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

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38 phylogenetic diversity, resource concentration, resource dilution

39 **Abstract**

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

59 **Introduction**

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

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

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

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

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

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

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

134 diversity of local plant communities should be accompanied by increased diversity in after-life
135 traits of litter. Examples of specialization in soil biota on particular plant lineages include
136 springtails becoming more abundant with the establishment of gymnosperms (Luque et al.
137 2011), soil-mediated interactions being strongest among closely related plant species (Anacker
138 et al. 2014), fungus gnats being moderately specialized on fungus lineages (Põldmaa et al.
139 2016), and particular soil microbes associating with particular plant species (Leff et al. 2018).

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

153 Overall, in local plant communities that are diverse, a species of generalist decomposer might
154 do well because it benefits from resource complementarity (Eisenhauer 2012), while a species
155 of specialist decomposer might suffer from resource dilution (Root 1973). Therefore, both low
156 and high phylogenetic or functional diversity of a local plant community might increase the
157 abundance and diversity of soil fauna, depending on its degree of dietary specialization. In
158 addition, high functional or phylogenetic diversity may support more diverse communities of

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

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

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

187

188 **Methods**

189 *Description of local plant communities*

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

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

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

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

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

247

248 *Sampling and determination of soil fauna*

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

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

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

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

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

291

292 *Data analysis*

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

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

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

336

337 **Results**

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

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

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

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

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

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

389

390 **Discussion**

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

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

408

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

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

440

441 Explaining interaction terms between plant phylogenetic and functional diversity

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

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

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

478 effects of phylogenetic and trait diversity were negative, contrary to predictions of resource
479 complementarity as presented in Figure 1a.

480

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

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

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

514

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

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

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

532

533 Do feedbacks between trait evolution and ecosystem processes exist?

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

553 still little treated (but see Yguel et al. 2016) compared to now classical approaches relating
554 ecosystem functioning to overall macroevolution as represented by phylogenetic diversity
555 (Cadotte et al. 2009), or to microevolutionary local adaptations within species (Harmon et al.
556 2019).

557

558 Conclusions

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

567

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574

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

583

584 **Data Availability Statement.** We propose to make the metadata accessible as a supplement-
585 tary file with metadata and correlation matrix.

586

587

588 **Tables**

589 Table 1. Relationships between soil fauna and phylogenetic and functional-trait diversity of
590 plant communities (PhylDiv, FunTraitDiv) and their interactions. Soil fauna is the dependent
591 variable and is characterized by Simpson diversity (a) and abundance (b) of major soil fauna
592 groups, and abundances of sub-groups expected to be strongly or weakly exposed to plant
593 diversity due to spatial position (c, d), trophic position (e-f) or life span (g). The functional traits
594 are specific leaf area (SLA) and leaf dry matter content (LDMC). Relationships between
595 independent and dependent variables are quantified as t values (and p values in brackets).
596 Significant ($p < 0.05$) relationships are in bold, and marginally significant ($0.05 \leq p < 0.1$) are
597 underlined. Phylogenetic diversity was calculated as Abu.mpd (abundance-weighted mean
598 pairwise phylogenetic distance). Covariates are the source of the plant community data
599 (VegData) and community-weighted mean of the respective functional trait (meanFunTrait), as
600 defined in Methods. The number of sites varied between soil fauna groups due to missing data
601 and the removal of outliers.

602

Functional trait	Soil fauna group	N sites	VegData	PhylDiv	meanFunTrait	FunTraitDiv	Phyl-Div*Fun-TraitDiv	R ²	R ² adj
a) Abundance of major soil fauna groups									
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)	<u>2.06 (0.07)</u>	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)	<u>2.15 (0.06)</u>	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 separated for groups expected to be strongly or weakly exposed to plant diversity due to spatial (c, d) or trophic (e-f) position or life span (g)									
b) Abundance per earthworm group									
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 per springtail group									
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	<u>2.02 (0.08)</u>	<u>2.21 (0.06)</u>	-1.36 (0.21)	<u>-2.01 (0.08)</u>	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 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)	<u>2.07 (0.08)</u>	0.30 (0.77)	-0.64 (0.54)	<u>2.05 (0.08)</u>	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 of nematodes per feeding guild									
SLA:	Phytophages	19	2.20 (0.05)	-0.90 (0.39)	0.80 (0.44)	<u>1.87 (0.08)</u>	-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:	Phytophages	19	<u>-1.97 (0.07)</u>	-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 accounting for abundances of long lived vs short-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 diversity									
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)	<u>0.81 (0.43)</u>	0.07 (0.94)	-0.72 (0.48)	<u>1.90 (0.08)</u>	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

