *et al.* 2008), which might give much space for synergistic effects due to litter mixing. Overall, we hypothesize that litter mixtures composed of poorly decomposable species (for instance, grasses) decompose most synergistically (Fig. 1), and that some traits decreasing decomposition *per se* increase synergy.

Here we tested whether and how the functional and phylogenetic neighborhood of litter mixtures drive synergistic or antagonistic decomposition of litter mixtures (see Fig. 1). We used a long-term mesocosm experiment with functionally or phylogenetically different neighborhoods, in which we exposed 2-species litter mixtures. We quantified phylogenetic and functional dissimilarities at all scales of the experiment (litter mixture, plant neighborhood, and between both), and we quantified functional dissimilarities using four traits: SLA, LDMC, WHC and C:N ratio. We measured litter decomposition and non-additive effects (synergy to antagonism) for each litter mixture. We tested the following prediction of our above hypotheses: synergy of litter decomposition within a litter mixture is favored by (i) high functional and phylogenetic dissimilarities within plant neighborhood;

(ii) low functional and phylogenetic dissimilarities between plant neighborhood and litter mixture;
(iii) high functional and phylogenetic dissimilarities within litter mixture; (iv) low decomposability of
litter species.

MATERIAL & METHODS

Selection and combination of litter-mixture species

Based on existing floristic regional datasets, we selected 20 species commonly present in grassland ecosystems of Brittany (Western France) to conceive litter mixtures: *Achillea millefolium* (L.), *Angelica sylvestris* (L.), *Brachypodium pinnatum* (L.), *Centaurea nigra* (L.), *Cirsium arvense* (L.), *Dactylis glomerata* (L.), *Deschampsia cespitosa* (L.), *Elytrigia repens* (L.), *Festuca rubra* (L.), *Filipendula ulmaria* (L.), *Holcus lanatus* (L.), *Holcus mollis* (L.), *Molinia caerulea* (L.), *Plantago lanceolata* (L.), *Potentilla erecta* (L.), *Potentilla reptans* (L.), *Ranunculus repens* (L.), *Rumex obtusifolius* (L.), *Succisa pratensis* (L.), and *Symphytum officinale* (L.). These species were selected to encompass various functional properties and phylogenetic positions (8 grasses, 12 eudicots, and various families within eudicots). From these 20 species, we conceived 120 distinct and contrasted combinations of 2-species litter mixtures in order to obtain a wide, continuous range of functional and phylogenetical dissimilarities (most combinations had only one replicate). 37 litter mixtures included two grass species, 48 mixtures included only one grass species and 35 mixtures included no grass species - see Tab. S1 for the occurrence of each species in litter mixtures.

Selection and floristic characterization of plant neighborhoods

We selected the plant neighborhoods in the mesocosm experiment of the University of Rennes 1 (Western France, 48°06'58.6"N 1°38'15.5"W; see Benot *et al.* 2013). In this experiment, set up in 2009, we selected 60 mesocosms, involving 6 different mixtures of grassland plant species replicated 10 times. These 6 mixtures corresponded to four levels of initial species richness (1, 4, 8, 12), with two different specific compositions for the level of 4 and 8 species richness. The different species

richness and the different specific compositions of mixtures were selected in order to mimic different plant communities of grassland ecosystems. The mesocosms were 1.30 x 1.30 m in surface and 0.25 m height. Soil was composed of 20% sand and 80% garden soil, and was homogenized before construction of mesocosms. At the beginning of the experiment in 2009, we applied a mineral fertilizer with slow release (N/P/K: 20/5/10) to fully homogenize the soil nutrient quantity among mesocosms. Initial mean soil nutrient properties were: $[\text{NO}_3^-] = 34.4 \mu\text{g.g}^{-1}$; $[\text{P}] = 0.37 \mu\text{g.g}^{-1}$; $[\text{PO}_4^{2-}] = 40.3 \mu\text{g.g}^{-1}$; C:N ratio = 7.21. Mesocosms were located outside in a microclimatically homogeneous common garden, and were watered by rain during most of the year, with an additional punctual artificial watering during dry summer weeks. The mesocosms harbored natural decomposer communities that were initially present in the soil, and decomposer communities that colonized the soil since the setting up of the experiment in 2009 (fauna as well as bacteria and fungi). Mesocosms were yearly mowed and plant material was exported to mimic semi-natural grasslands. The 12 sown species are very common and abundant in Western France and were: *Agrostis stolonifera* (L.), *Agrostis tenuis* (L.), *Brachypodium pinnatum*, *Centaurea nigra*, *Chamaemelum nobile* (L.), *Dactylis glomerata*, *Elytrigia repens*, *Festuca rubra*, *Holcus lanatus*, *Holcus mollis*, *Lolium perenne* (L.) and *Ranunculus repens*. We mapped plant species distribution in each mesocosm in early spring 2015, with an 80 x 80 cm square grid of 10-cm cell size (64 cells per grid, following Benot *et al.* 2013). The presence of each rooted species was noted in each cell. Based on this mapping, we selected in each mesocosm two distinct neighborhoods, separated by at least 30 cm. These neighborhoods were the experimental units of our design. Importantly, the realized range of species compositions in neighborhoods was very large and continuous due to major variation in plant species distribution within mesocosms. Plant neighborhood composition was quantified by calculating the number of cells occupied per each neighboring species in a radius of 15 cm around the center of the neighborhood (*i.e.* comprising the cell of the center of the neighborhood and the eight surrounding cells). Finally, we randomly assigned one litter mixture to each plant

neighborhood. A given neighborhood covered 707 cm², *i.e.* a distinctly larger surface than the 64 cm² of a given litterbag (see below).

