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Research article

Why oaks should stay with their close relatives: growing in a distantly related neighbourhood delays and reorganizes nutrient recycling during litter decomposition

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Closely related species often conserve similar niches despite interacting negatively. We suggest that close relatives may interact positively *via* ecosystem feedbacks: leaf litter produced or exposed in a closely related neighbourhood (low phylogenetic isolation) may decompose more quickly, leading to more rapid nutrient recycling. We studied decomposition of leaf litter of oaks *Quercus petraea* across 8 and 14 months, reciprocally transplanting leaf litters between low and high phylogenetic isolation to distinguish between effects mediated by leaf litter quality and by decomposition environment. We found that, by affecting litter quality, phylogenetic isolation reduced decomposition across 14 months (loss of litter mass and C). Moreover, by affecting litter quality and decomposition environment, phylogenetic isolation reduced microbial biomass and extensively altered relationships between C and N losses and abundances/diversities of different soil organisms across 8 and 14 months. Phylogenetic isolation was to a large extent driven by percentage of gymnosperms, explaining the decomposition-environment mediated effects. Such environment-mediated effects reflected decreasing soil humidity and pH with phylogenetic isolation, while litter-quality mediated effects reflected decreasing leaf phytophagy or increasing leaf phenolics. Tree-species richness, in contrast, did not explain effects of phylogenetic isolation, and had little effect overall. To conclude, coexistence of oaks with distant relatives partly impedes recycling of leaf litter and re-organizes the trajectories of this recycling. In contrast, oaks coexisting with close relatives may profit from a positive ecosystem feedback through increased

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nutrient recycling, possibly contributing to the conservation of the oak's niches. We suggest that such a positive ecosystem feedback among close relatives might exist in other late successional tree species.

Keywords: Eco-evolutionary feedback, leaf phenology, litter decomposition, litter quality, phylogenetic neighbourhood, plant-soil interaction

Introduction

Over millions of years, species often tend to conserve their niches across phylogeny despite major environmental changes (Wiens et al. 2010, Crisp and Cook 2012, phylogenetic signal sensu Losos 2008). As a result, related species share similar environmental preferences and co-occur (Prinzing et al. 2016a, 2017). Co-occurrence of related species, in turn, has been demonstrated to result in increased competition (Webb et al. 2002, Cavender-Bares et al. 2009), enemy pressure (Yguel et al. 2011), and a decrease in mutualist support (Verdú et al. 2012, Yguel et al. 2014, but see Gerhold et al. 2015). Some closely related species hence show niche divergence and reduce co-occurrence, thereby increasing performance of their individuals which find themselves back surrounded by phylogenetically distant species, i.e. phylogenetically isolated (Webb et al. 2002, Yguel et al. 2011, Fig. 1a). It remains unclear why many other species do not diverge from relatives but conserve shared niches: how do the individuals co-occurring with closely related species perform well? One possible mechanism is through ecosystem feedbacks. For plants, the recycling of nutrients is an essential ecosystem function and large plants like trees grow in

their own litter so that the recycling of its litter is essential for the performance of the tree (Austin et al. 2014). As we will argue below, leaf litter of a tree might be more decomposable and might decompose best when the neighbours of that tree are closely related. To our knowledge this idea has not been tested so far.

We hypothesize that the phylogenetic isolation of a focal tree from its neighbors influences the decomposition of the tree's leaf litter through the decomposition environment ('belowground mechanisms', Fig. 1). The environment may be favorable for decomposition under low phylogenetic isolation, i.e. in a phylogenetically close neighborhood. Trees constituting such a neighborhood produce a leaf litter that is dominated by plant lineages closely related to the focal species and may select for soil organisms particularly capable of decomposing the focal species (Ayres et al. 2009, Austin et al. 2014, Pan et al. 2015a, Cheng and Yu 2020). In contrast, under high phylogenetic isolation, decomposers may be naive to decompose the leaf litter of the focal tree. Thus, under low phylogenetic isolation, the number of decomposers available to decompose the focal species might be highest and the decomposers might be most efficient. Finally, abiotic conditions may be more favourable in some cases, e.g. higher

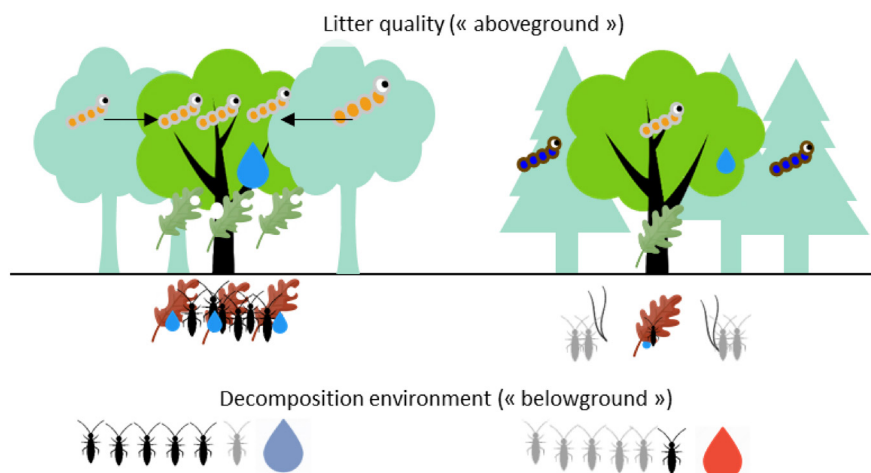


Figure 1. Multiple mechanisms by which phylogenetic isolation of a host tree (oak in this example) may reduce decomposition, as explained in the alternative hypotheses in the Introduction. Mechanisms affecting the decomposition environment (named 'belowground' in this study): under a tree (oak in this example) in a phylogenetically proximate neighborhood 1) ambient decomposers are experienced in decomposing the litter of the focal species (proportion of black Collembola in soil), increasing the abundance of decomposers and their efficiency (number and size of black Collembola on oak litter); 2) abiotic conditions may be more favorable such as higher pH in an angiosperm neighborhood compared to a gymnosperm neighborhood (blue versus red droplet). Mechanisms affecting litter quality ('aboveground'): a tree in a phylogenetically proximate neighborhood produces more decomposable litter: increased phytophagy (oak leaves with holes) 1) increases access for decomposers, thereby increasing decomposer abundance and efficiency (number and size of black Collembola on oak litter); 2) accelerates wetting and drying (size of droplets on oak litter). In contrast, a phylogenetically isolated tree produces less decomposable litter.

pH and soil moisture for an angiosperm in an angiosperm neighbourhood than for an angiosperm in a gymnosperm neighbourhood. For example, Yguel et al. (2014) reported a decrease of soil humidity and pH with phylogenetic isolation for an oak focal species. Overall, decomposition of the leaf litter of a phylogenetically non-isolated focal tree may benefit from a phylogenetic home-field advantage (HFA), a hitherto untested phenomenon. The idea is inspired by the HFA in decomposition, a phenomenon that has often been demonstrated (Negrete-Yankelevich et al. 2008, Vivanco and Austin 2008, Veen et al. 2015, Fanin et al. 2021, Quer et al. 2022): litter of a given species decomposes better under that species than under different species. Our idea of a phylogenetic HFA keeps the species under which the leaf litter decomposes constant, but compares it between different neighbourhoods, and these neighbourhoods are defined by phylogenetic distance from the focal species rather than in a binary way as con- versus heterospecific. Conversely, the decomposition environment may also be favorable when phylogenetic isolation is high because mixing of litter from focal and distantly related neighbouring trees may provide complementary resources to decomposers, thereby increasing their abundance, diversity and efficiency (Lummer et al. 2012, Handa et al. 2014, Porre et al. 2020). Also, abiotic conditions may be more favourable in some cases, such as less waterlogging for an angiosperm in a gymnosperm neighbourhood compared to an angiosperm neighbourhood. Overall, phylogenetic isolation of a focal tree affects the biotic and abiotic environment in which decomposition takes place, but it remains unknown how this affects the decomposer abundance and efficiency and abiotic forces, and thus overall decomposition.