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

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

630
631 Figure 3. Relationships between diversity of plant functional traits (Y-axis) and plant
632 phylogenetic diversity (X-axis) in permanent meadows in Brittany, France. Regression specific
633 leaf area : $t = 0.610$, $p = 0.551$, $N = 18$, $R^2 = 0.022$, Regression leaf dry matter content : $t =$
634 0.596 , $p = 0.560$, $N = 18$, $R^2 = 0.022$, excluding one outlier with extreme phylogenetic diversity.

635

636 Figure 4. Relationships between the abundance of major groups of soil fauna (Y-axis) and the
637 diversity of specific leaf area (X-axis) for plant communities with below and above median
638 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.

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

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

654

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946

Figure 1

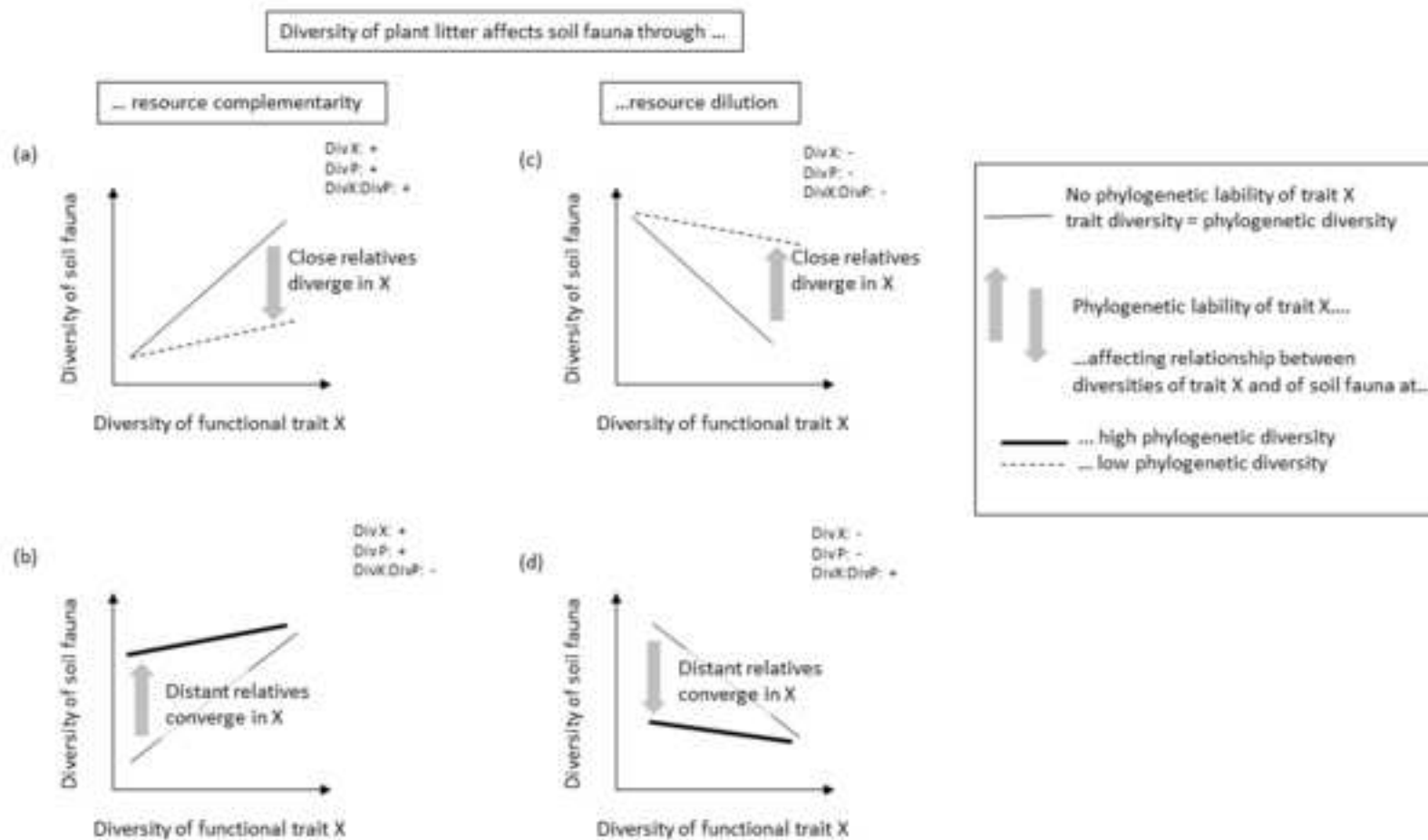


Figure 2

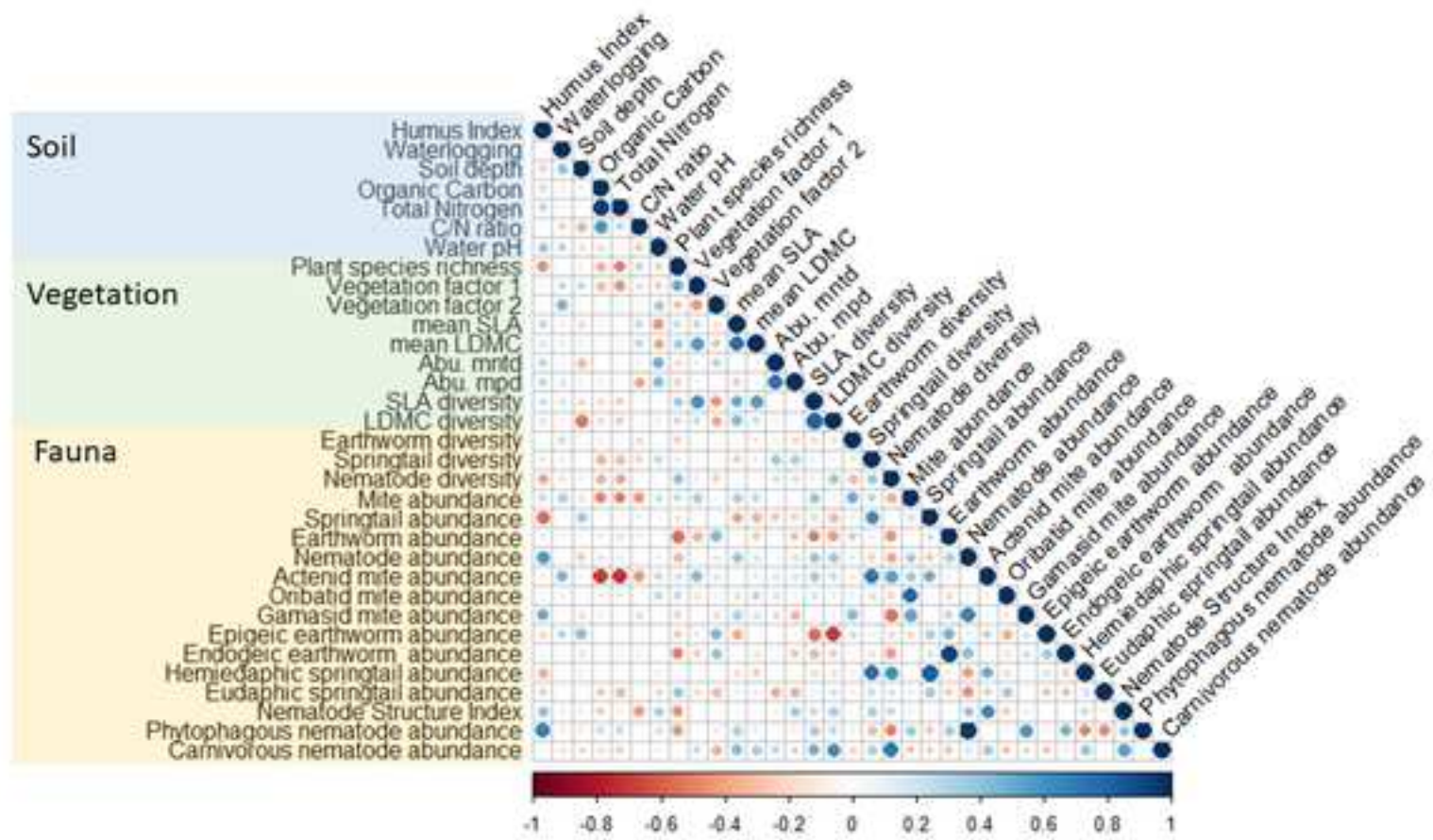


Figure 3

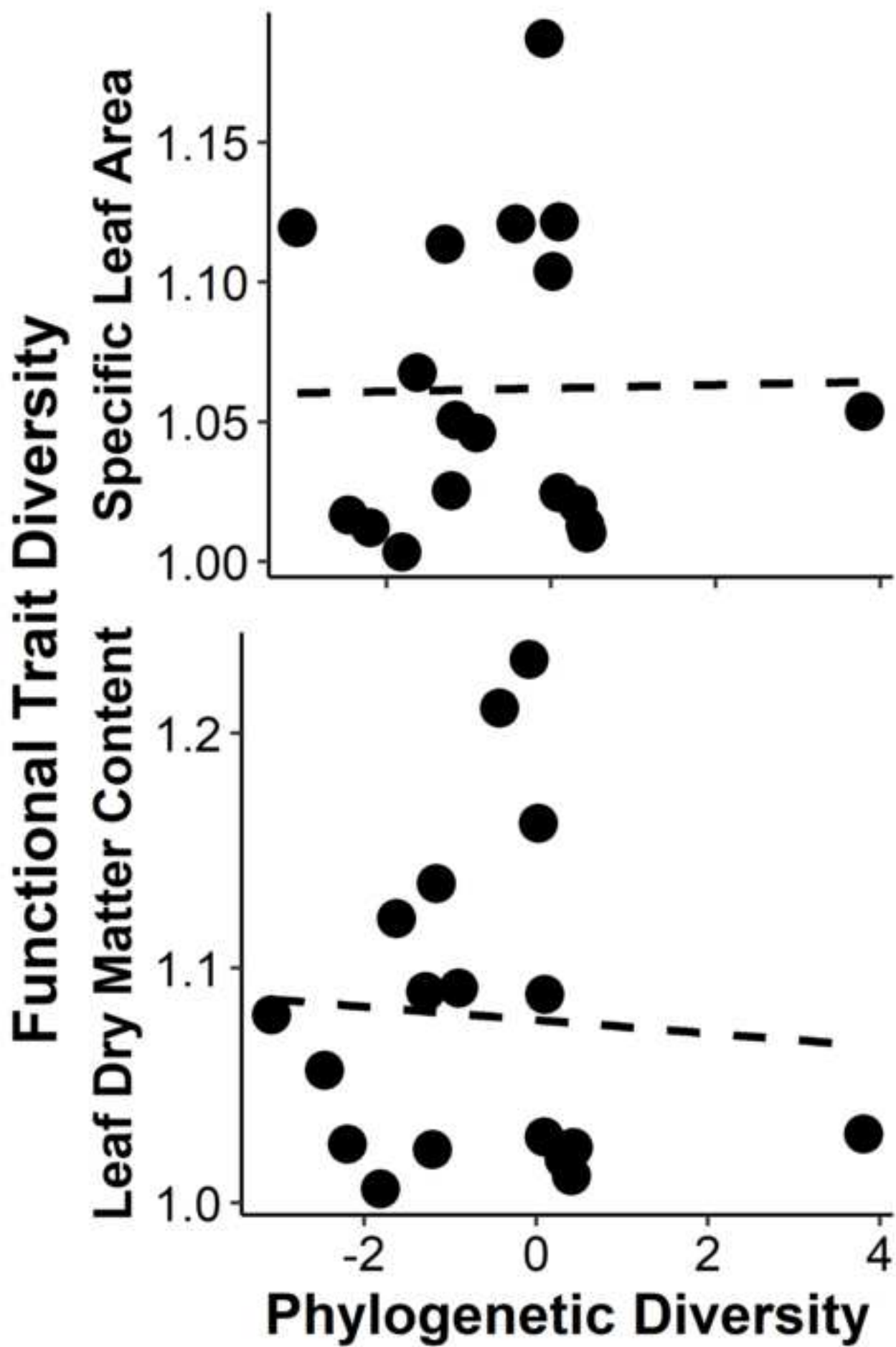


Figure 4

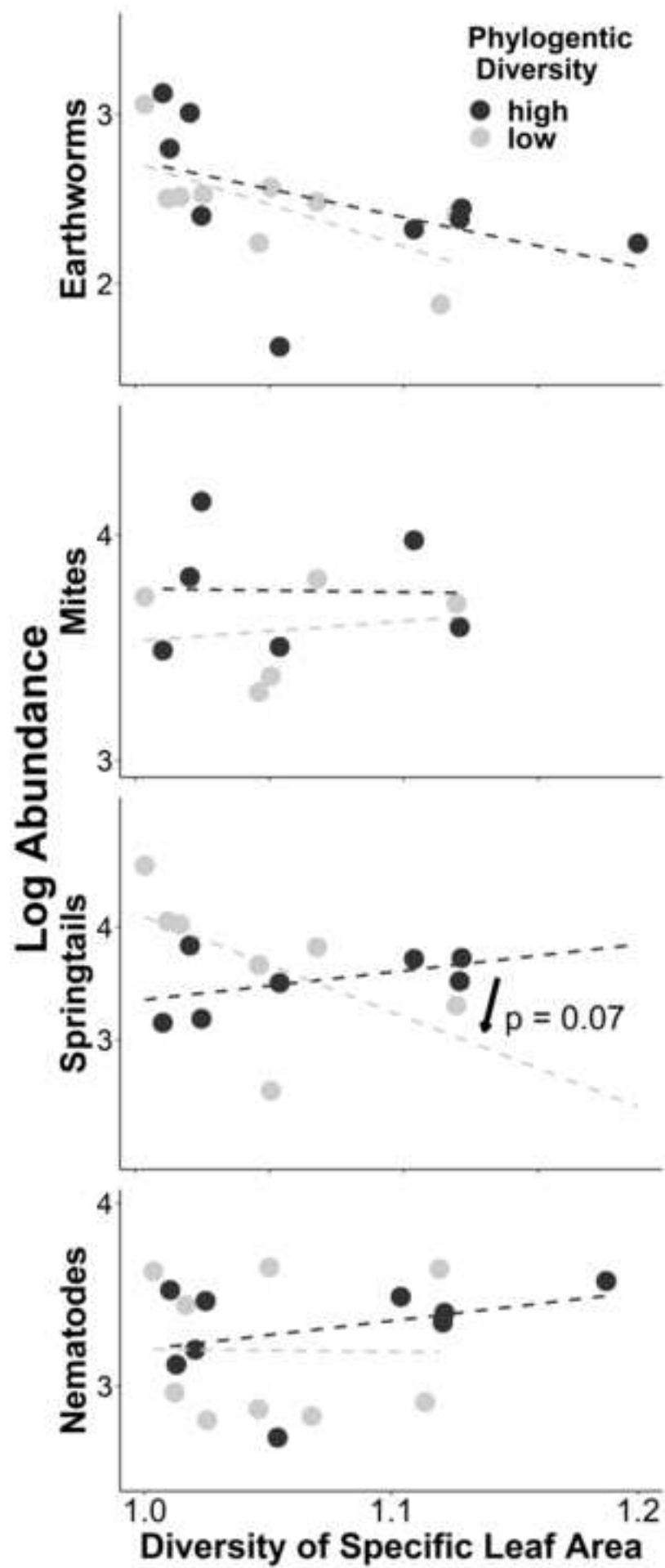


Figure 5

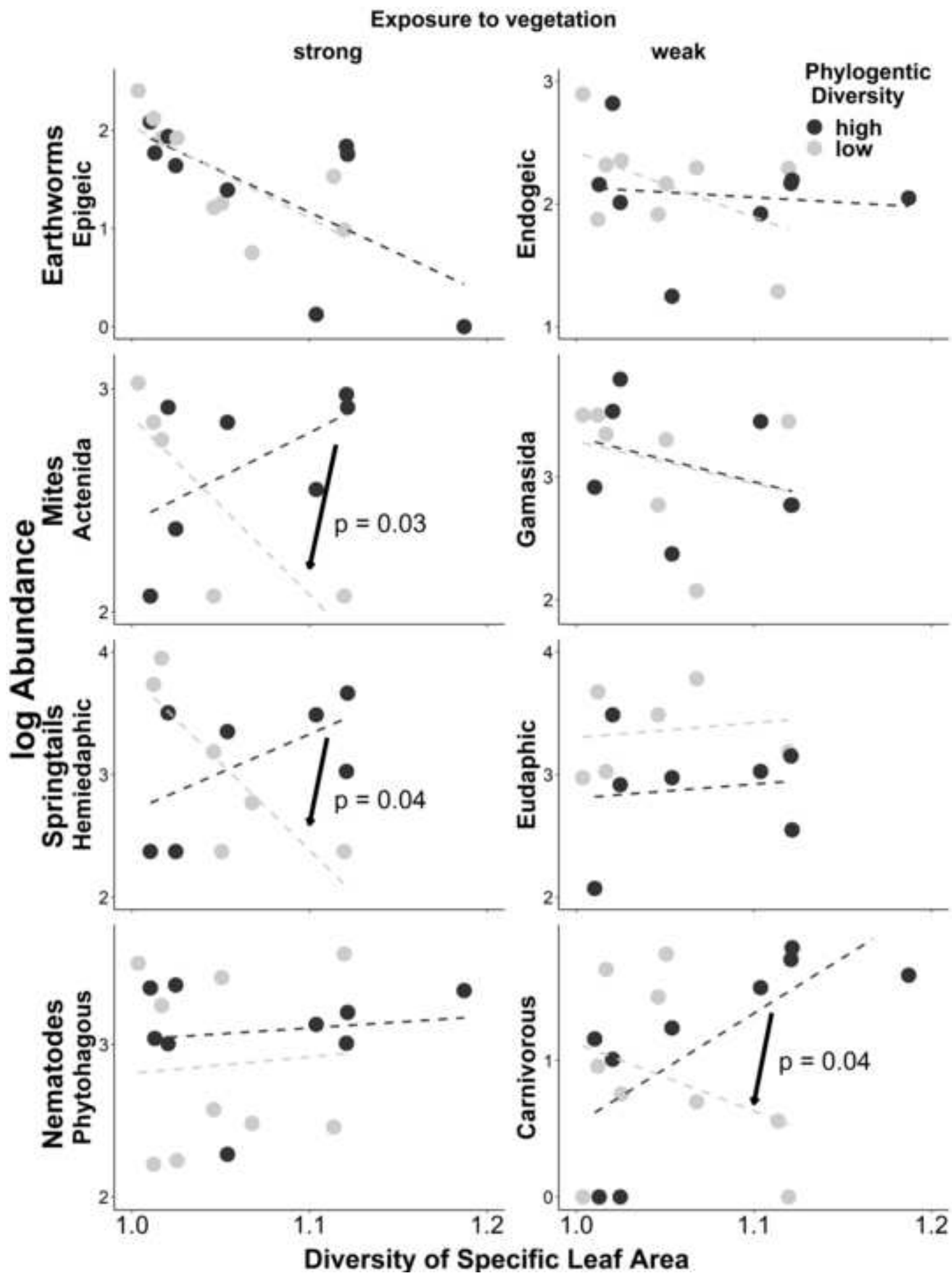


Figure 6

