

Why phylogenetic signal of traits is important in ecosystems: uniformity of a plant trait increases soil fauna, but only in a phylogenetically uniform vegetation

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39 Abstract

Phylogenetically closely related plant species often share similar trait states (phylogenetic 40 signal), but local assembly may favour dissimilar relatives and thereby decouple the diversity 41 of a trait from the diversity of phylogenetic lineages. Associated fauna might either benefit from 42 plant trait diversity because it provides them complementary resources, or suffer from it due to 43 dilution of preferred resources. We hence hypothesize that decoupling of trait and phylogenetic 44 diversity weakens the relationship between the plant-trait diversity and the abundance and 45 diversity of associated fauna. Studying permanent meadows, we tested for combined effects of 46 plant phylogenetic diversity and diversity of two functional traits (specific leaf area, leaf dry 47 matter content) on major groups of soil fauna (earthworms, mites, springtails, nematodes). We 48 found that only in phylogenetically uniform plant communities, was uniformity in the 49 functional traits associated with (i) high abundance in springtails, and (ii) high abundance of 50 the sub-group that feeds more directly on plant material (in springtails and mites) or those that 51 are more prone to disturbance (in nematodes), and (iii) high diversity in all three groups tested 52 (springtails, earthworms, nematodes). Our results suggest that soil fauna profits from the 53 resource concentration in local plant communities that are uniform in both functional traits and 54 phylogenetic lineages. Soil fauna would hence benefit from co-occurrence of closely related 55 plants that have conserved the same trait values, rather than of distantly related plants that have 56 converged in traits. This might result in faster decomposition and a positive feedback between 57 trait conservatism and ecosystem functioning. 58

59 **Introduction**

Phylogenetically closely related plant species often share similar trait states (Peterson 2011), 60 even locally. However, in disturbed habitat types like meadows in temperate regions, local 61 phylogenetic signal of traits may be weak (Prinzing et al. 2021). This pattern of low 62 phylogenetic signal suggests that local assembly favours distant relatives that converged in trait 63 64 states or close relatives that diverged. Such convergent or divergent trait states exist because during diversification, trait evolution was sometimes labile (Ackerly 2004; Grime 2006). For 65 simplicity, we hence below refer to the pattern of low local phylogenetic signal as "trait 66 lability", acknowledging that this pattern results from local assembly of species and traits that 67 have evolved elsewhere. As a result of such local trait lability, the local diversity of a given 68 functional trait may be decoupled from the local phylogenetic diversity: local communities will 69 sometimes be diverse in states of a given trait but uniform in phylogenetic lineages, or uniform 70 in trait states but diverse in lineages (Losos 2008). Local diversity of a plant trait may, in turn, 71 72 affect associated fauna (Beugnon et al. 2019), but we do not know whether this effect depends on whether the trait diversity is coupled with phylogenetic diversity. We will below develop 73 how local diversity of a trait may affect associated fauna, and then how this effect may depend 74 on coupling of this trait to phylogenetic diversity. 75

76 Local plant communities that have a large diversity of trait states may provide a large diversity of resources to associated fauna, thereby increasing the abundance and diversity of animals due 77 to increased complementarity among resources (Eisenhauer 2012). For instance, generalist 78 folivorous Orthoptera can balance their diet by feeding on multiple plant species and are worse 79 than specialists at coping with feeding on a single plant species that provides a non-balanced 80 81 diet (Raubenheimer and Simpson 2003). On the other hand, if the diversity of resources is large, none of them is abundant, so that the preferred resources for any given animal species are 82 diluted, potentially reducing their abundance or even preventing their subsistence (Root 1973). 83

The diversity of resources for animals within a local plant community has often been inferred from the diversity in particular key functional traits, each being supposed to be locally related to many other traits through evolutionary conserved "economic spectra" (e.g. Flores et al. 2014; Jardine et al. 2020; Li et al. 2017).

However, when in a local plant community a given trait is evolutionary labile, the diversity of 88 that trait does not coincide with high phylogenetic diversity or the diversity of other conserved 89 traits (Tucker et al. 2018). First, the local plant community may be composed of closely related 90 species that diverged in this particular trait but remained similar in many other traits. We 91 hypothesize that due to this similarity, the abundance and diversity of fauna may neither 92 increase due to complementarity, nor decrease due to resource dilution (Figures. 1a, c). As an 93 extreme example, a large diversity of plant sizes represented by phylogenetically diverse 94 Fabaceae, Poaceae, Salicaceae, and Fagaceae on a continent may produce more complementary 95 (or more diluted) resources than the same diversity of plant sizes represented by 96 phylogenetically closely related Boraginaceae species on an oceanic island (Nürk et al. 2019). 97 Second, the local plant community may be composed of distantly related species that converged 98 in this functional trait but remained different in many other functional traits (Figures. 1b, d). 99 We hypothesize that in that case, resources for animals might be complementary (or diluted) 100 despite low diversity in this particular trait, because other traits are different. Overall, we predict 101 that the evolutionary lability of a plant trait alters the relationship between the diversity of that 102 trait and the diversity and abundance of soil fauna (arrows in Figure 1). This altered relationship 103 results in a statistical interaction term between phylogenetic and functional diversity on soil 104 fauna (different types of lines in Figure 1). 105

The effect of phylogenetic position and functional traits of plants on associated fauna has been studied mostly for phytophages feeding on living plants, and rarely for soil animals living in dead litter. For phytophages, it has been shown that evolutionary histories of plant lineages are

intimately related to co-evolutionary histories of associated phytophagous arthropods: many 109 species of phytophages feed only on a small number of closely related plant species, probably 110 mediated in part by phylogenetic signals in leaf quality (Brändle and Brandl 2006). 111 Consequently, the phylogenetic diversity of a local plant community has major effects on the 112 diversity, abundance, and trophic structure of its phytophagous arthropod community (Jactel et 113 al. 2005; Jactel and Brockerhoff 2007; Molleman et al. 2022; Schuldt et al. 2019; Vialatte et al. 114 2010; Yguel et al. 2011). Furthermore, it has been shown that the Specific Leaf Area (SLA) and 115 Leaf Dry Matter Content (LDMC) of a leaf may determine which phytophages can use it 116 (Bisigato et al. 2015; Castagneyrol et al. 2017; Descombes et al. 2017; Schädler et al. 2003; 117 Schuldt et al. 2012), and higher diversity in such traits may increase the diversity of 118 phytophagous arthropods (Marini et al. 2009). 119