We also hypothesize that the phylogenetic isolation of a focal tree from its neighbors influences the decomposition of the tree's litter through litter quality and thus decomposability ('aboveground mechanisms', Fig. 1, mechanisms that are not part of the HFA concept). Again, decomposability might be favored under low phylogenetic isolation, i.e. in a phylogenetically close neighborhood. Low phylogenetic isolation of a given focal tree strongly increases phytophagy of the focal tree by increasing resources for specialist phytophages (Yguel et al. 2011). Leaf damage by phytophagy may in turn increase the accessibility of leaf litter for soil decomposers (Cárdenas and Dangles 2012), which thus increase in number and efficiency. Leaf damage may also increase the contribution of abiotic decomposition by increasing leaching of dissolved organic material from the litter (Berg and McClaugherty 2014, Prescott and Vesterdal 2021). Conversely, litter decomposability may be favored when phylogenetic isolation is high. In particular, low levels of phytophagy may reduce the production of secondary metabolites such as polyphenols (Schultz and Baldwin 1982, Karban and Myers 1989, Coley and Barone 1996, Strauss and Agrawal 1999). Such compounds negatively affect the abundance and efficiency of decomposer organisms as well as the abiotic decomposition of leaf litter (Schädler et al. 2003). Overall, phylogenetic isolation of a focal tree affects litter quality through leaf damage and leaf chemistry, but it remains unknown how this affects

decomposer abundance and efficiency and abiotic forces, and thus overall decomposition.

Here we studied the effects of phylogenetic isolation through litter quality and decomposition environment on leaf litter decomposition in oaks *Quercus petraea* (and hybrids), a system for which effects of phylogenetic isolation on enemy pressure and budburst have been demonstrated already (Yguel et al. 2011, 2014). Since decomposition under a given tree is the result of a mixture of litter quality and decomposition environment, we designed a litter transplantation experiment transplanting leaf litter from oaks growing among phylogenetically close or distant related neighbors, i.e. under low or high phylogenetic isolation (Fig. 1), ranging from conspecifics to gymnosperms. To our knowledge, this is the first 'phylogenetic litter-transplantation' experiment. To test the effect of phylogenetic isolation that is mediated by litter quality, we used oak leaf litter from more or less phylogenetically isolated oaks. To test the effect of phylogenetic isolation that is mediated by decomposition environment, we used the location where the oak litter bags actually decompose, i.e. under more or less phylogenetically isolated oaks. We hypothesized that increasing phylogenetic isolation will negatively affect oak litter decomposition and we tested a series of increasingly mechanistic predictions for this purpose: 1) phylogenetic isolation per se alters litter mass loss, C loss and N loss. 2) Phylogenetic isolation alters the trajectories by which litter decomposes: the abundances and diversities of different soil organisms that control decomposition, the efficiency by which a given group of soil organisms decomposes litter, the putative abiotic effects that are not attributable to the soil organisms considered (Fig. 2). 3) The effects of phylogenetic isolation in the above two predictions can be replaced, and thus likely explained, by litter traits or environmental characteristics such as leaf damage by phytophages, leaf chemistry (polyphenols, C:N ratio), soil pH and soil moisture, or by drivers of microclimate such as budburst date, all of which relate to phylogenetic isolation (Yguel et al. 2014).

Material and methods

Site description and phylogenetic isolation estimation

Our study was conducted in the Forest of Rennes (surface area: 2000 ha), Brittany (France). The forest and selection of trees was detailed in Yguel et al. (2011) (Supporting information). Overall 11 pair of oaks with contrasting phylogenetic distance of neighbours were chosen, with neighbours belonging to 10 different species (8 angiosperms and 2 gymnosperms, details in the Supporting information). For each focal oak, phylogenetic isolation was quantified as its mean phylogenetic distance to all neighboring trees with which its crown was in contact, and phylogenetic distances were extracted from published phylogenies following procedures applied previously (Vialatte et al. 2010, Yguel et al. 2011, Supporting information). The phylogenetic isolation from

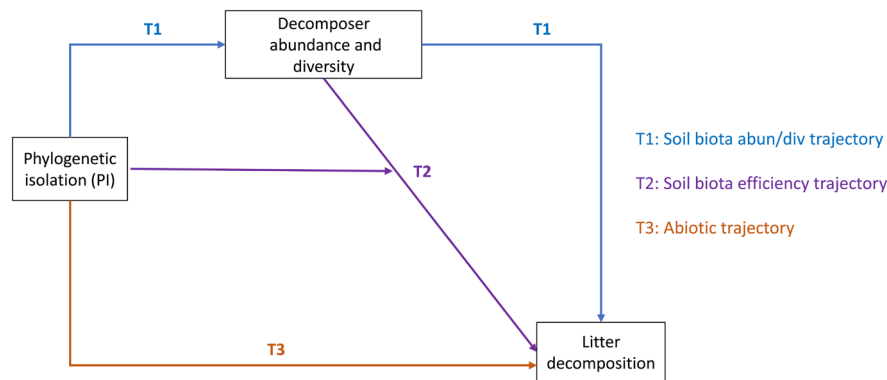


Figure 2. Role of different trajectories by which phylogenetic isolation may affect decomposition. The soil biota abundance/diversity trajectory (T1, blue arrow) can be tentatively inferred from the ‘phylogenetic isolation (PI)’ terms in multiple regression analyses explaining abundance or diversity combined with the ‘abundance’ or the ‘diversity’ terms in a final multiple regression analysis explaining decomposition: $\text{decomposition} \sim \text{abundance (or diversity)} + \text{PI} + \text{abundance (or diversity)} \times \text{PI}$. The soil biota efficiency trajectory (T2, purple arrow) can be tentatively inferred from the ‘abundance/diversity * PI’ interaction term in the before multiple regression analysis explaining decomposition. The abiotic trajectory (T3, brown arrow) can be tentatively inferred from the ‘PI’ term in the before multiple regression analysis explaining decomposition. Finally, an increase in decomposition resulting from the biotic trajectories T1 and T2 may also increase the proportion of ^{13}C accumulated through the food chain.

one oak to another oak was 0. Oaks were treated as one species as we do not account for phylogenetic relationships within *Quercus petraea* and its hybrids. These oak-oak phylogenetic distances will be minuscule compared to phylogenetic distances from oaks to non-oaks. Trees within a pair were less than 150 m apart. Such a pairwise design permitted to compare contrasting levels of phylogenetic isolation unbiased by the effect larger-scale environmental variation between pairs (Legendre et al. 2004).