Characterization of functional dissimilarities

Functional dissimilarities were calculated measuring four functional traits indicative of litter quality: Specific Leaf Area (SLA), Leaf Dry Matter Content (LDMC), Water Holding Capacity (WHC) and Carbon:Nitrogen ratio (C:N). These functional traits mainly determine the physical properties of litter (thinness of leaves, and their physical capacity to store water) and the litter microclimate (Santiago 2007; Makkonen *et al.* 2013) as well as the litter nutrient content (Pérez-Harguindeguy *et al.* 2000; Quested *et al.* 2007). We measured these traits on all species present in the pool of litter mixtures and plant neighborhoods. We measured on two green leaves collected on five different individuals the SLA and the LDMC, following the protocols of Pérez-Harguindeguy *et al.* (2013). The five individuals were collected in different local environments, to obtain a representative mean value for each trait and each species. For each of the 5 individuals, we also measured the C:N ratio on naturally senesced leaves, using an elemental analyzer (FLASH EA 1112 Thermo Finnigan, Waltham, Massachusetts, USA). We also measured the WHC, on dead leaves that were immersed in distilled water during 24h, drained and weighed, then dried at 65°C during 48h and weighed again. WHC was calculated following the formula: water-saturated weight / dry weight. A Principal Component Analysis (PCA) ordination of the four litter traits of the 20 litter species is shown in Fig. S1. The mean and variance of trait values for each species and each trait are described in Tab. S1.

For each pair of species present in the pool of litter mixtures and plant neighborhoods, we extracted the Euclidian distance between both species in the 4-dimensional space with an axis for each trait we measured (Villéger, Mason & Mouillot 2008). Trait 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 (all $r < 0.14$, except for LDMC vs WHC: $r = -0.52$). We calculated three types of functional dissimilarity:

(i) functional dissimilarity within litter mixture, as the Euclidian distance between both species composing the litter mixture; (ii) functional dissimilarity within plant neighborhood, as the abundance-weighted mean Euclidian distance between all pairs of species composing the neighborhood; (iii) functional dissimilarity between litter mixture and plant neighborhood, as the abundance-weighted mean Euclidian distance between each species of the litter mixture and each species of the neighborhood. The distance of a litter species to a conspecific neighbor was zero. Such zero distances did not impact further calculations as no multiplications were involved, only averaging. Moreover, averaging always involved some non-zero distances, which was inevitable given the study design. The variation range of functional dissimilarities is described in Tab. S2.

Characterization of phylogenetic dissimilarities

We calculated phylogenetic dissimilarities using a recent angiosperm phylogeny corresponding to a dated tree of the Dutch flora based on *rbcL* DNA sequences (see Hermant *et al.* 2012). The tree is highly congruent with, but often more resolved than that of Durka & Michalski (2012) for the larger region of Europe. The tree is also congruent with that of Zanne *et al.* (2013). Zanne *et al.*'s tree covers some 10-15% of the global Angiosperm flora, which renders it inevitably less complete and representative of the Western France grassland genera than the complete tree we used. We note that estimation of age of the crown node of Angiospermae from dating molecular phylogenies is still an issue of considerable uncertainty (Bell *et al.* 2010; Smith *et al.* 2010; Magallon *et al.* 2013). However, the congruence among several dated molecular reconstructions of the earliest evolution in Eudicotyledoneae and paleobotanic records (Doyle & Hotton, 1991) suggest that age estimate provides a robust constraint for calibrating phylogenies in this large taxon (see Magallon *et al.* 2013). We therefore used this estimate as a fixed age constraint for the crown node of Eudicotyledoneae in our dating analyses of Dutch angiosperms. Hermant *et al.* (2012, Appendix E) provide details on other node calibrations. For each pair of species present in the pool of litter mixtures and plant neighborhoods, we calculated the patristic distance, *i.e.* distance among both species as path-length

distance along branches of tree from one species to the other one. These distances represent twice the age of the species' last common ancestor. Calculations were made using Mesquite software (Maddison & Maddison 2017).

We calculated phylogenetic dissimilarities within litter mixture, within plant neighborhood and between both, as we did for functional dissimilarities. We calculated the phylogenetic dissimilarity within litter mixture as the patristic distance between both species composing the litter mixture, and we calculated the phylogenetic dissimilarity within plant neighborhood as the abundance-weighted mean patristic distance between all pairs of species composing the neighborhood. Finally, we calculated the phylogenetic dissimilarity between litter mixture and plant neighborhood as the abundance-weighted mean patristic distance between each species of the litter mixture and each species of the neighborhood. The variation range of phylogenetic dissimilarities is described in Tab. S2, and the correlations between functional and phylogenetic dissimilarities are given in Tab. S3, showing that both variables did not correlate across litter mixtures, but correlated positively across plant neighborhoods and partly across litter mixture-plant neighborhood comparisons. Correlations between phylogenetic and trait distances across the 20 litter-mixture species were at most weak, and only that involving LDMC was significant ($R^2=0.04$, Tab. S3). The PCA ordination in Fig. S1 shows that along the first, LDMC-related axis Poaceae are distinctly separated from the other (dicotyledons) families, while these remaining families are little separated among each other. Position along the second axis and the three other traits clearly does not correspond to family membership.