In contrast, it has been much less studied how local plant traits or the phylogenetic clades to 120 which plants belong affect soil fauna. Contrary to phytophagous arthropods, many soil 121 organisms feed on dead plant material which has been previously conditioned by microbes, thus 122 with much less active plant defences. Furthermore, leaf litter is typically mixed at small spatial 123 scales so that individual soil animals are more likely to have mixed diets than for example the 124 most often studied folivores, Lepidopteran larvae. Finally, soil animals are usually hidden from 125 view so that there is no selection for visual crypsis which promotes host-plant specialization in 126 folivores (Lichter-Marck et al. 2015). Nevertheless, plant functional traits have been shown to 127 affect leaf-litter traits and hence soil fauna (Eisenhauer and Powell 2017). In particular, 128 structure-related traits such as captured in SLA and LDMC are important to decomposition and 129 soil fauna, as they play an important role in determining the nutritional quality of leaf litter 130 (Cornelissen 1996; Lin et al. 2019; Zukswert and Prescott 2017). Furthermore, some after-life 131 traits of plant litter that affect soil fauna show phylogenetic signal (Cornelissen et al. 2004; 132 Grime et al. 1996; Pan et al. 2015a; Pan et al. 2015b). As a result, increased phylogenetic 133

diversity of local plant communities should be accompanied by increased diversity in after-life traits of litter. Examples of specialization in soil biota on particular plant lineages include springtails becoming more abundant with the establishment of gymnosperms (Luque et al. 2011), soil-mediated interactions being strongest among closely related plant species (Anacker et al. 2014), fungus gnats being moderately specialized on fungus lineages (Põldmaa et al. 2016), and particular soil microbes associating with particular plant species (Leff et al. 2018).

Local plant communities that are diverse might produce leaf litter that is nutritionally 140 complementary or diluted, thereby potentially favouring or disfavouring decomposer fauna, 141 depending on their degree of specialization. For example, if plant species with divergent 142 functional traits are nutritionally complementary, then a given generalist decomposer species in 143 a diverse plant community may be able to balance its diet using the complementarity of material 144 from different plant lineages. Such effects of complementarity among plant species on 145 decomposer fauna may explain results of experiments in which diverse litter mixtures 146 decomposed faster than predicted from decomposition rates of litter from single species (Bila 147 et al. 2014; Gessner et al. 2010; Meier and Bowman 2008; Rabelo et al. 2022; Tardif and Shipley 148 2014; Vos et al. 2013). If however decomposer fauna is composed of specialist species that are 149 good at coping with nutritional challenges of the litter of particular plant species, decomposer 150 species might suffer from dilution of preferred resources under high phylogenetic or functional 151 trait diversity (Barbe et al. 2018; Pan et al. 2015a; Plazas-Jiménez and Cianciaruso 2021). 152 Overall, in local plant communities that are diverse, a species of generalist decomposer might 153 do well because it benefits from resource complementarity (Eisenhauer 2012), while a species 154 of specialist decomposer might suffer from resource dilution (Root 1973). Therefore, both low 155 and high phylogenetic or functional diversity of a local plant community might increase the 156 abundance and diversity of soil fauna, depending on its degree of dietary specialization. In 157 addition, high functional or phylogenetic diversity may support more diverse communities of 158

specialists (Chesson 2000; Clavel et al. 2011; Jactel et al. 2021; Proches et al. 2009). While 159 local phylogenetic or functional diversity of plant communities has been shown to relate to 160 decomposition rates (Barbe et al. 2017; Barbe et al. 2018; Chamagne et al. 2016), its 161 relationship to soil fauna has been very little studied. Milcu et al. (2013) found little effect of 162 plant phylogenetic diversity on macroscopic decomposers in experimental plant communities, 163 and positive effects on soil microbial biomass. Interacting effects of diversities of phylogenetic 164 lineages and a given functional trait of plants on soil fauna (such as the hypotheses in Figure 1) 165 have to our knowledge never been studied. Overall, further studies are needed on effects of 166 plant phylogenetic diversity and diversity of individual functional traits, and their interaction, 167 168 on multiple classes of soil organisms in naturally assembled plant communities.

We tested the predictions in Figure 1 on relationships between phylogenetic diversity and the 169 diversity of a given key functional trait of local plant communities and soil fauna, considering 170 meadows in Brittany, France. For each plant community, we first calculated the diversity of 171 phylogenetic lineages and of two functional traits known to be major determinants of 172 decomposition – SLA, and LDMC (Cornelissen 1996; Cornelissen et al. 2004; Lin et al. 2019). 173 We tested for associations between plant phylogenetic and functional diversity and the 174 abundance of earthworms, nematodes, springtails, and mites. Within each group, we 175 differentiated sub-groups that are likely to be more exposed to plant diversity from those that 176 are less exposed. Exposure may be due to spatial proximity (epigeic earthworms and 177 hemiedaphic springtails being more exposed than endogeic earthworms and eudaphic 178 springtails), trophic proximity (plant-feeding nematodes and mites vs. carnivorous nematodes 179 and mites), or long life-span and disturbance sensitivity (summarized by nematode community 180 indices; Bouché 1972; Ferris et al. 2001; Gisin 1943; Walter and Proctor 2013). We also 181 considered the diversity of three major soil fauna groups; earthworms, nematodes, and 182 183 springtails (mites were not identified to species). We used the two functional traits in separate

models with as dependent variable the various soil fauna parameters (Table 1). To test our
hypotheses (Figure 1), we were especially interested in the statistical interaction between plant
phylogenetic diversity, and the diversity of functional traits.

187

188 <u>Methods</u>

189 Description of local plant communities

The plant community data were collected as part of the 'Réseau de Mesures de la Qualité des Sols' (RMQS), a campaign to systematically sample and analyse soils across France. When these plant community data were not available, we used those from RMQS-BioDiv. RMQS-BioDiv is a research program based at the University of Rennes 1 that provided data on soil fauna from the RMQS sites in the French Region of Brittany (Ponge et al. 2013). We selected all 19 sites with permanent meadows that were sampled.