Experimental design studying decomposition of oak leaf litter

For each pair of the focal oaks, we sampled the litter at leaf fall by gently shaking the branches and collecting the leaves before falling on the ground to avoid contamination by soil microbes and arthropods prior to the experimental treatment (Santonja et al. 2017). Oak leaf litter was air dried in the lab at ambient temperature for at least two weeks. For each tree, four samples of each oak litter (about 10 g in equivalent dry weight) were placed in litter bags (25 × 15 cm) with 5 mm-mesh size allowing colonization by microbes and soil fauna (Santonja et al. 2017). This 5 mm-mesh size is considered a coarse mesh bag with a mesh opening large enough to ensure that the entire community of litter consumers can access the litter (Makkonen et al. 2012, Santonja et al. 2017, Yang et al. 2022) and small enough to avoid loss of litter fragments and thereby avoid overestimating litter mass loss. The litter was evenly spread out across the litter bag to maximize the amount of litter in contact with the soil. Moreover, for each focal oak, five samples were weighted and oven-dried to estimate the water content of the initial leaf litter, i.e. (oven dry weight-air dry weight)/air dry weight. This ratio permitted to estimate the oven-dry weight equivalents of litter samples in the litter bags.

With this litter we conducted a transplant experiment. Litter transplantations have been used to test the effect of

litters being ‘home’ or ‘away’ in the sense of being below the tree species producing the litter versus below another tree species (Ayes et al. 2009). In contrast, in our case, leaf litter was transplanted between conspecific oaks which differed in being phylogenetically non-isolated or isolated from their neighbours. The interest of transplantation was then to separate effects operating via litter quality versus those operating via biotic and abiotic conditions at the ground (Fig. 1, cf. Barbe et al. 2017 for an equivalent approach using functional isolation). Therefore, a given litter bag was characterized by two phylogenetic isolations: the phylogenetic isolation of the oak from which the litter was sampled, which we named ‘aboveground phylogenetic isolation (PIA)’, and the phylogenetic isolation of the oak under which the litter was exposed, named ‘belowground phylogenetic isolation (PIB)’ (Fig. 1). Transplantation ensured independence of PIA and PIB: for each pair of focal oaks, litters from the high-phylogenetic isolation oak (high PIA) were exposed below that oak (high PIB) and below the oak of low phylogenetic isolation (low PIA). Inversely, litter from the low-phylogenetic isolation oak (low PIA), were exposed under that oak (low PIB) and under the isolated oak (high PIB). Litter bags were put on the top of the litter horizon to mimic as much as possible the natural process occurring in the field at approx. 1 m from the trunk of the focal tree, i.e. close enough to avoid impact from other trees (Deniau et al. 2017). Additional metal-mesh protection was used to avoid physical disturbance by large mammals (wild boars, humans). We started the experiment in early December, i.e. at the end of the leaf shedding season. The litter bags were collected after 8 and 14 months of incubation (44 litter bags each sampling time) for a total of 88 litter bags. Eight months corresponds to the first significant litter mass loss of the study species, 14 months to a further distinct increase (Pan et al. 2015a, Vaydelis et al. 2020), reaching up to approximatively 50% (Handa et al. 2014, Horodecki and Jagodziński 2019). Further mass loss would

lead to methodological problems, such as loss of litter fragments through the mesh and insufficient remaining substrate for chemical analyses.

Measurements of microbial biomass, arthropod abundances and fungal community composition

Litter bags were retrieved and transported in individual plastic bags to the laboratory. We carefully spread leaf litter equally across the litter bag and cut the litter bag into two parts in the lab: one part was 3 cm of the 25 cm length of the litter bag (75 cm² out of 625 cm², i.e. a 12% aliquot of the total litterbag surface) and used for the microbial measurements (microbial biomass and fungal community composition) and the other part was used for soil arthropod extraction. This procedure has been done in a standardized manner and fresh weight of both litter subsamples were measured.

Microbial biomass was analyzed using the substrate-induced respiration (SIR) method (Anderson and Domsch 1978). The microbial respiratory response was measured in an electrolytic O₂ microcompensation apparatus at hourly intervals for 24 h at 22°C (Scheu 1992). Microbial biomass was measured after the addition of glucose to saturate the catabolic activity of microorganisms. The maximum initial respiratory response (MIRR: ml O₂ g⁻¹ DW h⁻¹) was calculated as the mean of the lowest three readings within the first 10 h and the microbial biomass for each litter bag was calculated as $C_{mic} = 38 \times MIRR$ (mg C_{mic} g⁻¹ DW; Beck et al. 1997). Fungal community composition in the remaining leaf litter after eight months were measured using ITS1-ITS2 barcoding primers to sequence the total fungal community (Supporting information). The number of reads for each litterbag was determined and illustrated, based on the OTUs of each genus identified. As is common practice we excluded singleton taxa (i.e. taxa represented by a single DNA read) or rare taxa (i.e. taxa below a specified number of reads) prior to conducting diversity analyses using DNA-based community data. Specifically, we removed from 454 results whose hits represented ≤ 0.01% of all the hits. Using the same proportion, we removed rare taxa from Illumina reads when they represented less than 0.01% of total hits. We then used Simpson index (Rosenzweig 1995) to illustrate fungal diversity at the OTU level.

Soil arthropods were extracted from the remaining litter by heat (Kempson et al. 1963) and stored in saturated salt solution (NaCl) at -10°C for further measurement and identification (Pausch et al. 2016). Soil arthropods were counted and identified at the class, sub-class or order levels using a binocular microscope (Santonja et al. 2017, Aupic-Samain et al. 2021a, Supporting information). Acari and Collembola together represented 97% of the animals extracted from the litterbag (Supporting information), with an average abundance of 367 and 203 individuals per litterbag, respectively. By consequence, we decided to consider only these two groups as the representative of the fauna decomposer community in the present study. We acknowledge that Acari is a diverse group including Oribatid which are classically considered to

be decomposers while Mesostigmata and Prostigmata classically considered not to be decomposers (Coleman et al. 2004, Santonja et al. 2017), albeit their functions can be more complex (Potatov et al. 2022). By quantifying Acari, we primarily quantified Oribatid Acari, which are known to be microbidetritivorous organisms, as are also Collembola (Aupic-Samain et al. 2021b, Potatov et al. 2022). We found in additional 24 soil faunal samples from the Rennes forest that the Oribatid dominates the Acari community (77% of the community), and an increase in Acari strongly reflects an increase on Oribatid mites ($R^2 = 0.86$, $p < 0.001$, Supporting information).

Measurements of litter decomposition and leaf litter traits

After the extraction of soil arthropods, litter was oven dried at 65°C to weight constancy and weighed at 0.1 g. The moisture content of the litter subsample used for soil arthropod extraction was used to calculate the dry weight of the litter subsample used for microbial measurements. Both values were to estimate the oven dry weight of the leaves remaining in each litterbag. The litter mass loss was then calculated as (pre-exposure oven-dry weight equivalent - post-exposure oven-dry weight)/pre-exposure oven-dry weight equivalent. Oven-dried litter was ground using a ball mill. Carbon and nitrogen concentrations were determined by using an elemental analyser (N1500, Carlo Erba). The changes in C and N concentrations were calculated in the same way as for mass loss. A decrease of C concentration reflects rapid decomposition. Inversely, an increase of N concentration reflects an accumulation of N in the litter due to decomposition, improving resource conditions for plants. We refrained from using changes of absolute C or N values to avoid bias from among-site variation of C or N. For instance, high-N sites would always show higher absolute changes of N than low-N sites. Total phenolic concentration of initial leaf litter was measured colorimetrically using the method of Santonja et al. (2015) with gallic acid as a standard. Leaf powder samples (250 mg) were suspended in 20 ml of a 70% aqueous methanol, shaken for 1 h and then filtered (0.45 µm filter). Filtered extracts (0.25 ml) were mixed with 4 ml of distilled water, 0.5 ml of saturated aqueous Na₂CO₃ and 0.25 ml of Folin-Ciocalteu reagent. After 60 min, phenolic concentrations were determined at 765 nm on the same UV/Vis spectrophotometer (Biomate 3, Thermo Electron Corporation) and expressed as mg of gallic acid equivalent g⁻¹ DW.