Decomposition of litter mixtures and comparisons to monospecific litters

In autumn 2014, we collected naturally senesced litter for the 20 litter-mixture species. Species present both in mesocosms and litter mixtures (8 species) were collected in mesocosms and species only present in litter mixtures (12 species) were collected nearby grasslands in the Rennes region. For a given field-sampled species, litter was collected in the same grassland and was homogenized

after. Also, litter of species sampled in mesocosms was homogenized. Litter was air-dried, and the 120 litter mixtures were assembled and placed into 8 x 8 cm litterbags. We tried to have identical masses for both species composing each litter mixture and the precise mass of each species were noted. Litterbags had 2 mm mesh on their upper side to avoid contamination by allochthonous litter – which is important in grassland ecosystems since grass species produce litter throughout the year – and 5 mm mesh on their lower side to facilitate access for the numerous detritivores that shuttle between litter and soil (Santonja *et al.* 2016). During the period of exposure, litter always remained moist and was never brittle, preventing the loss of small fragments of litter. Each litterbag contained 1g of litter, oven-dried equivalent (air-dry/oven-dry ratio calculated from subsamples that were oven-dried but not exposed to decomposition).

We exposed each litter mixture in its respective plant neighborhood, positioning litter mixture on bare ground by gently pushing aside plant neighbors (*i.e.* without removing any neighbor), and we started the decomposition experiment in February, 2015. To calculate synergistic or antagonistic effects during litter-mixture decomposition, *i.e.* non-additive effects (NAE), we also exposed in each neighborhood two litterbags containing the corresponding mono-specific litters alone (the three litterbags occupied around 27% of the soil surface of the neighborhood, leaving enough space for the neighboring vegetation to recover). These mono-specific litterbags were exposed very close (one to two centimeters) to the litter mixture, contained 1g of litter (oven-dried equivalent) and had mesh identical to mesh of litter-mixture litterbags. All litterbags were collected 6 weeks later: a phase that is of particular interest as litter-mixture interactions mainly occur in the initial stages of litter decomposition (Hoorens, Aerts & Stroetenga 2002; Hättenschwiler *et al.* 2005; Srivastava *et al.* 2009). At that moment, litter mixtures had reached between 30-60% mass loss, reflecting the rapid decomposition during the humid and relatively warm, frost-free winter in the study region which increases decomposer activity. High decomposition also results from the high decomposability of herbaceous eudicots (Cornelissen 1996; Cornwell *et al.* 2008). We cleaned the litter by hand, oven-dried it at 65°C for three days and calculated mass loss (%) as $(1-(m_1/m_0)) \times 100$, where m_1 is the

oven-dry weight at collection and m_0 the initial oven-dry equivalent dry weight. We calculated the expected decomposition of litter mixtures, as the mean of the decomposition of the two species in mono-specific treatment, weighted by the precise proportion of the two species in the litter mixture.

Then, we calculated non-additive effects (NAE) of litter-mixture decomposition as:

Where O is the observed decomposition of litter mixture and E is the expected decomposition of litter mixture. Division by E ensures a similar scale of non-additive effects for highly and poorly decomposable litter mixtures. Litter-mixture decomposition could be additive ($NAE=0$, *i.e.* no significant difference between observed and expected decomposition), synergistic ($NAE>0$, *i.e.* observed decomposition higher than expected), or antagonistic ($NAE<0$, *i.e.* observed decomposition lower than expected; Wardle *et al.* 1997). Note that alternative quantifications of non-additive effects (*i.e.* log-ratios) led to the same results thereafter.

Statistical analyses

Prior to analyses, we center-reduced all independent and dependent variables (*i.e.* for each variable, subtracting from each value the mean of the variable and then dividing this difference by the standard deviation of the variable), permitting comparisons between regression coefficients of different variables within a given model and among models. We used multiple ordinary least squares regression models to test the effects of functional and phylogenetic dissimilarities on (a) non-additive effects of litter-mixture decomposition and (b) litter-mixture decomposition *per se*. As independent variables, we also included in these models the mean functional characteristics of litter mixtures (SLA, LDMC, WHC and C:N) as they may also influence decomposition; we also included the percentage of grasses within litter mixture, to account for phylogenetic position of litter species and not only for phylogenetic distances between them. As non-additive effects can by definition only be quantified for litter mixtures, we also restricted the analysis of decomposition *per se* to litter

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mixtures. To understand the effect of overall functional dissimilarities on non-additive effects tested in (a), we tested (c) how non-additive effects depended on dissimilarities of each of the individual traits (SLA, LDMC, WHC, C:N ratio) within litter mixture, within plant neighborhood and between both (see Tab. S4). The identity and abundance of species (in both neighborhood and litter-mixture species) might also affect non-additive effects (Wardle *et al.* 2003; Wardle *et al.* 2006; Ball *et al.* 2008; Nielsen *et al.* 2011), we hence tested (d) the effect of abundance of species composing the litter mixtures and the plant neighborhoods on non-additive effects (see Tab. S5). Note that we also included the abundances of all litter species and the neighborhood species richness in the initial set of variables tested in (a), as well as mesocosm as a random factor (because per mesocosm there were two data points, which could result in statistical non-independence), but all these variables were excluded during model selection. Finally, we tested (e) the effect of decomposability of litter mixtures (averaged decomposition from the two monospecific litterbags) on non-additive effects, through a simple ordinary least squares regression model. For analyses in (a), (b), (c) and (d) we built all possible models, *i.e.* all possible combinations of independent variables, including in (a), (b) and (c) the interaction terms between dissimilarity within litter mixture and dissimilarity within plant neighborhood - testing whether dissimilar litter mixtures decompose better if the plant neighborhood is dissimilar too. Then, we performed a best subset search and selected the 10 best models based on AIC and BIC (Burnham & Anderson 2003; Chen & Chen 2008). This procedure is more robust than a backward stepwise selection procedure when independent variables are numerous compared to replicates and differences between models are likely to be small (Miller 2002). We graphically explored residuals using probability plots and predicted vs residual plots, and we excluded five major residual outliers (out of 120 data points) to fulfill the assumption of normality and homogeneity of residuals. Not excluding outliers reduced explained variance, but changed only one minor result of the analyses: the effect of mean C:N of litter mixtures on non-additive effects became slightly non-significant. The 10 best models explaining non-additive effects by functional and phylogenetic dissimilarities were highly significant and were very close in terms of

likelihood and explained variance, with AIC and BIC always varying from a given model to its closest one by less than 2, giving high confidence in the variables selected in all models (Tab. S6, and Tab. S7 for models for decomposition *per se*). Results were robust despite the somewhat large number of variables (relative to 120 replicates), with best models of a given analysis all identifying the same set of variables (Tab. S6 and Tab. S7). As AIC and BIC gave priority to the best model, we hence only present that model in Results. All statistical analyses were performed with R 3.0.3 software (R Development Core Team, 2014), with the packages *car* and *leaps*.