RMQS plant community data were collected with a variant of the point-centred quarter method, 196 originally developed for forest plots (Cotham and Curtis 1956) and also applied to grassland 197 communities (Dix 1961). Classically, in each of the four cardinal directions, the distance of the 198 first individual of each species to the central point is measured. In RMQS, instead of using the 199 central point, the points at the corners of a 20x20m sampling plot were taken as bases for 200 distance measurements in all directions, extending to 3.5 meters from each of the four points. 201 The density of a given plant species was approximated by the inverse of the square of the 202 average distance to the point $(1/d^2)$, reflecting that plant species encountered closer to the 203 observation points tend to be more abundant. In case of an average distance of zero across the 204 four corners, it was substituted by one cm. Subsequently, we multiplied this 'average density' 205 by its frequency in the four corners, where the absence in a corner was regarded as a density of 206 zero. We then scaled the resulting densities so that the total was one within sites, which is 207

comparable to proportional abundance. For technical reasons, the plant community of six of the sites was not determined by RMQS, but was determined by RMQS-BioDiv using cover estimates. Both methods provide measures of plant cover per species, which in grasslands should correlate reasonably well with litter biomass produced (Röttgermann et al. 2000). We used RMQS data to characterize sites by the soil properties: humus index, waterlogging, soil depth, organic carbon, total nitrogen, C/N ratio, and water pH (Arrouays et al. 2002; Terrat et al. 2017).

Plant community composition was summarized using Principal Component Analysis, 215 extracting the two main factors for each site. To calculate phylogenetic diversity, we obtained 216 phylogenetic distances (in millions of years) among the species from the higher-plant 217 phylogeny database Daphne (Durka and Michalski 2012). Some plants were identified only to 218 genus level, but were then replaced by a species taken randomly from the same genus because 219 there was always only one member of that genus present at a given site. We calculated 220 phylogenetic diversity using the Picante package in R (Kembel et al. 2010; R Core Team 2021) 221 as the average across phylogenetic distances within all pairs of species (Webb 2000). We 222 accounted for the abundance of species using "MPD-abundance" which quantifies abundance-223 weighted mean phylogenetic distances between pairs of individuals (Abu.mpd; Kembel et al. 224 2010). To control for variation in species richness, we compared these mean distances to those 225 from a null model produced by reshuffling species across communities. We calculated 226 standardized effect size (SES) values as (observed minus mean-null) / (SD-null), and used SES 227 values in further analyses. We calculated in the same way for each community the abundance-228 weighted phylogenetic distances within pairs of most closely related species, their averages and 229 the SES of that average. The resulting "mean nearest taxon distances" (Webb 2000) were 230 closely correlated to the above phylogenetic diversity calculated across pairs of species 231 (Abu.mntd; Fig. 2) and we hence limited further analyses to phylogenetic diversity. 232

To calculate the functional trait diversity of the plant communities, we obtained SLA and 233 LDMC for each species from the LEDA database (Klever et al. 2008). When several values 234 were present for one species, the median value was calculated. Not fully identified species were 235 treated as missing values. We calculated single-trait functional diversity for SLA or LDMC 236 using Rao's quadratic entropy index. The Rao Index expresses the probability that two 237 randomly-picked individuals in the community are functionally different. Rao = $\sum p_i \cdot p_j \cdot d_{ij}$ 238 where p is the abundance of species i and j in the plot, respectively; d_{ii} the dissimilarity in trait 239 value between the two species (Botta Dukát 2005). Trait values were first scaled between zero 240 and one, and then the dissimilarity matrix was calculated as the Euclidean distance between 241 trait values for a pair of species. Thus, the dissimilarity d can range from zero (same trait value) 242 243 to one (complete dissimilarity between species). Overall, both phylogenetic and functional diversity measures account for the abundance of species. Phylogenetic diversity measures 244 distance in evolutionary time, functional diversity measures distance in a functional space. 245 Otherwise, both measures are technically equivalent (Swenson 2011). 246

247

248 Sampling and determination of soil fauna

Soil fauna was sampled for each site across multiple subsites to integrate the major small-scale 249 variation of soil fauna. Specifically, soil fauna was sampled 5 m northward from the RMQS 250 sampling plots, in 3 x 34 m plots that were homogeneous in plant cover and soil features (see 251 Cluzeau et al. 2010 for further details). This zone was subdivided into 1 x 3 m sub-plots 252 (Cluzeau et al. 2012). Earthworms were sampled in three sub-plots using protocols developed 253 by Bouché (1972) and adapted by Cluzeau et al. (1999; 2003), where the soil is watered with 254 diluted formalin which drives earthworms up to the surface. Earthworms that emerged at the 255 surface were collected and preserved in 4% formalin. To assess how many earthworms 256

remained in the soil after completion of earthworm extraction, a 0.25 x 0.25 x 0.25 m block of 257 soil was dug out at the centre of each quadrat and spread on a plastic sheet and the remaining 258 earthworms were collected. Species identification was performed using a key based on Bouché 259 (1972). Earthworm species were grouped into three categories; epigeic (living at the surface in 260 litter, no burrows), anecic (making deep vertical burrows and feeding at the surface in litter at 261 night), and endogeic (living fully underground in shallow horizontal, branched burrows) based 262 on Bouché (1972) and OPVT (2013). Diversity and abundance of earthworm species were 263 calculated on the pooled sample. Here and below, species diversity was calculated using the 264 Simpson index (1-D, with values ranging from 0 for no diversity to 1 for high diversity), as it 265 266 is particularly robust against differences in numbers of animals sampled among sites (Rosenzweig 1995). Note also that Simpson diversity corresponds to a Rao diversity where all 267 species differences are equal (Botta Dukát 2005), contributing to the consistency of our 268 measures. 269

Sampling of springtails (Collembola) and mites (Acari) was done in triplicate using a corer that 270 took a cylinder of soil of 6 cm diameter and 5 cm deep (Block 1966; ISO 2006). 271 Microarthropods were extracted from the soil samples using the high gradient method 272 (Macfadyen 1961), where invertebrates avoid a heat source and move down to fall through a 273 gauze into a cooled collection container. Springtails were identified to species, while mites were 274 identified to suborder. Springtails were identified using Gisin (1960) and later updates 275 (Fjellberg 1998; Hopkin 2007; Potapow 2001; Thibaud 2004). Springtails were classified as 276 euedaphic (living inside the soil), hemiedaphic (living both at the surface and in the soil), and 277 epigeic (living at the surface, being exceptional in our samples) according to Gisin (1943). 278

Nematodes were sampled from the surface soil layer (0 to 15 cm) in 32 samples (to capture microspatial heterogeneity; e.g. Delaville et al. 1996) that were then pooled. Nematodes were extracted from about 300 g of wet soil by elutriation with water, followed by an active passage

through a cotton wool filter for 48 h. Nematodes were then counted under a binocular 282 microscope. After that, nematodes were fixed with a formaldehyde-glycerol mixture and 283 transferred to mass slides. On average, ca. 200 nematodes were identified per mass slide to 284 family or genus level (Andrássy 1984; Bongers 1994; Siddiqi 2000). We ranked trophic groups 285 of nematodes, according to family membership as in Parmelee and Alston (1986). We also 286 calculated the Structure Index which best reflects the absence of disturbance (Ferris et al. 2001). 287 The Structure Index increases with the presence of long-lived species and of 288 carnivores/omnivores vs. fungivores/bacterivores, and hence is an indicator of stable 289 development of the community. 290

