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► To cite this version:

Pierre Ganault, Johanne Nahmani, Stephan Hättenschwiler, Lauren Michelle Gillespie, Jean-François David, et al.. Relative importance of tree species richness, tree functional type, and microenvironment for soil macrofauna communities in European forests. *Oecologia*, 2021, 196 (2), pp.455-468. 10.1007/s00442-021-04931-w . hal-03280113

HAL Id: hal-03280113

<https://hal.science/hal-03280113v1>

Submitted on 7 Jul 2021

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2 **Relative importance of tree species richness, tree functional type,**
3 **and microenvironment for soil macrofauna communities in European**
4 **forests**

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8 Received: 19 June 2020 / Accepted: 26 April 2021

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10 **Abstract**

11 Soil fauna communities are major drivers of many forest ecosystem processes. Tree species diversity and composition shape
12 soil fauna communities, but their relationships are poorly understood, notably whether or not soil fauna diversity depends on **AQ1**
13 tree species diversity. Here, we characterized soil macrofauna communities from forests composed of either one or three tree
14 species, located in four different climate zones and growing on different soil types. Using multivariate analysis and model
15 averaging we investigated the relative importance of tree species richness, tree functional type (deciduous vs. evergreen), litter
16 quality, microhabitat and microclimatic characteristics as drivers of soil macrofauna community composition and structure.
17 We found that macrofauna communities in mixed forest stands were represented by a higher number of broad taxonomic **AQ2**
18 groups that were more diverse and more evenly represented. We also observed a switch from earthworm-dominated to
19 predator-dominated communities with increasing evergreen proportion in forest stands, which we interpreted as a result of a
20 lower litter quality and a higher forest floor mass. Finally, canopy openness was positively related to detritivore abundance
21 and biomass, leading to higher predator species richness and diversity probably through trophic cascade effects. Interestingly,
22 considering different levels of taxonomic resolution in the analyses highlighted different facets of macrofauna response to **AQ3**
23 tree species richness, likely a result of both different ecological niche range and methodological constraints. Overall, our
24 study supports the positive effects of tree species richness on macrofauna diversity and abundance through multiple changes
25 in resource quality and availability, microhabitat, and microclimate modifications.

26 **Keywords** Community ecology · Forest ecosystems · Biodiversity-ecosystem functioning · Aboveground-belowground
27 linkages

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28 **Introduction**

29 Forests are a major type of ecosystem in Europe, covering
30 42% of land surface (Paivinen et al. 2001) and provid-
31 ing a multitude of key ecosystem services, such as timber
32 production, watershed protection and carbon sequestra-
33 tion (Scherer-Lorenzen et al. 2005). These services depend
34 strongly on tree taxonomic richness and on the proportion
35 of different functional type (e.g., evergreen vs. decidu-
36 ous) in forest stands (Gamfeldt et al. 2013). In addition,
37 tree species richness may determine the abundance and
38 diversity of other groups of organisms (Ampoorter, et al.
39 2019) that could affect ecosystem processes. Especially,
40 trees shape communities of soil invertebrates, which are
41 key regulators of soil functioning and primary productiv-
42 ity (Wardle 2004; Wall et al. 2012). However, the direct
43 and indirect mechanisms underlying soil invertebrate
44 responses to tree species diversity and composition remain
45 poorly understood, even in temperate forest ecosystems
46 (Korboulewsky et al. 2016).

47 Trees can influence soil fauna through the provision
48 of energy and matter via living and dead plant products
49 such as leaf and root litter, dead wood, and rhizodepo-
50 sition. Many soil organisms such as macrodetritivores
51 (earthworms, millipedes, woodlice) feed directly on plant
52 debris (Lavelle and Spain 2001), imposing stoichiometric
53 constraints with lower and narrower carbon to nutrient
54 ratios in animal biomass than that of their feeding resource
55 (Sterner and Elser 2002). Resource nutrient concentrations
56 are therefore particularly important as they determine lit-
57 ter palatability for macrodetritivores, and have important
58 consequences on the structure of their communities, nota-
59 bly on their biomasses (Ott et al. 2014). In mixed forest
60 stands, litter may be of overall higher quality relative to
61 monospecific stands when tree species with high quality
62 litter may compensate for those with low nutrient con-
63 centrations or high contents in recalcitrant compounds
64 (e.g., polyphenols or lignin; Korboulewsky et al. 2016).
65 Another pattern often highlighted in the literature is the
66 strong effect of evergreen trees on soil fauna communities
67 (Reich et al. 2005), which can be related to the low lit-
68 ter quality of most evergreen species. Additionally, other
69 evergreen traits such as leaf life span and the phenology of
70 leaf senescence together determine tree canopy properties
71 which affect microhabitats and microclimate conditions at
72 soil surface (Monk 1966).