RESULTS

In general, litter mixtures decomposed quickly if composed of species that each decomposed quickly (Fig. S2), but 24% of the variance in litter-mixture decomposition remained unexplained by the decomposition of single litters, which may at least in part reflect the effect of synergies or antagonisms. Litter-mixture decomposition triggered strong non-additive effects, from antagonistic effects with 60% less decomposition than expected to synergistic effects with 80% more decomposition than expected (Fig. S3). Around 40% of litter mixtures showed only minor non-additive effects, *i.e.* comprised between -10% and +10%. Overall, the mean of non-additive effects was around 8% synergy and was significantly larger than 0 ($t=3.0$, $P=0.004$, $df=114$).

Phylogenetic dissimilarity within plant neighborhood and functional dissimilarity between litter mixture and plant neighborhood render decomposition synergistic

Non-additive effects were explained by several variables concerning trait dissimilarity and trait means of litter mixtures, plant neighborhoods and both (Tab. 1). The model with these retained variables explained more variance than models using only species identities (see Tab. S5): retained variables explained 19% of the variance of non-additive effects, in a highly significant model ($P=5.10^{-5}$). We note that variance inflation factors were distinctly smaller than what is usually considered indicative of overly multicollinearity (Tab. 1). Species identities and interaction terms among dissimilarities were excluded from the best model, therefore we did not present them in Tab. 1.

Overall, we observed that phylogenetic dissimilarity within plant neighborhood triggered synergy during litter-mixture decomposition, and functional dissimilarity between litter mixture and plant neighborhood turned antagonism into synergy (Tab. 1, Fig. 2, A, B). For instance, when the plant neighborhood was composed of grasses as well as eudicotyledons, and of various families within eudicotyledons, litters decomposed more rapidly compared to alone; when the litter mixture had functional traits different from that of the plant neighborhood, litters also decomposed more rapidly compared to alone. These results are not biased by the correlation between functional and phylogenetic dissimilarities within plant neighborhoods (Tab. S3): even after exclusion of phylogenetic dissimilarity within plant neighborhood, functional dissimilarity within plant neighborhood remained non-significant (albeit showed a tendency: $P=0.08$). Contrary to the neighborhood effect, functional dissimilarity within litter mixture turned synergy into antagonism, but with a weaker effect than the previously-mentioned effects related to plant neighborhood (Tab. 1, Fig. 2 C). The effect of functional dissimilarity within litter mixture and between litter mixture and plant neighborhood was especially due to one functional trait, LDMC (see Tab. S4). For example, when the litter mixture was different from the plant neighborhood in terms of LDMC, litters decomposed much more quickly together compared to alone; in contrast, when litters composing the litter mixture had different LDMC, litters decomposed more slowly compared to alone.

Poorly decomposable litters decompose more synergistically

Synergy among litter mixtures was high if species composing mixtures, in monospecific treatments, were poorly decomposable: mean monospecific decomposability of litter-mixture species decreased synergy among species ($P=0.001$, $r^2=0.08$, $F=11.4$, $df=114$, Fig. 3, A). Consistently, several variables that decreased litter-mixture decomposition *per se* increased synergy (see Tab. 1). Specifically, low WHC and high percentage of grasses within litter mixture decreased litter-mixture decomposition *per se*, but increased synergy (Fig. 3, B, C – note that high C:N ratio, in contrast, increased both

decomposition and synergy). We note that decomposition *per se* was very well explained (adj-R²=0.55) in comparison to non-additive effects (adj-R²=0.19).

DISCUSSION

We demonstrated that litter mixing in temperate grassland communities triggered both synergy and antagonism during decomposition, and that synergy and antagonism were driven by the characteristics of litter-mixture species as well as those of species of the plant neighborhood. We observed that, within litter mixtures, functional dissimilarity tended to turn synergy into antagonism. However, plant neighborhoods had stronger and opposing effects: phylogenetic dissimilarity within neighborhood and functional dissimilarity between litter mixture and neighborhood tended to turn antagonism into synergy. We also showed that poorly decomposable litter mixtures decomposed more synergistically.

A neighborhood of phylogenetically distant species might harbor diverse decomposers and detritivores thereby favoring synergistic decomposition of litter mixtures

We observed that phylogenetic dissimilarity within plant neighborhood triggered synergy during decomposition of litter mixtures. The synergistic decomposition rate in dissimilar neighborhoods might be due to a larger range of biotic and abiotic conditions, caused by more distantly related species ultimately harboring a more diverse pool of detritivores and decomposers. From such a diverse pool, the litter-mixture patch might recruit the decomposers and detritivores capable of benefiting from litter mixing, which might be more efficient in decomposing litter mixtures than mono-specific litters (Wardle *et al.* 1999; Spehn *et al.* 2000; Milcu *et al.* 2006). As phylogenetic dissimilarity within neighborhood increased synergy and functional dissimilarity did not, the neighbors' functional traits involved in the effect of phylogenetic dissimilarity were not those we measured. Moreover, as phylogenetic dissimilarity influenced synergistic effects only within plant neighborhood, these unmeasured traits acted only at the scale of the plant neighborhood, *i.e.* acted rather on the pool of detritivores and decomposers than on the properties of litter mixture.