291

292 Data analysis

We first tested for correlations between soil parameters, plant community parameters, and soil 293 fauna parameters using Pearson's correlations, using the rcorr function in the R package Hmisc 294 (Harrell 2020), and visualized them using the corrplot package (R Core Team 2021; Wei and 295 Simko 2021). We then tested for a relationship between the diversity in SLA and LDMC, and 296 the phylogenetic diversity of a plant community across our study sites using Ordinary Least 297 Squares regression (OLS) in R (R Core Team 2021). Finally, we tested the relationships 298 between functional-trait and phylogenetic diversities of the local plant communities, and the 299 abundance and species diversity of soil fauna using OLS regression models. Separate models 300 were run with SLA and with LDMC. Because plant community parameters tended to differ 301 within sites between RMQS and RMQS-BioDiv data when both sources were available, the 302 source of the plant community data was included as a factor in the models (where both sources 303 were available we used RMQS plant community data). The average value of SLA or LDMC 304 weighted by abundance was included in the models as predictors alongside plant functional trait 305

diversity, because diversities may change with average values, and average values will capture 306 some of the variation in soil parameters and management across sites (Figure 2, Supplement 3). 307 To test the predictions in Figure 1, the interaction between phylogenetic diversity and diversity 308 of the functional trait in question (SLA or LDMC) was included in the models. We tested for 309 associations with overall abundances of earthworms, springtails, mites, and nematodes, and 310 within these groups the abundances of sub-groups considered to be particularly strongly versus 311 particularly weakly exposed to plant diversity. For earthworms and springtails this was in space 312 (epigeic vs endogeic earthworms, hemiedaphic vs euedaphic springtails), for mites and 313 nematodes the exposure to plant traits was based on diet (mainly herbivorous actinid vs. entirely 314 carnivorous gamasid mites, phytoparasite vs. carnivorous nematodes). For nematodes, we also 315 fitted models with Structure Index as the dependent variable, an indicator of stable development 316 of the community based on life history and trophic position. Abundance data were log-317 transformed, which generally led to more normally distributed residuals. In addition, we also 318 studied the species diversities of earthworms, springtails, and nematodes. All models were run 319 with scaled predictors using the function 'summ' of the R package jtools (Long 2022). For some 320 sites, particular soil fauna parameters were not available. Furthermore, up to three outlier data-321 points were excluded (based on Q-Q plots). This exclusion permitted to have models that 322 represent almost all but not all data points, rather than models that are biased by one or few data 323 points and do not represent the majority of data points (Quinn and Keough 2002). We note that 324 there were no general problems of residual distribution, only individual outliers that would have 325 been outliers for any possible assumed distribution of residuals. Given small numbers of sites, 326 the results of any single regression analysis must be interpreted with caution, and we hence 327 interpreted relationships only when consistent between plant traits within animal taxon, or 328 among animal taxa for a given plant trait, or both. We checked whether there are cases indicative 329 of too many explanatory variables: no explanatory variable being significant but adjusted R² 330

being high. There were none. Moreover, variance inflation factors were below 2 for all predictors main effects and below 3 for all interactions). Results were illustrated by plotting simple regression relationships between functional trait diversity of plant communities and soil fauna separately for sites with below- and above-median phylogenetic diversity of the plant community, using the R package ggplot2 (R_Core_Team 2021; Wickham 2016).

336

337 **<u>Results</u>**

We identified 91 plant species across 19 permanent meadows (Table S.1.). Correlation analysis 338 did not suggest major effects of soil parameters on plant community parameters and only 339 limited effects on soil fauna parameters, notably not on several of those that show strong signals 340 in our below regression analyses: diversities of earthworms, springtails or nematodes, 341 abundances of hemiedaphic springtails and carnivorous nematodes, or nematode structure index 342 (Fig. 2). Vegetation factors 1 and 2 (from principal component analysis of plant community 343 composition) were correlated with diversity of SLA, which thereby represented general patterns 344 in the plant community. Vegetation factor 1 was correlated also with means of LDMC, so that 345 inclusion of mean LDMC in the below regression analyses also accounted for vegetation 346 composition. With the exception of soil pH being correlated with one measure of vegetation 347 phylogenetic diversity (Abu.mntd), neither soil nor vegetation factors were strongly related to 348 measures of phylogenetic diversity (Abu.mntd and Abu.mpd), further reducing the risk of our 349 below regression analyses identifying pseudo-relationships between phylogenetic community 350 composition and soil fauna being in reality attributable to the abiotic or biotic environment. 351

Phylogenetic diversity of plant communities was not significantly related to diversity in plantfunctional traits (Figure 3). While phylogenetically uniform plant communities tended to be

also uniform in SLA and LDMC, phylogenetically diverse plant communities had trait diversity
values for SLA and LDMC that ranged from low to high.

The abundance of springtails appeared to decline with SLA and LDMC diversity of plant communities when plant phylogenetic diversity is low (Figure 4, interaction terms in Tab. 1a). Thus, springtail abundance was higher when plant functional diversity was lower only when plant phylogenetic diversity was low.

Sub-groups of springtails that live spatially exposed to plants in upper soil strata responded to 360 plant community diversity, contrary to groups dwelling in deeper strata. Specifically, abundance 361 of hemiedaphics decreased with plant functional diversity (of SLA and LDMC) when plant 362 phylogenetic diversity was low (see interaction terms in Table 1c, Figure 5), while abundances 363 of eudaphics did not show such change. A similar trend was observed for mites that are often 364 plant-feeding (actinedids) and SLA, while for LDMC the interaction of plant phylogenetic and 365 functional diversity was only marginally significant, and similar for both groups of mites 366 (actinedids and gamasids, Table 1d, Figure 5). For earthworms, no such effects were observed, 367 and for nematodes the pattern was opposite to expected: the interaction was significant for 368 carnivores but not phytophages (Table 1e, Figure 5). Among nematodes, we also tested whether 369 groups indicative of undisturbed soils (long-lived, higher trophic level, as summarized by 370 Structure Index) mostly responded to plant community diversity, contrary to groups that are 371 indicative of disturbed soils. The Structure Index showed a significant interaction between plant 372 phylogenetic and functional diversity for SLA (Table 1f). When plant phylogenetic diversity 373 was low, lower plant functional diversity was associated with lower values for the nematode 374 Structure Index. The pattern found in Structure Index was distinctly stronger than that for 375 376 carnivorous nematodes (F = 15.9 vs. 11.5, Table 1 e and f), suggesting that additionally accounting for life-history information in the Structure Index is pertinent. 377