73 Beyond litter quality and its consequences for the het-
74 erotrophic soil food web, different tree species also vary
75 in a number of physical characteristics that may influ-
76 ence soil fauna communities. For instance, differences in
77 leaf size, leaf shape, and amount of litterfall (including
78 deadwood), determine the total volume of habitats, and

79 their spatial organization for both detritivore and predator
80 species (Aubert et al. 2006, Kaspari and Yanoviak 2009).
81 The structural complexity of litter layers, and the resulting
82 diversity of microhabitats for the soil fauna, also vary from
83 one tree species to another and are likely higher in mixed
84 than pure stands (Hättenschwiler et al. 2005). This may
85 contribute to an increase in abundance, biomass, diversity,
86 and evenness of soil invertebrates in mixed when com-
87 pared to monospecific forest stands (Hansen and Coleman
88 1998; Perry and Herms 2016), especially when the mixed
89 stands include deciduous broadleaved trees among ever-
90 green conifers (Kaneko and Salamanca 1999).

91 The influence of the previously mentioned litter prop-
92 erties (nutrient content, shape, litter layer depth) on soil
93 and forest floor properties and on invertebrate communi-
94 ties also varies with tree canopy richness and composition
95 (Augusto et al. 2002; Ponge 2003). Tree canopy openness
96 is an important but overlooked forest stand characteristic
97 that has important effects on forest floor conditions. By
98 modulating light availability at the soil surface, canopy
99 openness may influence soil communities by altering forest
100 floor microclimate and understory vegetation (Prescott and
101 Vesterdal 2013; Henneron et al. 2015; Mueller et al. 2016).
102 This again can differ depending on tree species richness that
103 can affect canopy openness and litter production through
104 increased canopy packing, as was reported for different
105 European forests (Jucker et al. 2015). In addition, evergreen
106 tree species distinctively affect microclimatic conditions, in
107 particular through a permanent canopy cover, and high leaf
108 area index (LAI) all year round which leads to higher rainfall
109 interception and evaporation and thus drier soils (Augusto
110 et al. 2015).

111 Characterizing soil fauna responses to the diversity and
112 composition of the standing vegetation is thus complex
113 and often made even more difficult by taxonomic impedi-
114 ments and our lack of knowledge of certain taxa. Indeed,
115 it is difficult if not impossible to obtain rapid and reliable
116 taxonomic assignments at a species level for most of the
117 soil biota (Decaëns 2010). A classic strategy to avoid this
118 problem in soil macrofauna studies is to target assignments
119 to higher taxonomic ranks, which allows the whole com-
120 munity to be considered without prior selection of target
121 taxa (Williams and Gaston 1994; Andersen 1995). Another
122 option is to make species-level identifications possible by
123 restricting the study to a small number of taxa, for which
124 taxonomic expertise is available, that are further assumed to
125 be representative of the whole community or of a particu-
126 lar trophic group thereof. The implication of each of these
127 approaches for our ability to describe community patterns
128 reliably, and the importance of the level of taxonomic reso-
129 lution they imply, has never been formally addressed with
130 regard to soil fauna. However, it is probable that some of
131 these patterns (e.g., diversity—area, or diversity—available

energy relationships) may vary in their shape depending on the fundamental taxonomic units of the study, which could consequently affect observed community responses to environmental gradients (Williams and Gaston 1994; Kaspari 2001; Storch and Šizling 2008).