Candidate traits that differ among distantly related species and likely to drive the composition of the pool of detritivores and decomposers may be root traits such as root density, root microbiota or root exudates (Kuzyakov, Hill & Jones 2007; Lindahl & Tunlid 2015; Soudzilovskaia *et al.* 2015). We stress, however, that we did not sample detritivores and decomposers nor measure their activity, so this decomposer-pool mechanistic hypothesis remains to be tested: do neighborhoods composed of distantly related plant species harbor pools of decomposers that are more efficient in decomposing mixed than mono-specific litters, and does this reflect the diversity of niche conditions in the neighborhood?

Functional dissimilarity between neighborhood and litter mixture might favor synergy through Away-Field Advantage

We found that ambient plant neighborhoods that are functionally dissimilar to the litter mixture tended to turn antagonism into synergy. This is contrary to our hypothesis that similarity between litter mixture and neighborhood should favor synergy due to a Home-Field Advantage, *i.e.* the availability of decomposers and detritivores being particularly adapted to litter-mixture quality (Ayres *et al.* 2009; Freschet *et al.* 2012; Austin *et al.* 2014; Veen *et al.* 2015). Instead, our result suggests that synergy within a litter mixture might be favored by the uniqueness of this patch within its neighborhood: a functionally unique litter patch is one that attracts across a large scale the decomposers preferring the characteristics of this patch, possibly leading to an over-proportional decomposer activity facilitating synergy. Specifically, litter patches that have high or low LDMC compared to their neighborhood decomposed most synergistically (Tab. S4). These patches possibly attracted across a large neighborhood decomposers whose activity benefited from extreme LDMC: either decomposers whose colonization and activity was facilitated by low LDMC, or detritivores performing compensatory feeding on high LDMC (*i.e.* enhanced consumption rate on poor-quality litter to ensure sufficient resource assimilation to meet metabolic needs; Gessner *et al.* 2010). We may also speculate that this synergy might compensate for a possible negative effect of dissimilarity

between litter mixture and neighborhood on decomposition *per se* (as predicted by Home-Field Advantage), and might explain why we and other authors (Gießelmann *et al.* 2011; Veen *et al.* 2015) did not find this negative effect on decomposition *per se*. Future research should test whether litter mixtures that are functionally unique within their neighborhood do indeed attract specialist decomposers across large surfaces. Also, the consequences of decomposer assembly for litter decomposition and synergistic effects require further investigation.

Functional similarity within litter mixture might favor synergy through increased resource concentration

We showed that functional similarity within litter mixtures tended to turn antagonism into synergy during decomposition. These results contradict numerous previous studies that mainly reported that functional trait similarity decreased synergistic effects (Pérez Harguindeguy *et al.* 2008; Berglund & Ågren 2012; Makkonen *et al.* 2013). We suggest that functional similarity among co-decomposing litter species increased concentration of litter resources for specialist decomposers and detritivores, in comparison to litter mixtures with high dissimilarity. Colonization of specialist decomposers or consumption by specialist detritivores might be favored, and these multiple specialists might have complementary effects on decomposition, leading to synergistic effects (Pan *et al.* 2015). Specifically, we showed that this effect of functional dissimilarity was especially due to one particular trait, LDMC (see Tab. S4). In litter mixtures with such high LDMC dissimilarity, the litter species with high LDMC might have inhibited colonization of the other litter species, due to the dilution of easily decomposable compounds by recalcitrant compounds such as lignin and cellulose (Hedde *et al.* 2010; Vos *et al.* 2011). In addition, synergy or antagonism during litter-mixture decomposition depended on functional dissimilarities within litter mixture or among litter mixture and plant neighborhood, but did not depend on phylogenetic dissimilarities. The traits we measured were hence likely important, albeit we remind that unmeasured traits like [P], [K], [Ca], lignin content are also likely important (Makkonen *et al.* 2012), and that some traits like litter acidity may

have little phylogenetic signal (Pan *et al.* 2015). Future studies would need to test whether abundance and activity of a given decomposer indeed declines overproportionally if traits of involved litter species become more dissimilar.

Poorly decomposable litters might decompose more synergistically due to a large margin between realized and maximal possible decomposition rate

Finally, and independently of the neighborhood effects, our results showed that high decomposability of litter species statistically decreased the synergy we observed when mixing these species. Consistently, some traits that increased litter-mixture decomposition *per se*, such as high mean WHC or low percentage of grasses, decreased synergy. These results validated our hypothesis that litter decomposition might have a maximum, basically the physiological optimum for fragmentation of leaves and respiration of carbohydrates. Synergy will not permit going beyond this maximal decomposition. For instance, in litter mixtures with high mean WHC, the moisture level was already favorably high and constant. Therefore, the litter species with the relatively lowest quality probably did not benefit much from the presence of the other litter species. In contrast, in litter mixtures with low mean WHC, moisture conditions were unfavorable for decomposers and the litter species with the lowermost WHC probably benefited more from the presence of another litter species with somewhat higher WHC. We note however that other studies have found a positive relationship between decomposability of litter mixtures and synergistic effects (Cuchiatti *et al.* 2014; Setiawan *et al.* 2016), the issue hence requires further investigation.