Taxonomic diversity of soil fauna declined with trait diversity of plant communities when plant 378 phylogenetic diversity is low. Specifically, higher diversity in SLA was associated with lower 379 diversity of springtails and nematodes when plant phylogenetic diversity is low, while higher 380 diversity in SLA was associated with increased or unchanged diversity of springtails and 381 nematodes when plant phylogenetic diversity was high (interaction terms in Table 1g, Figure 382 6). For earthworms, no significant statistical effects of SLA diversity were detected (interaction 383 terms in Table 1g, Figure 6). Higher diversity in LDMC was associated with lower diversity of 384 earthworms and springtails when plant phylogenetic diversity was low, while higher diversity 385 in LDMC increased diversity of earthworms and springtails when plant phylogenetic diversity 386 was high (interaction terms in Table 1g). For nematodes, no effect of LDMC diversity was 387 detected (interaction terms in Table 1g). 388

389

390 **Discussion**

We combined plant community data with soil fauna data for permanent meadows in Brittany, 391 France, and found interactions between phylogenetic and functional-trait diversity of plant 392 communities in determining multiple aspects of the soil fauna. To our knowledge, this is the 393 394 first time that such interactive effects have been tested, permitting us to explore novel hypotheses on the consequences of phylogenetic lability of a functional trait for how the local 395 diversity of this plant trait within a community drives associated biota. Overall, we found that 396 plant phylogenetic diversity and the diversity of functional traits combined have major power 397 of explaining abundances of several soil fauna groups and of diversity of soil fauna. In most 398 cases, significant effects were detected for those groups that we considered to be particularly 399 400 exposed to the plants: living close to the plants, or feeding directly on the plants. Importantly, one form of diversity not just complements the other - the interaction terms between 401 phylogenetic and functional trait diversity are also important. These statistical interactions 402

reflect the local assembly of different phylogenetic histories of traits. We found that communities representing trait divergence among close relatives often have reduced abundances and diversities of soil fauna, compared to communities representing close relatives that have similar functional trait values. Our study might hence contribute to identifying the possible local consequences of trait shifts among phylogenetically closely related species.

408

Our study has several limitations. First, it is a correlational study. We cannot prove causality. In 409 particular, diversities might reflect environmental conditions not accounted for and possibly 410 being the true underlying causes of the patterns observed. We tested for such relationships of 411 412 diversities to environmental conditions and found only few (Figure 2). Plant species composition correlated with the diversity of SLA, but not with the diversity of LDMC. 413 Nevertheless, diversities of both functional traits showed similar interaction terms with plant 414 phylogenetic diversity in determining soil fauna. Also, our study does integrate multiple 415 environmental conditions by accounting for community-weighted means of SLA and LDMC 416 as these trait means tend to vary with environmental conditions (Bisigato et al. 2015; Daou et 417 al. 2021; Kichenin et al. 2013; Reich et al. 1999). In our data, these trait means were of much 418 lower statistical importance than diversities and their interactions. Second, our study focused 419 on two important functional traits, but other functional traits such as carbon:nitrogen ratio may 420 also be important. However, these other traits may be related to the traits we considered (Wright 421 et al. 2004). Third, we did not have sufficient data to test for non-linear relationships, but data 422 visualization did not indicate that these are important here. Fourth, our study does not permit to 423 identify effects of diversity that operate through individual plasticity or within-population 424 variation, but focuses on the effects of sorting of species with certain traits into communities. 425 Future studies could sample sites multiple times for vegetation and soil fauna and measure plant 426 traits directly, rather than rely on a database (Fujii et al. 2020; Ganault et al. 2021). Fifth, our 427

results on plant phylogenetic diversity might be contingent on the particular phylogenetic 428 lineages present in this system. Meadows are dominated by grasses, and grasses tend to favour 429 closely related neighbours (Cahill et al. 2008). In addition, combinations of litters of different 430 grass species tend to decompose faster than combinations of grasses with non-grasses (Barbe 431 et al. 2018), consistent with our observation of increased diversity and often abundance of soil 432 fauna with a combined decrease in phylogenetic and trait diversity. So, while for the lineages 433 present in grassland, our results are consistent with the literature, future work on different, non-434 grass-dominated systems is needed to identify the generality of our results. Sixth, soil fauna 435 will also be affected by biomass removal such as by mowing and grazing (Galvánek and Lepš 436 2012; Liu et al. 2017; Todd et al. 1992), for which we have insufficient data for our study sites. 437 Even if hay is exported, the local vegetation composition drives the local litter composition. In 438 grasslands, between 50 and 90% of plant primary production ends up as litter (Cebrian 1999). 439

440

441 Explaining interaction terms between plant phylogenetic and functional diversity

Overall, for the abundances of the major groups of soil fauna, we found a significant and 442 positive effect of the interaction term between plant phylogenetic and functional diversity in 443 the respective subgroups that are particularly exposed to the plants due to their vertical 444 distribution (within earthworms and springtails), diet (within mites but not nematodes), or life 445 span (within nematodes). Only in earthworms did we find that exposure to plants (in epigeic 446 forms) did not increase the interaction between phylogenetic and trait distance. It may be that 447 earthworms can avoid exposure to vegetation by constructing niches as they construct tunnels 448 and may forage at the surface during the night. For the diversity of all three major groups of 449 450 soil fauna tested, we found a significant and positive effect of the interaction between plant phylogenetic diversity and the diversity of at least one functional plant trait. These positive 451 interaction effects are consistent with both hypotheses 1a and d in Figure 1: Plant phylogenetic 452

diversity reinforcing either complementarity of resource traits or dilution of preferred resource
traits. We will discuss below which of these hypotheses has more support.