Statistical analysis

Statistical analyses were performed with the R software ver. 3.3.3 (www.r-project.org). In all analyses, we identified and excluded outliers using the *plot* function to show the residuals and leverages, and the *outlierTest* function in package 'car' (Fox and Weisberg 2019). For all the analyses, we removed a maximum of three outliers from the analyses based on the diagnostic procedures.

Effects of phylogenetic isolation on leaf litter decomposition, soil organisms and carbon isotopes mediated via litter quality and via decomposition environment, i.e. phylogenetic isolation aboveground (PIA) and belowground (PIB)

We used multiple regression analyses to test how phylogenetic isolation of the tree that had produced the litter and of the tree where the litter was exposed (above and belowground phylogenetic isolation, PIA and PIB, respectively) jointly affect 1) the decomposition parameters (litter mass loss, C loss and N loss) after 8- and 14-months, and 2) the decomposer organisms, i.e. Acari abundance, Collembola abundance and microbial biomass after 8- and 14-months of decomposition, and number of reads per OTU and diversity of the fungal community based on barcoding after 8 months of decomposition. The regression results were illustrated in partial residual plots.

Combined effects of PIA, PIB and soil organisms on leaf litter decomposition

We then explored the role of different trajectories by which PIA or PIB may affect decomposition as follows (Fig. 2). Abundance/diversity trajectory (T1): PIA or PIB influences significantly a particular group of decomposers (abundance/biomass or diversity) which in turn influences the decomposition parameters (Fig. 2, blue arrow). Efficiency trajectory (T2): PI affects the efficiency of a given decomposer group, reflected by a significant interaction term between either of the phylogenetic isolations and the decomposer group (abundance or diversity) in their effect on decomposition (Fig. 2, purple arrow). Abiotic trajectory (T3): PI affects abiotic conditions and thereby decomposition: PIA or PIB maintain a significant main effect on decomposition after accounting for abundances/biomass and diversity of decomposers groups and the corresponding interaction terms (Fig. 2, brown arrow).

As outlined above, we explained decomposition parameters by including PIA and PIB and decomposer organisms (Acari abundance, Collembola abundance and microbial biomass) as predictors, as well as the interaction terms of decomposers with both PIA and PIB, using multiple regression models. The full models were then simplified to determine the most parsimonious models using the *stepAIC* function of the 'BMASS' package (Venables and Ripley 2002), an established model-selection procedure with both forward and backward selection algorithms, which ranks all candidate models (all initial predictor variables included in the full model) based on the lowest AICs (Crawley 2013). We used the t values of these variables to calculate effect sizes as Pearson's r as $\sqrt{t^2/(t^2 + df)}$ (Rosenthal 1986). We conducted a separate analysis for the number of reads and diversity of the fungal community based on barcoding (instead of microbial biomass), as these variables were only available for the 8-month sampling. The procedure of including interaction terms was the same as before. We finally conducted a separate analysis for the number of reads and diversity of saprotrophic fungi. We refrained from a formal structural equation modeling as the interaction terms, being essential in our approach to identify Trajectory 2, would produce inflated, uninterpretable path coefficients (Grewal et al. 2004). Note that 'tree pair' did not

significantly affect the six dependent variables of decomposition. For consistency and to avoid over-parametrization we hence refrained from including 'tree pair' in the analysis of any of the six decomposition variables.

Explaining PIA and PIB effects on leaf litter decomposition

Finally, we further explored whether the observed direct or interaction effects of PIA or PIB could be explained by the percentage of gymnosperms, since it is inevitably a major part of the phylogenetic distance of the oak's neighbours (Supporting information). The question is whether phylogenetic distance is something more than gymnosperm percentage, i.e. whether there is an effect of phylogenetic distance within angiosperms. If so, gymnosperm percentage should perform less strongly than phylogenetic distance in statistical analyses. Therefore, we replaced either PIA or PIB with gymnosperm percentage. We note that such an approach, comparing performance or %Gymnosperms with that of phylogenetic isolation, avoids taking a somewhat arbitrary decision on which data points to consider or not.

We further investigated whether the observed direct or interaction effects of PIA or PIB could be explained by specific litter traits (such as leaf phenolics, leaf phytophagy or leaf litter C/N ratio) or specific characteristics of the abiotic environment (such as soil humidity and pH) affected by phylogenetic isolation, as listed in the Supporting information. We performed the same statistical analysis using PIA or PIB as explanatory variables, replacing either PIA or PIB with a specific litter trait or environmental characteristic in order to improve our mechanistic understanding of the effect of PI on the decomposition process. Replacing phylogenetic isolation with the appropriate factor should result in an increase in explained variance. We refrained from including both phylogenetic isolation and soil parameters simultaneously into the same analysis, as this would result in large multicollinearity between causes and effects included as explanatory variables into the same analysis.

Results

Throughout, effects of phylogenetic isolation mediated *via* litter quality were inferred from aboveground phylogenetic isolation (PIA), i.e. the isolation of the tree that had produced the litter. Effects mediated via decomposition environment were inferred from belowground phylogenetic isolation (PIB), i.e. the isolation of the tree where the litter was exposed.

Effects of phylogenetic isolation on leaf litter decomposition and soil organisms

Loss of mass, C and N

After 8 and 14 months, the litter mass loss was on average 25.5 and 49.7%, leading to 7.4 and 5.0 g of remaining litter, respectively. PIA increased C loss after 8 months, but decreased C loss after 14 months and decreased mass loss after 14 months (Fig. 3). PIB decreased C loss after 8 months

(Fig. 3) but had no effect after 14 months. PIA and PIB never affected N loss.

Abundances/diversity of decomposers

PIA had no effect on microbial biomass after 8 months but decreased microbial biomass after 14 months (Fig. 3). PIA had no effect on Collembola or Acari abundances at 8 or 14 months. PIB decreased microbial biomass and Collembola abundance after 8 and 14 months. PIB increased Acari abundance only after 8 months (Fig. 3). PIA or PIB did not affect the number of reads and the diversity of the fungal community after 8 months (Supporting information).

Combined effects of phylogenetic isolation and soil organisms on leaf litter decomposition

Above we found that PIA and PIB affect certain groups of decomposers. In the below analyses we will hence verify the

main effects of these decomposers on decomposition, in addition to the main effects of PIA and PIB on decomposition and the interactive effects decomposers $\times$ PI. If an interaction term of a given variable was statistically significant, we interpreted a significant main effect of that variable only if it was as strong as the interaction effect.