Possible feedbacks on community assembly processes

Synergistic or antagonistic nutrient recycling within a litter mixture correlated with the functional and phylogenetic characteristics of the mixture but also with those of the neighborhood. We hence demonstrated the combined effects of plant assemblages across multiple scales on litter species interactions. At the local scale of a litter mixture, synergistic decomposition was favored by similarity among litters suggesting that decomposers profited from high resource concentration. At the larger

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scale of neighborhoods, in contrast, synergistic decomposition within a local litter mixture was favored by dissimilarities among neighbors (or between mixture and neighbors), suggesting that such neighborhoods provided complementary resources and conditions which maintained detritivores and decomposers capable of profiting from a highly concentrated local patch. Overall, the results suggest that nutrient recycling is most synergistic in a homogenous litter mixture within a heterogeneous and distinct matrix. Such spatial vegetation structures occur for instance through clonal growth or low-dispersal distances (Herben & Hara 2003; Semchenko *et al.* 2013). We may hypothesize that synergistic decomposition among litters of two coexisting species might possibly contribute to the maintenance of such vegetation structures, through an increased availability of soil nutrient benefiting to the growth of both coexisting species (*i.e.* facilitation). Increased soil nutrient availability could also mainly benefit the most resource-acquisitive species, providing the most decomposable litter in the mixture, so that increased synergy during decomposition might represent an indirect competitive strategy. However, our study was too short duration (6 weeks) to verify this hypothesis and more long-term studies (Mao, Yu & Zeng 2015) are needed.

Mixed litters also decomposed more synergistically when composed of species of low WHC or of grasses. Low WHC may be representative of a resource-conservative strategy as we find it in stressful environments (Wright *et al.* 2004). It has been suggested that facilitation is particularly important in such environments (Maestre *et al.* 2009; López *et al.* 2016). The observed synergy in decomposition might be another form of facilitation, which has not been recognized so far: synergistic decomposition might indeed increase nutrient availability and benefit to both species providing the mixed litter. Similarly, facilitation through synergistic decomposition might also favor coexistence of grasses. Surprisingly, grasses very often coexist despite being very similar (Cahill *et al.* 2008; Linder *et al.* 2017). Coexistence among grass species increases the number of patches that can be occupied per species and might thereby reduce extinction probability (Prinzing *et al.* 2016). We may speculate that ultimately such facilitation in nutrient recycling has contributed to the impressive

success of grasses (Linder et al. 2017), through feedback between ecological coexistence, ecosystem functioning and evolutionary diversification of lineages (Prinzing et al. 2017).

CONCLUSION

Our results suggest that decomposition of litter mixtures was synergistic if (i) mixed species provided similar resources, (ii) the ambient plant neighborhood provided complementary resources, and (iii) individually, mixed litters were poorly decomposable. Thus, the relationship between increasing diversity due to mixing litters and the ecosystem function of decomposition was highly dependent on the plant community context. We hope these results open new insights and contribute to a more pluralistic view on diversity-ecosystem functioning relationships.

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AUTHOR'S CONTRIBUTION

L. Barbe, V. Jung, C. Mony and A. Prinzing conceived the experiments. L. Barbe performed the experiments, with help of V. Jung, C. Mony and A. Prinzing. L. Barbe analyzed the data, with help of A. Prinzing. L. Barbe wrote the manuscript, with help of V. Jung, C. Mony, A. Prinzing, M. Santonja and I. Bartish, who also provided the phylogenetic tree.

DATA ACCESSIBILITY

Data is available at: <https://doi.org/10.5281/zenodo.1165521> (Barbe et al., 2018)

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TABLES

Table 1. Summary of the best model explaining (i) non-additive effects of litter-mixture decomposition and (ii) decomposition *per se* of litter mixtures. Non-additive effects of litter-mixture decomposition as well as litter-mixture decomposition *per se* depended on phylogenetic and functional dissimilarities of litter-mixture (LM) and plant neighborhood (PN), on litter-mixture trait means (Specific Leaf Area, SLA; Leaf Dry Matter Content, LDMC; Water Holding Capacity, WHC; Carbon:Nitrogen ratio, C:N) and on percentage of grasses within litter mixture. Variance inflation factors of independent variables ranged from 1.06 to 1.82 in the best model of non-additive effects and from 1.03 to 2.39 in the best model of decomposition *per se*. Moreover, variable selection was very stable (see Tab. S6 and Tab. S7). Multiple regression analysis was hence not biased by the partial correlation between LDMC and WHC. Given model parameters are the selected variables with their coefficient and significance (*: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$), the degree of freedom (Df) the adjusted- R^2 (adj- R^2), the F statistic (F) and the probability of the model (P).

| Variable | Phylogenetic dissimilarity | | | Functional dissimilarity | | | Litter-mixture trait mean | | | | Grass % within LM | Df | adj- R^2 | F | P |
|------------------------------------|----------------------------|-----------|-------------------|--------------------------|-----------|-------------------|---------------------------|------|--------|-------|-------------------|-----|------------|------|--------------|
| | within PN | within LM | between LM and PN | within PN | within LM | between LM and PN | SLA | LDMC | WHC | C:N | | | | | |
| Non-additive effects | 0.18* | | | | -0.30** | 0.36** | | | -0.22* | 0.21* | 0.46*** | 108 | 0.19 | 5.5 | 5.10^{-5} |
| Decomposition <i>per se</i> | | 0.16 | | 0.23*** | -0.13 | | -0.21** | | 0.19** | 0.15* | -0.52*** | 107 | 0.55 | 20.7 | 2.10^{-16} |

FIGURE CAPTIONS

Figure 1. Illustration of our conceptual framework and predictions of hypotheses for how functional and phylogenetic dissimilarities might drive synergy or antagonism during decomposition of a litter mixture – *i.e.* litter mixture decomposing faster or slower than the corresponding mono-specific litters alone. Litter-mixture decomposition might become synergistic with: (A) high functional or phylogenetic dissimilarity within plant neighborhood, resulting in a pool of decomposers capable of decomposing mixed litters ; (B) low functional or phylogenetic dissimilarity between plant neighborhood and litter mixture, resulting in availability of adapted decomposers ; (C) high functional and phylogenetic dissimilarity within litter mixture, resulting in complementarity effects ; (D) low decomposability of litter mixture, resulting in large margin between realized and maximal possible decomposition rate. Only the hypothesis on functional dissimilarity within litter mixture has been tested so far.