Plant phylogenetic diversity reinforcing complementarity of resource traits (Figure 1a): a 455 positive interaction term *phylogenetic*functional-trait diversity* might reflect an increase of 456 resource complementarity due to increasing diversity of the functional trait with increasing 457 plant phylogenetic diversity (Eisenhauer 2012). High diversity of a given functional trait may 458 provide complementary resources for soil fauna only if represented by phylogenetically distant 459 species, and not by phylogenetically closely related species diverging only in a single or few 460 traits. Soil organisms may benefit from such complementarity of multiple resources (consistent 461 with Barbe et al. 2018). For instance, phylogenetically more diverse plant communities might 462 463 select for a higher proportion of generalist soil fauna that benefit more from resource complementarity due to a more diverse functional trait (for herbivores: Castagneyrol et al. 2014; 464 Grandez-Rios et al. 2015). Moreover, it might be impossible for soil fauna to profit from the 465 diverse values of a given trait if the differences in that trait are not integrated with differences 466 in other plant traits (Pigliucci 2003). Such phenotypic integration of traits seems to be the rule 467 in plants due to trade-offs or allometries, and different phylogenetic lineages of plants occupy 468 different positions along these axes of phenotypic integration (Pigliucci 2003). Soil fauna might 469 have evolved solutions to these phylogenetically conserved, integrated combinations of traits, 470 but not to disintegrated combinations of traits that recently diverged while other traits remained 471 phylogenetically conserved (Alonso and Herrera 2003 but see; Damián et al. 2020 on integrated 472 defenses). A diversity of values of one trait would hence not permit the establishment of a 473 diversity of resource specialists. This scenario of Figure 1a, however, is unlikely to be the major 474 explanation of the patterns we found. First, we hardly observed high trait diversity for low plant 475 phylogenetic diversity (contrary to Prinzing et al. 2008). Low plant phylogenetic diversity 476 hence usually cannot cancel out the effect of high diversity of a given trait. Second, the main 477

effects of phylogenetic and trait diversity were negative, contrary to predictions of resourcecomplementarity as presented in Figure 1a.

480

Plant phylogenetic diversity reinforcing dilution of preferred resource traits (Figure 1d): A 481 positive interaction term *phylogenetic*functional trait diversities* on soil fauna might also 482 reflect an increase of resource dilution due to trait diversity with increasing plant phylogenetic 483 diversity, or in other words, an increase of resource concentration due to trait uniformity with 484 increasing phylogenetic uniformity (Root 1973). Low diversity of a given trait may increase 485 the resource concentration for soil fauna only if represented by phylogenetically proximate 486 species, and not by phylogenetically distant species converging in only a single or few traits. 487 Again, soil fauna might have evolved solutions to integrated combinations of traits that have 488 been phylogenetically conserved, but not to disintegrated combinations of traits that recently 489 converged while others remained phylogenetically conserved (Alonso and Herrera 2003; 490 Damián et al. 2020). Low trait diversity of only one or few traits would not increase resource 491 concentration for soil fauna specialized on an integrated multi-trait plant phenotype 492 characteristic for a particular plant lineage. Phylogenetically diverse litters that are uniform in 493 SLA or LDMC might possibly be a mosaic of phylogenetically conserved and recently 494 converged traits, and only few soil-fauna species might be capable of using such a trait mosaic 495 (Pan et al. 2015b) if there has been little evolutionary time to adapt to it. This scenario of soil 496 fauna profiting from resource concentration (Root 1973) only under both trait and phylogenetic 497 uniformity is likely to be the major explanation for the patterns we found. First, we did observe 498 that low trait diversity could occur for both low and high plant phylogenetic diversity. High 499 plant phylogenetic diversity could hence potentially cancel out the effect of low diversity of a 500 given trait. Second, the main effects of phylogenetic and trait diversity were negative, consistent 501 with predictions of resource concentration as presented in Figure 1d. 502

503 Why uniformity of resources sometimes promotes consumer diversity and sometimes not.

The scenario of plant community uniformity increasing soil fauna through resource 504 concentration is consistent with parts of the literature (Barbe et al. 2018; Pan et al. 2015a) but 505 not with others (Milcu et al. 2013). Even within our own study, some results were inconsistent: 506 uniformity of a trait across phylogenetically uniform plant species did not always correspond 507 to increased soil fauna diversity. Inconsistency may result from the idiosyncratic responses of 508 different taxa of soil fauna to different traits of the plant community, and from reinforcement 509 of these idiosyncrasies by particular traits of soil fauna such as vertical distribution, diet, or life 510 span. Other factors like study system may come on top. Such effects would explain why low 511 diversity of a plant community does not always promote diversity of soil fauna or performance 512 of soil fauna (Ganault et al. 2021; Hooper et al. 2000; Wolters et al. 2000). 513

514

515 Why accounting for phylogenetic diversity advances our understanding of ecosystems.

Phylogenetic diversity has been related to ecosystem functioning by multiple authors (Cadotte 516 et al. 2008; Flynn et al. 2011; Narwani et al. 2013; Venail et al. 2015; Yguel et al. 2016), often 517 arguing that phylogenetic diversity might serve as a proxy for the diversity of functional traits 518 (see for critical discussion Cadotte et al. 2008; Gerhold et al. 2015; Srivastava et al. 2012). 519 These authors tend to find no relationships when applying measures of phylogenetic diversity 520 that are independent of species richness (like ours; Narwani et al. 2013; Venail et al. 2015; 521 Yguel et al. 2016). We here use the information on both trait diversity and phylogenetic 522 diversity of plants, to infer scenarios of phylogenetic trait lability or trait conservatism across 523 the species locally assembled into a community. We hence move from using phylogenetic 524 diversity as a proxy for trait diversity to phylogenetic diversity as a tool to interpret the 525 evolutionary origin of trait diversity (as suggested by Prinzing 2016). High functional diversity 526 may sometimes be of evolutionary recent origin due to local assembly of closely related species 527

that have diverged in trait states. Similarly, low functional diversity may be due to the assembly of distantly related species that have converged in trait states. We show that such low trait diversity of recent origin may be particularly disadvantageous for soil fauna and thereby likely also for soil food-webs and decomposition. We further develop this point below.

532

533 Do feedbacks between trait evolution and ecosystem processes exist?

Our results might also have implications for understanding eco-evolutionary feedbacks. Diverse 534 and abundant soil fauna have often been shown to improve litter decomposition (Heemsbergen 535 et al. 2004) and thereby potentially plant growth. The present study suggests that soil fauna 536 diversity and abundance may be low in a plant community in which key functional traits are 537 diverse but phylogenetic lineages are uniform (a community that is composed of close relatives 538 that have recently diverged in the respective traits). Equally, plant communities composed of 539 distant relatives that have converged in traits could be associated with low abundance and 540 diversity of important groups of soil fauna. It can be speculated that low abundance and 541 diversity of soil fauna then reduce litter decomposition rate. Reduced litter decomposition, in 542 turn, might be to the detriment of the plants that produced this litter (Hooper et al. 2000). This 543 544 (still highly speculative) reasoning suggests feedback between the recent macroevolution of plant traits, the ecological assembly of decomposers, the recycling of nutrients in ecosystems, 545 and the performance of plants: Recent phylogenetic lability of a trait has the potential of 546 reducing soil fauna, litter decomposition, and the performance of plants, hence feeding back 547 negatively on itself (Barbe et al. 2020). Such negative feedback might be particularly frequent 548 in disturbed habitat types given that they show a particularly strong pattern of phylogenetic 549 550 lability of traits (Prinzing et al. 2021). Our study hence contributes to exploring the interface between evolution and ecosystem functioning at an intermediate scale of "recent 551 macroevolution" (evolutionary lability of functional traits among species). This scale is so far 552

still little treated (but see Yguel et al. 2016) compared to now classical approaches relating
ecosystem functioning to overall macroevolution as represented by phylogenetic diversity
(Cadotte et al. 2009), or to microevolutionary local adaptations within species (Harmon et al.
2019).