Analyses accounting for microbial biomass and Collembola and Acari abundances after 8 and 14 months

Mass loss

PIA did not directly affect mass loss after 8 and 14 months. PIB increased mass loss after 8 months, but decreased mass loss after 14 months (main effects in Table 1). The observed positive effects of PIB after 8 months were replaceable by shorter vegetation period, delayed budburst and decreasing soil moisture (Supporting information). Moreover, Acari abundance (which was increased by PIB after 8 months,

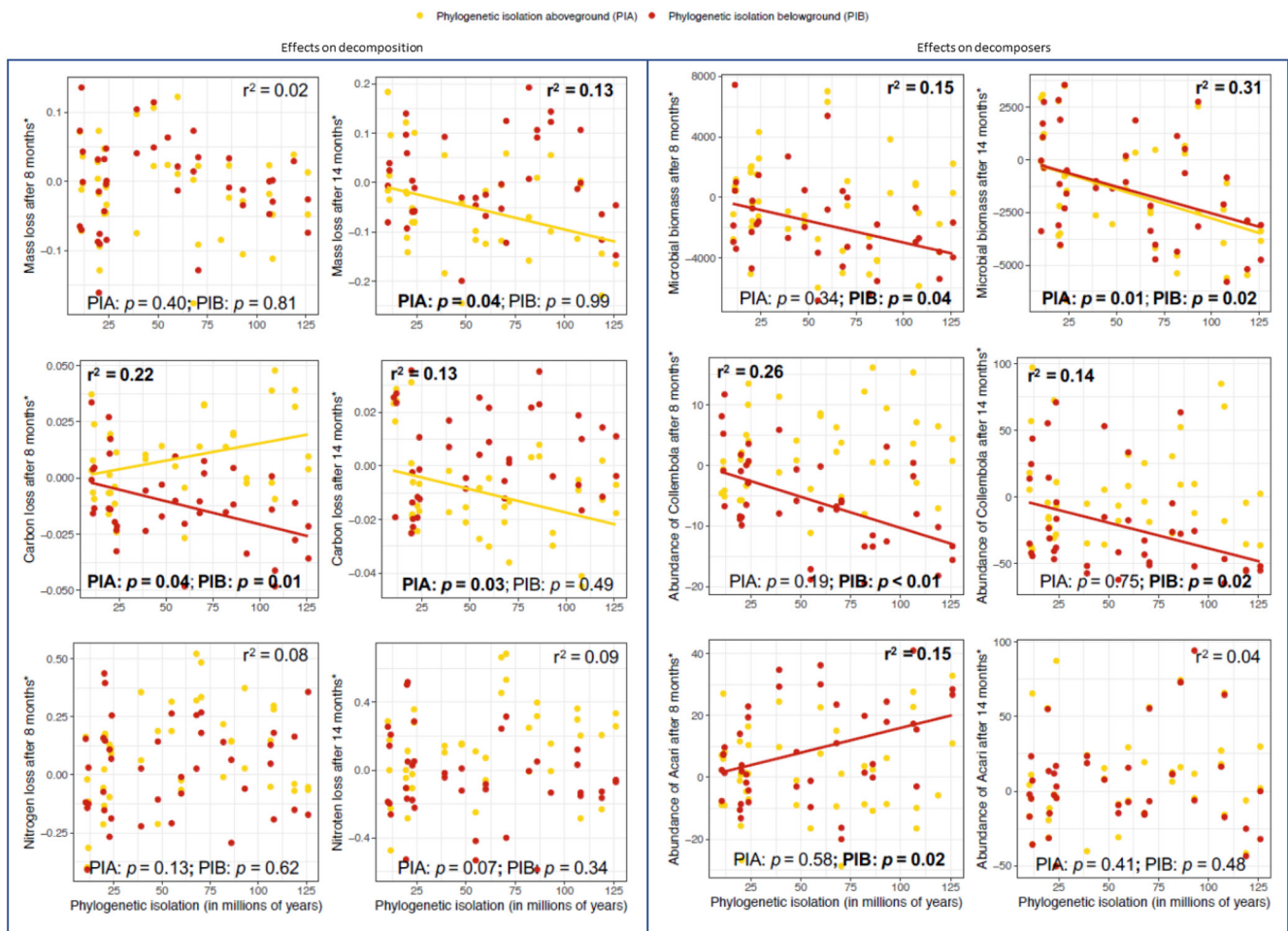


Figure 3. Effects of phylogenetic isolation aboveground (PIA, yellow, reflecting litter quality) and belowground (PIB, red, reflecting decomposition environment) included simultaneously into a multiple regression analysis explaining decomposition (left – the mass loss, C loss or N loss of oak litter), and explaining decomposers (right – microbial biomass, abundance of Acari or abundance of Collembola in the oak litter). * indicates 'partial residuals'. Significant effects ($p < 0.05$) are shown by a regression line. r^2 represents the explanatory power of each multiple regression model. Here and elsewhere phylogenetic isolation is determined between the focal oak and the trees that are in direct contact. This is the most pertinent spatial scale – phylogenetic isolation quantified across larger scales usually has weaker effects (Supporting information).

Fig. 3) directly increased mass loss after 8 and 14 months (main effects in Table 1). There was a negative interaction between PIB and Acari abundance on mass loss after 8 months, in which PIB was replaceable by delayed budburst (Table 1, Supporting information). Collembola abundance (which was decreased by PIB after 8 months, Fig. 3) directly increased mass loss after 8 months (main effects in Table 1). Also after 8 months, there was a negative interaction between PIB and Collembola abundance, in which PIB was replaceable by longer vegetation period. In addition, there was a positive interaction between PIB and microbial biomass on mass loss after 14 months, in which PIB was replaceable by increasing soil moisture (Table 1, Supporting information).

Carbon loss

PIA directly increased C loss after 8 months, but PIB directly decreased C loss after 8 months (main effects in Table 1). The observed positive effect of PIA on C loss was replaceable by decreasing phytophagy, and the observed negative effects of PIB was replaceable by delayed budburst (Table 1, Supporting information). Moreover, Collembola abundance (which was decreased by PIB, Fig. 3) directly increased C loss after 14 months. There was a negative interaction between PIA and Collembola abundance after 14 months, in which PIA was replaceable by both decreasing phytophagy and increasing phenolics (Supporting information). Acari abundance (which was increased by PIB after 8 months) directly decreased C loss after 8 and 14 months. Also after 8 and 14 months, there was a positive interaction between PIB and Acari abundance, in which PIB was replaceable by increasing budburst or decreasing soil pH (Table 1, Supporting information).

Nitrogen loss

Only PIB directly decreased N loss after 8 months (main effects in Table 1). This negative effect of PIB on N loss was replaceable by longer vegetation period (Supporting information). Moreover, microbial biomass (which was decreased by PIB after 8 months; Fig. 2) directly decreased N loss after 8 months. No interaction effects were found between either PIA or PIB and soil organisms (Table 1).

Analyses accounting for fungal community, and Collembola and Acari abundances at 8 months

Functional composition

The fungal community observed after 8 months was dominated by saprotrophs (84 out of 150 taxa, 267 out of 367 reads on average per sample) and plant pathogens (33 taxa, 42 reads). Other functional groups were rare, e.g. ectomycorrhiza (9 taxa, 11 reads). We conducted two sets of analyses: accounting for the number of reads and diversity of either all fungi (Supporting information), or of only saprotroph fungi (Supporting information). Analyses with all fungi explained more variance of mass loss and N loss than did analyses with saprotrophs, but less variance of C loss (Supporting information).

Table 1. Effects of phylogenetic isolation aboveground (PIA, reflecting litter quality) and belowground (PIB, reflecting decomposition environment) on decomposition of oak litter, i.e. mass loss, carbon loss and nitrogen loss, based on multiple regression analyses, which involved the soil organisms as explanatory variables, as well as their interaction terms with PIA and PIB. t-values and effect sizes (Pearson's r) are given. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Residual degree of freedom ranged from 27 to 36. The r -square and the adjusted r -square ($\text{adj}r^2$) for each model were listed in the table. Blanks: terms excluded by variable selection as explained in Methods.