Figure 2. Non-additive effects of litter-mixture decomposition (positive values indicating synergy) depending on phylogenetic dissimilarity within plant neighborhood (A, standardized regression coefficient = 0.18, $P < 0.05$), on functional dissimilarity between litter mixture and plant neighborhood (B, standardized regression coefficient = 0.36, $P < 0.01$), and on functional dissimilarity within litter mixture (C, standardized regression coefficient = -0.30, $P < 0.01$). Removing the isolated point at the right of the graph (A) does not reduce the strength of the relationship. Each graph presents partial residuals, *i.e.* accounting for the simultaneous effect of the other independent variables not presented in that graph – see Tab. 1 for full statistical results. Black dotted lines around slopes represent the 95% confidence interval.

Figure 3. Litter-mixture decomposability decreased synergy. Decomposability of litter species corresponds to the decomposition measured on monospecific litters within the same neighborhood. High decomposability of species composing litter mixtures (*i.e.* high average across their respective monospecific decomposition rates) was related to low synergy (A, $P=0.001$, $r^2=0.08$, $F=11.4$, $df=114$).

Grasses decomposed slower but the more synergistically (A, see Tab. 1; note that interaction term between grass percentage and decomposability was not significant). Also, high mean WHC of litter mixture increased litter-mixture decomposition *per se* (B, standardized regression coefficient = 0.19, $P < 0.01$, see Tab. 1) while it decreased synergy (C, standardized regression coefficient = -0.22, $P < 0.05$, see Tab. 1). Data points in B and C are partial residuals of the best model showed in Tab. 1, so account for other independent variables. Black dotted lines around slopes represent the 95% confidence interval.

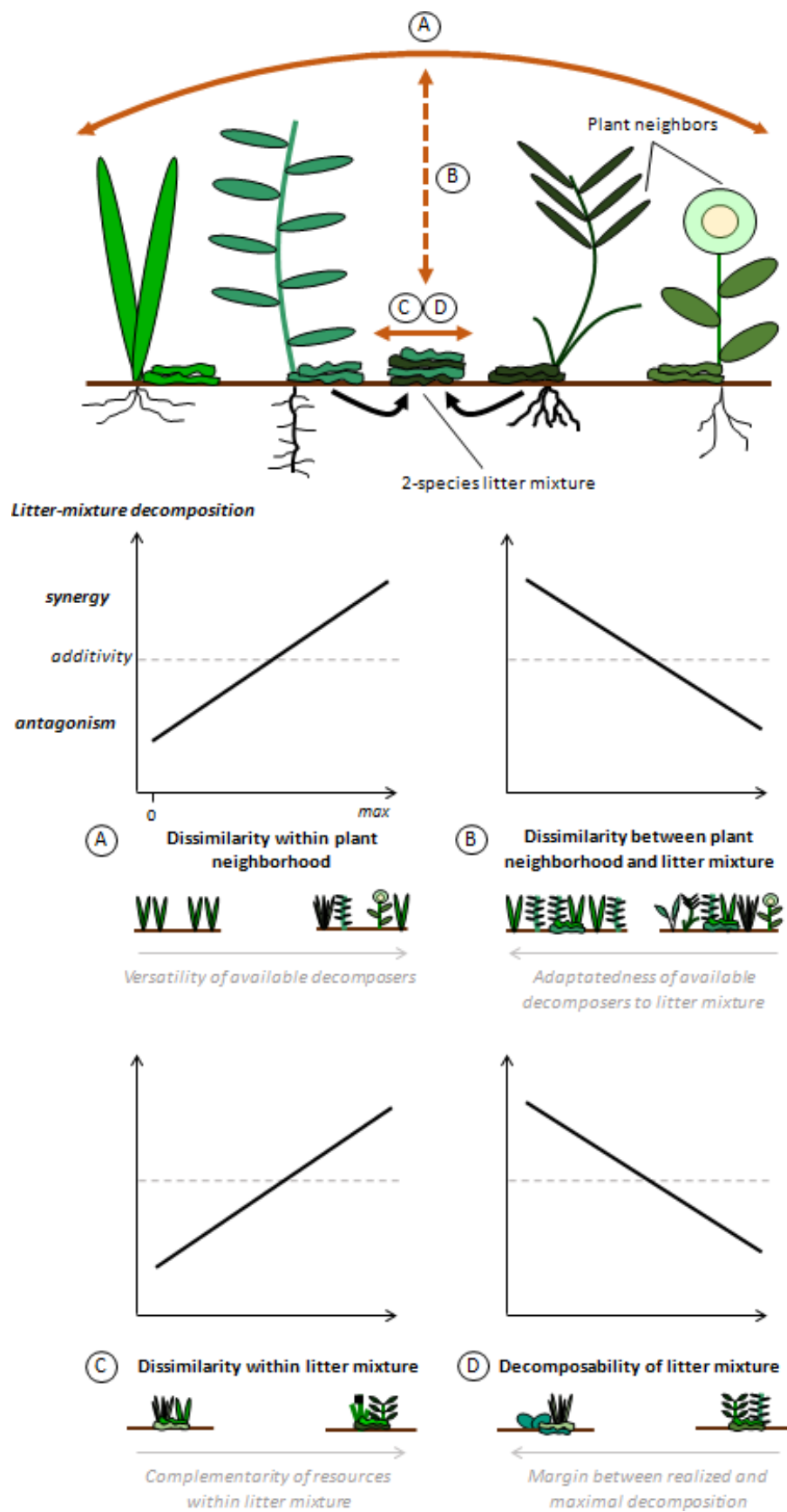


Figure 1.