557

558 <u>Conclusions</u>

Our results suggest that soil fauna only profits from resource concentration when both the 559 diversity of key plant functional traits and plant phylogenetic diversity are low. This is the case 560 in plant communities characterized by the co-occurrence of closely related plant species that 561 have conserved trait values, and not in plant communities consisting of distantly related plant 562 species that have converged in values of the key functional trait. Trait evolution across plant 563 lineages and the local assembly of these traits and lineages might drive the abundance and 564 diversity of soil fauna, which in turn control the recycling of plant litter and thereby potentially 565 influence the performance of the plants. 566

567

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575 Author Contribution Statement. FM performed statistical analyses and lead the writing, NR calculated functional trait parameters for the sites and contributed to MS writing, JFP 576 contributed to soil fauna identification and writing of the MS, GP was responsible for the 577 management of RMQS-BioDiv, DC lead the soil fauna data collection, NRC identified macro 578 arthropods, JC identified mites, CP identified springtails, CV identified nematodes, and AP was 579 580 responsible for the development of the concept of the paper, advised on statistical analyses and contributed greatly to the MS writing. All co-authors have read and approved the submitted 581 MS. 582

Data Availability Statement. We propose to make the metadata accessible as a supplementary file with metadata and correlation matrix.

586

587 588 **Tables**

589 Table 1. Relationships between soil fauna and phylogenetic and functional-trait diversity of plant communities (PhylDiv, FunTraitDiv) and their interactions. Soil fauna is the dependent 590 variable and is characterized by Simpson diversity (a) and abundance (b) of major soil fauna 591 groups, and abundances of sub-groups expected to be strongly or weakly exposed to plant 592 diversity due to spatial position (c, d), trophic position (e-f) or life span (g). The functional traits 593 are specific leaf area (SLA) and leaf dry matter content (LDMC). Relationships between 594 independent and dependent variables are quantified as t values (and p values in brackets). 595 Significant (p < 0.05) relationships are in bold, and marginally significant (0.05) are596 underlined. Phylogenetic diversity was calculated as Abu.mpd (abundance-weighted mean 597 pairwise phylogenetic distance). Covariates are the source of the plant community data 598 (VegData) and community-weighted mean of the respective functional trait (meanFunTrait), as 599 defined in Methods. The number of sites varied between soil fauna groups due to missing data 600 and the removal of outliers. 601

Functional trait	Soil fauna group	N sites	VegData	PhylDiv	meanFunTrait	FunTraitDiv	Phyl- Div*Fun- TraitDiv	\mathbb{R}^2	R ² adj
a) Abundance	e of major soil fau	na group	S						
SLA:	Mites	12	0.54 (0.61)	0.13 (0.90)	0.30 (0.78)	0.72 (0.50)	0.22 (0.83)	0.21	-0.44
	Springtails	15	0.10 (0.92)	-0.75 (0.47)	<u>-1.01 (0.09)</u>	-0.02 (0.98)	2.06 (0.07)	0.53	0.27
	Earthworms	19	2.75 (0.02)	-1.25 (0.23)	1.14 (0.27)	-1.53 (0.15)	0.57 (0.58)	0.60	0.44
	Nematodes	19	-1.58 (0.14)	0.84 (0.42)	0.85 (0.41)	1.60 (0.13)	0.33 (0.74)	0.35	0.10
LDMC:	Mites	12	0.83 (0.44)	1.26 (0.25)	1.04 (0.34)	-0.83 (0.44)	1.60 (0.16)	0.35	-0.18
	Springtails	15	0.89 (0.40)	1.17 (0.27)	-1.03 (0.33)	-1.76 (0.11)	2.15 (0.06)	0.50	0.21
	Earthworms	19	-2.37 (0.03)	-0.67 (0.52)	-0.28 (0.78)	-0.70 (0.49)	0.73 (0.48)	0.54	0.36
	Nematodes	19	-1.37 (0.19)	0.05 (0.96)	0.84 (0.42)	1.35 (0.20)	0.94 (0.37)	0.34	0.09
Analyses sep	arated for groups e	expected	to be strongly or	weakly exposed to	plant diversity due t	o spatial (c, d) or	trophic (e-f) posit	ion or life sp	an (g)
b) Abundance	e per earthworm g	roup							
SLA	Epigeic	19	0.82 (0.43)	0.2 (0.85)	-0.59 (0.56)	-1.42 (0.18)	0.88 (0.40)	0.39	0.15
	Endogeic	18	2.22 (0.04)	-1.91 (0.29)	0.79 (0.44)	-0.49 (0.63)	0.39 (0.70)	0.41	0.18
LDMC	Epigeic	17	-0.30 (0.77)	0.63 (0.54)	0.27 (0.79)	-2.45 (0.03)	1.33 (0.21)	0.45	0.23
	Endogeic	19	- <u>2.00 (0.07)</u>	-0.62 (0.55)	0.02 (0.98)	-0.10 (0.92)	0.52 (0.61)	0.39	0.15
c) Abundance	e per springtail gro	oup							
SLA:	Hemiedaphic	14	0.72 (0.49)	0.69 (0.51)	1.01 (0.34)	-0.71 (0.50)	2.45 (0.04)	0.53	0.24
	Eudaphic	14	0.47 (0.65)	-0.87 (0.41)	-0.28 (0.79)	0.21 (0.84)	0.23 (0.82)	0.17	-0.35
LDMC:	Hemiedaphic	14	2.02 (0.08)	2.21 (0.06)	-1.36 (0.21)	-2.01 (0.08)	2.45 (0.04)	0.56	0.29
	Eudaphic	14	0.18 (0.86)	-1.08 (0.59)	0.06 (0.95)	0.52 (0.62)	-0.58 (0.58)	0.20	-0.30
d) Abundance	e per mite group								
SLA:	Actenida	13	0.77 (0.47)	1.38 (0.21)	-0.92(0.39)	1.08 (0.32)	2.45 (0.04)	0.63	0.36
	Gamasida	15	-1.51 (0.16)	-0.65 (0.53)	1.04 (0.33)	0.33 (0.75)	0.62 (0.55)	0.34	-0.02
LDMC:	Actenida	13	1.34 (0.22)	2.07 (0.08)	0.30 (0.77)	-0.64 (0.54)	2.05 (0.08)	0.48	0.10
	Gamasida	15	-0.66 (0.52)	0.69 (0.51)	1.38 (0.20)	-0.97 (0.36)	<u>1.92 (0.09)</u>	0.48	0.20
e) Abundance	e of nematodes per	r feeding	guild						
SLA:	Phytopahages	19	2.20 (0.05)	-0.90 (0.39)	0.80 (0.44)	1.87 (0.08)	-0.13 (0.89)	0.39	0.16
	Carnivores	19	1.23 (0.24)	2.53 (0.03)	1.39 (0.19)	0.26 (0.80)	2.33 (0.04)	0.59	0.43
LDMC:	Phytopahages	19	-1.97 (0.07)	-0.34 (0.74)	0.78 (0.45)	1.60 (0.13)	0.28 (0.78)	0.33	0.06
	Carnivores	19	0.90 (0.39)	1.59 (0.14)	0.96 (0.35)	1.53 (0.15)	0.95 (0.36)	0.54	0.36
f) Nematode	Structure Index ac	counting	for abundances	of ling lived vs sho	ort-lived species				
SLA:		19	-1.19 (0.25)	2.56 (0.02)	0.28 (0.78)	0.74(0.47)	3.04 (0.01)	0.53	0.35
LDMC:		19	-0.82 (0.43)	1.53 (0.15)	0.14 (0.89)	1.14 (0.28)	0.91 (0.38)	0.32	0.06
g) Simpson d	iversity								
SLA:	Earthworms	19	1.43 (0.18)	-0.39 (0.71)	0.66 (0.52)	-0.37 (0.72)	0.96 (0.35)	0.24	-0.05
	Springtails	13	0.11 (0.92)	1.68 (0.14)	-0.67 (0.52)	-0.02 (0.99)	2.64 (0.03)	0.56	0.25
	Nematodes	18	6.73 (<0.01)	4.68 (<0.01)	0.36 (0.72)	-3.21 (0.01)	3.65 (<0.01)	0.86	0.80
LDMC:	Earthworms	19	-1.00 (0.34)	0.81 (0.43)	0.07 (0.94)	-0.72 (0.48)	1.90 (0.08)	0.35	0.10
	Springtails	13	0.81 (0.44)	2.63 (0.03)	-0.75 (0.48)	-0.25 (0.81)	2.43 (0.05)	0.52	0.18
	Nematodes	18	3.84 (<0.01)	1 65 (0 13)	0.82 (0.43)	-0.61 (0.55)	0.59 (0.56)	0.63	0.48