	Mass loss						Carbon loss						Nitrogen loss					
	8 months			14 months			8 months			14 months			8 months			14 months		
	t-value	effect size		t-value	effect size		t-value	effect size		t-value	effect size		t-value	effect size		t-value	effect size	
PIA	1.76	0.30		1.05	0.20		2.37	0.39*		0.99	0.18		-0.47	0.08		-1.33	0.22	
PIB	2.76	0.44**		-2.39	0.42*		-3.65	0.55***		-0.27	0.05		-2.35	0.38*				
Acari abundance (AA)	2.41	0.39*		3.60	0.57**		-3.13	0.49**		-4.61	0.65***		-0.24	0.04		-1.25	0.20	
Collembola abundance (CA)	2.87	0.45**		0.57	0.11					4.59	0.65***							
Microbial biomass (MB)	1.34	0.23		-1.25	0.23		-0.02	0.00		1.92	0.34		-2.42	0.39*		1.96	0.31	
PIA × AA													-1.99	0.33				
PIA × CA										-3.29	0.52**		1.88	0.32				
PIA × MB										4.64	0.65***		1.69	0.29				
PIB × AA	-2.40	0.39*					2.59	0.42*										
PIB × CA	-2.20	0.36*		-1.29	0.24													
PIB × MB		0.30		2.51	0.43*		0.55			-1.85	0.32		1.84	0.31		0.31		
r^2	0.34			0.52			0.46			0.61			0.33			0.18		
Adj r^2	0.18			0.39						0.51						0.16		

Mass loss

Mass loss increased with number of fungal reads. In contrast, mass loss decreased when diversity of fungal saprotrophs increased (Supporting information).

Carbon loss

There was a negative interaction between PIB and total fungal diversity on C loss (Supporting information): Fungal diversity favored C loss mainly under low PIB. By contrast, there was a positive interaction between PIB and saprotroph fungal diversity on C loss (Supporting information): Saprotroph fungal diversity favored C loss mainly under low PIB.

Nitrogen loss

There was a positive interaction between PIA and fungal diversity on N loss (Supporting information): an increase of the number of fungal reads was related to a reduction of N loss mainly under low PIA. No effect of the number of reads and the diversity of saprotrophic fungi on N loss was observed (Supporting information).

Balance on different types of effects

Accounting for multiple trajectories by including decomposer $\times$ PI interaction terms was important and allowed identification of significant direct or indirect effects of PI on decomposition in 10 out of 12 analyses on 5 out of the 6 dependent variables (Table 1, Supporting information), compared to 3 out of 6 models that did not account for multiple trajectories (Fig. 3). The biotic trajectories mediated via decomposer communities represented 3 out of 5 observed relationships of decomposition to PIA. At 8 months, this biotic trajectory of PIA was mediated by fungi, at 14 months (when no information on fungi was available) biotic trajectories of PIA were mediated by Collembola abundance and microbial biomass (Fig. 4). These biotic trajectories were more numerous belowground, representing 12 out of 17 relationships of decomposition to PIB (Fig. 4), involving Collembola and Acari abundance, and to a lesser extent microbial biomass and number of fungal reads.

Discussion

Many authors have suggested that phylogenetically closely related species may occupy different niches and unrelated species the same niche to reduce negative interactions between neighbours in a niche (reviewed by Webb et al. 2002, Cavender-Bares et al. 2009). Here, we investigated the consequences of co-occurrence of a focal species with phylogenetically distant neighbours, i.e. phylogenetic isolation (PI). We focused on a process that has the potential to contribute to positive interactions between neighbours (Aponte et al. 2013, Barbe et al. 2020a): litter decomposition, contributing to nutrient recycling. We showed that PI of a focal oak might significantly affect and mostly reduce the decomposition of its own litter. Phylogenetic isolation

operated *via* both the litter quality and the decomposition environment, tested as aboveground and belowground phylogenetic isolation (PIA and PIB) (Fig. 5): PIA effects often being replaceable by decreasing leaf phytophagy or increasing leaf phenolics, and PIB effects by microclimate-drivers such as tree vegetation period, budburst, decreasing soil pH or decreasing soil moisture. Accounting for multiple trajectories by including decomposer $\times$ PI interaction terms was important and allowed identification of most significant direct or indirect effects of PI on decomposition. Overall, we found that phylogenetic isolation may re-organize biotic trajectories of decomposition in addition to cases where phylogenetic isolation reduces overall decomposition rates.

Our study has inevitable limitations. First, we focused only on decomposition of leaf litter, without considering root litter. Root litter usually decomposes close to the parent tree and should therefore be strongly affected by PI. On the other hand, root phytophages might be less specialized on particular tree species and phylogenetic lineages than foliar phytophages (Novotny et al. 2010), possibly because roots may show less inducible defense than leaves, Kaplan et al. 2008), which would reduce a possible effect of PI. Second, we did not sample all groups of soil organisms such as nematodes, some of which do contribute to decomposition. Third, we experimentally separated effects of above- and belowground PI, but did not manipulate PI as such, nor the presence of particular decomposer species or particular abiotic conditions. Manipulating PI would be impossible given the lifespan of trees. Our experimental design with replication across pairs (each less and one more PI tree at less than 150 m) limits the problem of correlational evidence, but does not entirely resolve it. Also, manipulating particular decomposer species is difficult, but would be needed to assess whether a significantly positive PI $\times$ decomposer interaction reflects rather a shift towards more efficient decomposer species (Deniau et al. 2018), a shift within each decomposer species towards increased decomposition performance, or a support of decomposers by nutrients from dung and urine of the phytophages above (Cherif and Loreau 2013). Fourth, we examined whether observed effects of phylogenetic isolation might be due to one of the drivers of phylogenetic isolation (percentage of gymnosperms) or one of the possible consequences of phylogenetic isolation (such as litter microclimate). For instance, we found that the percentage of gymnosperms performs less well as an explanatory variable than does the litter-quality driven ('aboveground') effect of phylogenetic isolation (Supporting information). We concluded that the litter-quality mediated effect of phylogenetic isolation goes beyond the gymnosperm–angiosperm distinction and includes in addition phylogenetic distance within-angiosperm. Importantly, we do not pretend that the gymnosperm–angiosperm distinction is unimportant, it just does not explain all of the effect of phylogenetic isolation aboveground. In contrast, we found that the percentage of gymnosperms performs better as an explanatory variable than does the decomposition–environment driven ('belowground') effect of phylogenetic isolation (Supporting