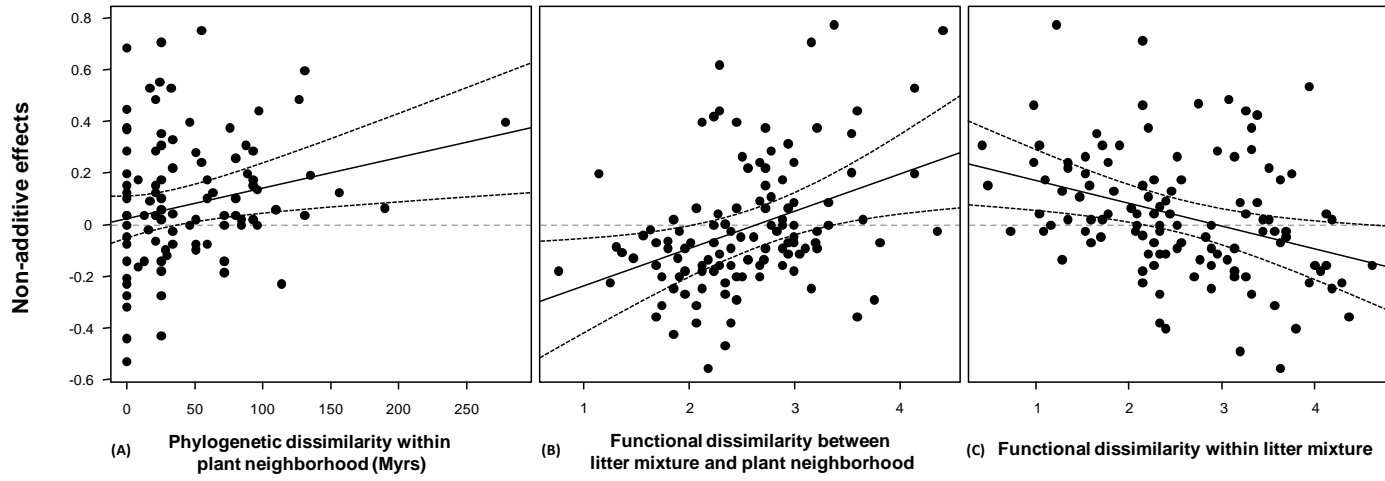


Figure 2.

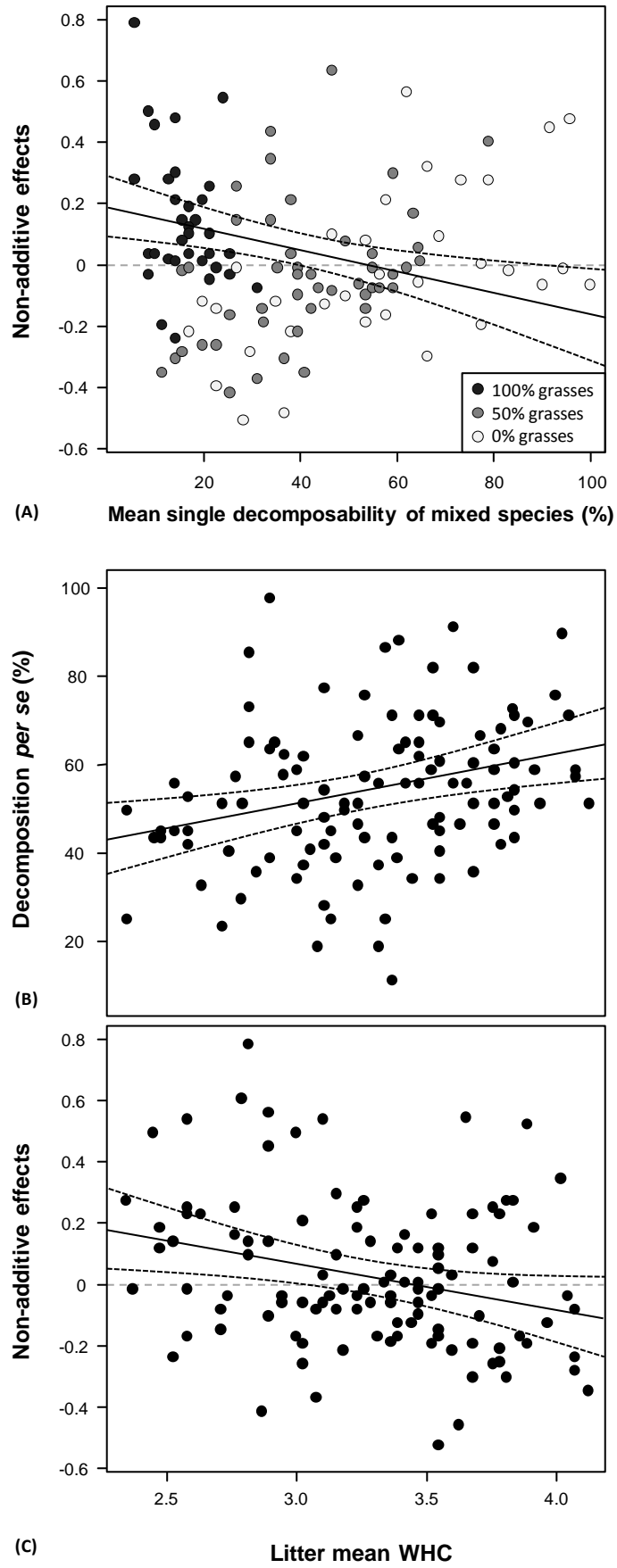


Figure 3.