Figure 1. How the phylogenetic diversity of plants and the diversity of a functional plant trait 606 may interact to determine abundance of associated animals. Abundance of animals is favoured 607 by the diversity of plant resources through complementarity among litters (a, b), or reduced 608 through dilution of preferred resources for any individual animal species (c, d). High or low 609 diversity for a given functional trait X (X-axis) corresponds to high or low phylogenetic 610 diversity if X locally shows phylogenetic signal (thin straight line). However, if among the 611 locally represented species the trait X was evolutionary labile (grey arrows), we may expect 612 locally high diversity of X also through past divergence of close relatives (dotted lines in a 613 and c), or locally low diversity of X also through past convergence among distant relatives 614 (thick straight lines in b, d). High diversity of X among otherwise similar, closely related plant 615 species may imply less resource complementarity or dilution than high diversity of X among 616 distantly related species (inversely for low diversity of X through convergence among 617 distantly related species). Div X, Div P, and DivX:DivP represent expected effects of diversity 618 of functional litter trait X, phylogenetic diversity, and their interaction on faunal diversity, 619 respectively. The interaction term hence describes how the evolutionary lability of an 620 individual plant trait changes the relationship between the diversity of that trait and the 621 diversity of associated animals. Similar relationships may be posited for animal abundance. 622 623

<u>Figure 2.</u> Pearson's correlations between soil parameters, vegetation parameters, and soil
fauna parameters. Vegetation factors were obtained using PCA analysis. Abu.mntd =
abundance-weighted mean nearest taxon distance. Abu.mpd = Abundance-weighted mean
phylogenetic distance, referred to as phylogenetic diversity in the results, abbreviated as
PhylDiv in Table 1. Smaller p-values are depicted with larger circles. Abundances were logtransformed before analysis. Details can be found in Supplement S3.

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Figure 3. Relationships between diversity of plant functional traits (Y-axis) and plant phylogenetic diversity (X-axis) in permanent meadows in Brittany, France. Regression specific leaf area : t = 0.610, p = 0.551, N = 18, $R^2 = 0.022$, Regression leaf dry matter content : t = 0.596, p = 0.560, N = 18, $R^2 = 0.022$, excluding one outlier with extreme phylogenetic diversity.

635

Figure 4. Relationships between the abundance of major groups of soil fauna (Y-axis) and the diversity of specific leaf area (X-axis) for plant communities with below and above median phylogenetic diversity (< / > -0.8), illustrating interactions terms listed in Table 1b. The 639 interaction term between diversities is significant in springtails, as indicated by arrow and p-640 value in figure.

Figure 5. Relationships between the abundance of sub-groups of soil fauna (Y-axis) and the 641 diversity of specific leaf area (X-axis) for plant communities with below and above median 642 phylogenetic diversity (< / > -0.8). Sub-groups are strongly (left column) exposed or weakly 643 (right) exposed to vegetation, and hence likely or unlikely to respond to plant community 644 diversity. Exposure is due to spatial position (epigeic vs endogeic earthworms, hemiedaphic vs 645 eudaphic springtails), or diet (plant-feeding acteneid vs carnivorous gamasid mites, 646 phytophagous vs carnivorous nematodes). Figures illustrate interaction terms as listed in Table 647 1c, d, and e, respectively, significant interaction terms are indicated by arrow and p-value in 648 figure. 649

<u>Figure 6.</u> Relationships between the diversity of soil fauna (Y-axis) and the diversity of specific
leaf area (X-axis) for plant communities with below and above median phylogenetic diversity,
illustrating interaction terms listed in Table 1g. Significant interaction terms are indicated by
arrow and p-value in figure.

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