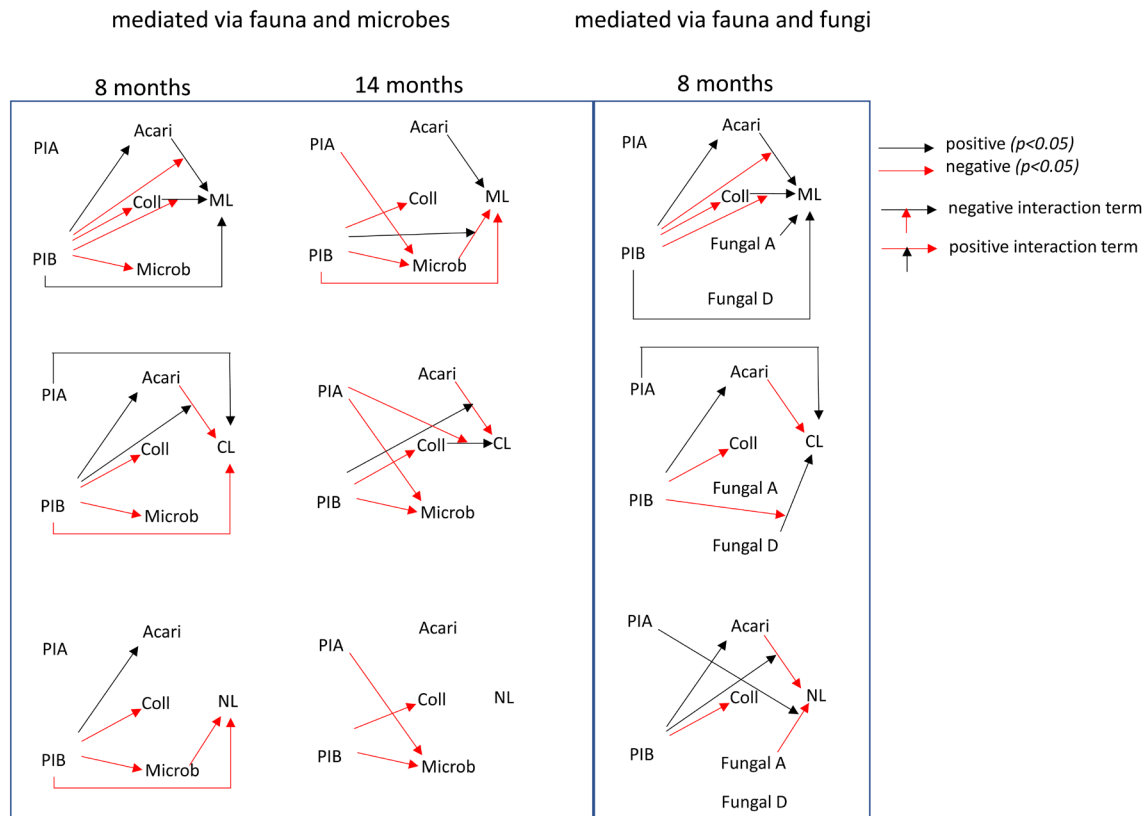


Figure 4. Schematic summary of relationships observed in two types of regressions: 1) the regressions using phylogenetic isolation aboveground (PIA, reflecting litter quality) and belowground (PIB, reflecting decomposition environment) to explain decomposers, i.e. abundances of Acari ('Acari') or of Collembola ('Collembola'), or microbial biomass ('Microb') or number of fungal reads ('Fungal A') or fungal diversity ('Fungal D') based on barcoding, as presented in Fig. 3 and the Supporting information; 2) the regressions using phylogenetic isolation, decomposers and their interactions to explain mass loss ('ML'), carbon loss ('CL'), N loss ('NL'), as presented in Table 1 and the Supporting information. Note that six out of nine summaries contain interaction terms where PIA or PIB change the effect of decomposers on decomposition, i.e. trajectory T2 from Fig. 2 (purple arrow). Total microbial biomass is treated separately from fungal diversity and number of fungal reads based on barcoding as information on fungi was available only for the first sampling date.

information). The observed effects of phylogenetic isolation that are driven by the decomposition–environment are hence specific to our oak study system, where largest phylogenetic distances correspond to a high proportion of gymnosperms. Finally, we describe the neighbourhood of the trees in terms of phylogenetic distance from oaks, but other properties of the neighbourhood may change, too, in particular, tree species richness. We hence redid the analysis in Fig. 3 including in addition tree-species richness, (Supporting information). We found that species richness has no effect.

Overall, we profit from a quasi-experiment of phylogenetic isolation established by foresters, and could separate effects of phylogenetic isolation that are mediated by the litter quality from such mediated by the decomposition environment. However, we only use correlational approaches. Hence, conclusion about mechanisms remain interpretations of patterns, causal terminology refers to statistical relationships rather than direct proof of mechanisms.

Our analyses were hierarchical: We first identified general relationships of phylogenetic isolation to decomposition using analyses that only accounted for phylogenetic isolation

above and below ground, i.e. PIA and PIB (Fig. 3 left). To explain these general relationships, we then used detailed analyses of pathways. In the rest of the Discussion we will hence identify for each of these general relationships the detailed trajectory by which PIA and PIB operate (Fig. 2).

Effect of phylogenetic isolation on decomposition environment partly reduces and reorganizes leaf litter decomposition, reflecting the action of microclimate and fungi

The effect of phylogenetic isolation mediated *via* the abiotic and biotic environment in which decomposition takes place was expressed by phylogenetic isolation belowground (PIB) the isolation of the tree under which the litter was exposed. We found that PIB mainly related to lower C loss at 8 months in analyses only accounting for PIA and PIB (Fig. 3). This relationship was partly direct (abiotic trajectory T3, Fig. 2), and PIB was replaceable by tree phenological effects on microclimate, i.e. late budburst increasing microclimatic fluctuations at the ground and decreasing decomposition.

Partly this relationship appeared to be indirect, i.e. mediated by decomposers (trajectories T1 and T2, Fig. 2): first, PIB increased Acari abundance after 8 months, which in turn related to strongly decreased C loss (albeit the PIB $\times$ Acari interaction had the inverse effect). Interestingly, the increase in Acari abundance was concomitant to a decrease in Collembola abundance, leading to an increase of Acari dominance through the mesofauna communities under PI. This shift is explained by the highest sensitivity of Collembola to soil desiccation compared to Acari (Santonja et al. 2017), as soil moisture decreased with increasing PI (Supporting information). Second, PIB rendered the effect of fungal diversity on C loss more negative. These relationships might reflect a naiveté of decomposers in, or a transfer of toxins from, the ambient phylogenetically distant litter (consistent with high decomposability of functionally uniform litter; Grossmann et al. 2020), but also less favorable abiotic conditions for decomposer activity (Sellan et al. 2020) since soil pH decreased with increasing PI (Supporting information). At 14 months, PIB did not relate to C loss in analyses only accounting for PIA and PIB. Nevertheless, at 14 months PIB decreased Collembola abundance which in turn related positively to C loss. Overall, there appears to be a phylogenetic home-field advantage where C loss is stronger when surrounded by a 'phylogenetic home litter' produced by closely related neighbourhood (consistent with Aponte et al. 2012). As a consequence, oaks may have difficulties to penetrate into a phylogenetically distant neighbourhood.

Regarding mass loss and N loss, litter mostly decomposed equally well when exposed in a phylogenetically closely or distantly related belowground neighbourhood. Processes that decrease decomposition were likely compensated by such that increase decomposition, and we could indeed identify the corresponding opposite relationships when comparing different trajectories (Fig. 4). Specifically, PIB directly increased mass loss and decreased N loss after 8 months, while decomposer-mediated effects were opposite: PIB decreased the effect of Collembola or Acari on mass loss, and PIB decreased microbial biomass itself decreasing N loss. Moreover, PIB might also have relatively little effect on mass loss, as in our system high PIB often corresponds to a gymnosperm-dominated neighbourhood with highly recalcitrant litter (Kaneko and Salamanca 1999, Cornwell et al. 2008, Berendse and Scheffer 2009). Being 'trained' in decomposing such recalcitrant litter, decomposers in a high PIB environment might efficiently reduce the mass of any litter, with little specific preference for a phylogenetically closely related 'home' litter (consistent with Milcu and Manning 2011, Wallenstein et al. 2013). Overall, despite similar mass loss and N loss in decomposition environments created by phylogenetically proximate and distant neighbourhoods, the trajectories of decomposition have become different. There is hence a 'phylogenetic home-field functioning' of the decomposition environments created by phylogenetically proximate neighbours (see also Vivanco and Austin 2008, Ayres et al. 2009 for changes in functioning but not net effects). Shift in belowground trajectories of functioning while maintaining net effects of functioning suggests

redundancy among different trajectories of decomposition, and a flexibility to shift in neighbourhood. Nevertheless, different trajectories may depend on different litter traits and penetration into a phylogenetically distantly related neighbourhood might impose new selection pressures on litter traits (Guénon et al. 2017).

Effect of phylogenetic isolation on litter quality overall reduces and reorganizes decomposition, mainly reflecting the action of phytophages, soil microbes and soil fauna

The effect of phylogenetic isolation mediated via the litter quality was expressed by phylogenetic isolation aboveground (PIA) the isolation of the tree from which the litter had been sampled. First, we found that PIA shows no effect on mass loss after 8 months, and a negative effect after 14 months (in analyses only accounting for PIA and PIB, Fig. 3). Analysis of trajectories fails to reproduce this negative effect. Instead, the trajectory analysis reveals among others a negative effect of PIA on the role of fungal diversity on mass loss after 8 months. Second, PIA shows a positive effect on C loss after 8 months (in analyses only accounting for PIA and PIB, Fig. 3). This effect is explicable by a direct, abiotic effect of PIA (trajectory T3), which in turn, is replaceable by low phytophagy: less attacked leaves might have kept more labile and soluble carbon rendering these leaves abiotically more degradable. In contrast, PIA shows a negative effect on C loss after 14 months. Analyses of trajectories suggests that this relationship is mediated by a decline in the relationship between Collembola and C loss, the latter being replaceable and possibly explicable 1) by reduced phytophagy, as low phytophagy damage might reduce the access to leaves for detritivores such as Collembola, or 2) by higher litter phenolics, consistent with the hypothesis of an increased competition for resources and/or on allelopathic interaction between oaks and distantly related gymnosperms increasing leaf phenolics (Fernandez et al. 2016) and decreasing litter quality for decomposers (Hattenschwiler and Vitousek 2000, Chomel et al. 2014). We note that main effects of PIA not necessarily reflect abiotic decomposition, as suggested in the definition of our trajectory T3: the increased phytophagy under low PIA might also contribute to decomposition by increasing phyllosphere microbial abundance (Stadler and Müller 2000), favouring in particular microbes capable of using $\text{NO}_3^-/\text{NH}_4^+$ and thereby potentially reducing N-loss (Müller et al. 2003). Phyllosphere microbial community, in turn, can contribute to the litter microbial community and the decomposition process (Osono 2006, Fanin et al. 2021).

In the present study, phylogenetic isolation negatively affected mass and C losses without major impact on N loss during the decomposition process. This differential impact on C and N losses led to an increase of the C:N ratio of the litter organic matter under phylogenetic isolation. Since microbes need to immobilize N to consume the excess of C (Mooshammer et al. 2014), phylogenetic isolation might lead to a deficit of N available for trees and by consequence might

potentially reduce tree growth. Thus, leaf litter that is produced in a neighbourhood of closely related lineages becomes more decomposable in the long run. This can be considered as a form of a phylogenetic home-field advantage, albeit one that is non-standard for three reasons. First this positive effect of neighbourhood is mediated in part by litter quality, which so far has not been accounted for in the home-field research on decomposition (Ayres et al. 2009, Freschet et al. 2012, Veen et al. 2015). Second, existing research defined ‘home’ taxonomically: as litter from the particular plant species under which the decomposers had been living (Austin et al. 2014). Phylogenetic proximity and neighbourhoods were not accounted for. Finally, outside research on decomposition, a kind of phylogenetic home-field advantage has been proposed as an explanation why phylogenetic lineages of early land plants were dominant for so long: they were competitively superiority ‘at home’ and for long outcompeted other lineages (DiMichele and Bateman 1996). We suggest that, besides competition, improved recycling of nutrients through decomposition might have contributed to the local dominance of a single lineage on land. Such phylogenetic home-field advantage might possibly result from dominance of lineages whose species synergistically accelerate decomposition when mixed (Barbe et al. 2018), and it may explain large unexplained variance in home field advantages in studies not accounting for phylogeny (Barbe et al. 2020a,b). Home-field advantages might be more important for plants that create a home field, i.e. plants that can be dominant and that hence grow in their own litter and attract specialist phytophages when surrounded by close relatives. Such species are often late-successional species, and we hence suggest that phylogenetic home-field advantages might be more important in late-successional species.

Conclusion

Trees may be exposed to a distantly related neighbourhood if niches were conserved in the past and at present individuals leave their ancestral niche and converge with niches of distantly related species. In oaks, such coexistence of trees with distant relatives appears to impede carbon and nitrogen recycling and the trajectories of this recycling may be reorganized. The processes involved operate through the litter quality and the decomposition environment, and may reflect both pedoclimatic and biotic drivers of decomposition (Supporting information), affecting microbes, in particular fungi, Collembola and Acari. Low nutrient recycling during litter decomposition reduces the fitness of trees (Binkley and Giardina 1998), so that trees in a phylogenetically distant neighbourhood should suffer a selective disadvantage, counteracting a possible competitive advantage. Plants indeed appear to avoid neighbourhoods where nutrient recycling is low (Barbe et al. 2020a, b). Therefore, reduced nutrient recycling under local phylogenetic isolation might possibly prevent oaks and trees distantly related to oaks from converging into the same niches, ultimately contributing to a

feedback between niche-evolution and ecosystem functioning (Srivastava et al. 2012, Prinzing et al. 2016b, 2017). Future studies might test this evolutionary speculation, and they might experimentally test ecological mechanisms behind the observed patterns, such as the sources of recruitment of decomposer organisms from surrounding litter or soil or phyllosphere. Finally, future studies should expand to other focal taxa of angiosperms and in particular of gymnosperms: do both angiosperms and gymnosperms profit from increased decomposition when growing with close relatives, or do gymnosperms suffer decreased decomposition (for reasons suggested in the Introduction), selecting for gymnosperms to approach angiosperms?

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Author contributions

Mathieu Santonja and **Xu Pan** contributed equally to this publication. **Mathieu Santonja**: Data curation (equal); Formal analysis (equal); Methodology (equal); Validation (equal); Writing - original draft (equal); Writing - review and editing (equal). **Xu Pan**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Methodology (equal); Validation (equal); Writing - original draft (equal); Writing - review and editing (equal). **Pierre-Emmanuel Courty**: Data curation (equal); Validation (equal); Writing - review and editing (equal). **Olaf Butenschön**: Data curation (equal); Validation (equal); Writing - review and editing (equal). **Matty P. Berg**: Data curation (equal); Validation (equal); Writing - review and editing (equal). **Phil Murray**: Data curation (equal); Validation (equal); Writing - review and editing (equal). **Benjamin Yguel**: Data curation (equal); Validation (equal); Writing - review and editing (equal). **Daphne Brule**: Data curation (equal); Validation (equal); Writing - review and editing (equal). **Keliang Zhang**: Data curation (equal); Validation (equal); Writing - review and editing (equal). **Andreas Prinzing**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Methodology (equal); Supervision (lead); Validation (equal); Writing - original draft (equal); Writing - review and editing (equal).

Data availability statement

Data are available from the Figshare Repository: <https://doi.org/10.6084/m9.figshare.12448850.v1> (Santonja et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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