In this study, we described soil macrofauna communities in forest plots composed of either a single dominant tree species or three co-dominant tree species in four different pedoclimatic zones ranging from boreal to Mediterranean. These plots were part of an existing network of natural forest plots with different tree species richness and composition across Europe (Baeten et al. 2013). We tested three complementary hypotheses. First (H1) higher tree richness in forest stand will promote soil macrofauna richness, diversity, evenness, abundance, and biomass, likely by increasing the probability of including at least one tree species that significantly improve life conditions for invertebrates (e.g., by producing a high quality litter, having a denser canopy that limits microclimatic variations, or promoting more diversified microhabitats in the litter layer). Alternatively, (H2) increasing the proportion of evergreen species will negatively affect detritivore assemblages due to their low-quality litter and soil-acidification effect, but may favor predator organisms by the production of a thicker litter layer and the consecutive provision of more microhabitats. Combined, these expected effects will result in changes in the whole macrofauna community composition. Finally, because of the tighter trophic link between litter characteristics and detritivores species (Scherber et al. 2010; Beugnon et al. 2019), we expect that (H3) tree species richness and composition will induce a stronger response in detritivore than in predator communities. These three hypotheses were tested at different levels of taxonomic resolution to assess the response of the whole macrofauna community and of specific groups with narrower ecological niche.

Material and methods

Study sites and tree stand composition

The study was carried out within the framework of the Soil-ForEUROPE project in four forest sites selected to represent four major European forest types along a broad climatic gradient in Europe: thermophilous deciduous forests (Colline Metallifere, Italy), mountainous deciduous forests (Râșca, Romania), temperate mixed coniferous and broadleaf forests (Bialowieza, Poland), and boreal forests (North Karelia, Finland). The sampled plots are part of the FunDivEUROPE exploratory platform (Baeten et al. 2013) excluding within site variation in climate, soil and land use history between plots and specifically designed to disentangle the species diversity and identity effect in the biodiversity—ecosystem

functioning relationship (Nadrowski et al. 2010). In each site, replicated forest plots of 30×30 m were selected to represent either monospecific stands (34 plots) or 3 species mixtures (30 plots), further referred to as pure and mixed stands, respectively. Selected tree species (i.e., target species) are 13 locally dominant and representative tree species, including evergreen conifers and evergreen or deciduous broadleaved trees (Table 1). These plots were selected in 2012 during the FunDivEUROPE project and relative basal area of tree species was re-estimated in 2018 for this study. The relative proportion of tree species was based on their relative basal area, and non-targeted species basal area in the plot was kept below 5%. In each plot we selected three subplots based on tree triplets forming a triangle of three individual trees with a minimal diameter at breast height of 5 cm, composed of either the same target species in the pure stands or the three target tree species in the mixed stands (Fig. S1).

Invertebrates sampling and community descriptors

Sampling was conducted in 2017 during the phenological spring at each of the four sites. In each plot, soil macrofauna was sampled by excavating one soil block of 25×25×10 cm within each tree triplet (i.e., three soil blocks per plot). Invertebrates were hand sorted in the field, and immediately fixed and preserved in 70% ethanol. They were further assigned to broad taxonomic groups (usually orders), with additional consideration of trophic position or ecological categories when relevant. This resulted in 16 groups: Araneae, predatory Coleoptera (Carabidae adults and larvae, Staphylinidae), Opilionidae, Dermaptera, Chilopoda, Blattodea, rhizophagous Coleoptera (larvae of Melolonthinae, Curculionidae, Elateridae), coprophagous Coleoptera (Geotrupinae), endogeic, epigeic, and anecic Lumbricidae, Diplopoda, Isopoda, Diptera larvae, Gastropoda, and Lepidoptera larvae. Species level identifications were done for all Lumbricidae, Isopoda, Diplopoda, Chilopoda, and Araneae specimens. For the few individuals for which this was not possible, genus or family levels were kept for the analysis; as this only concerned a small fraction of specimens, these higher rank taxonomic identifications were treated without distinguishing them from species-level identifications. All invertebrates were counted per broad group or species and weighed individually to the nearest 0.01 mg after gently drying them with a paper towel. The abundance and biomass of the 16 different groups is given in Table S1. We then organized the data into three different matrices: one with the numbers of individuals per plot for each broad group, further referred to as “*all macrofauna*”, and two with the numbers of individuals per plot and per species (or finest level achieved) for the detritivore and predator groups previously mentioned,

Table 1 Description of the four sample sites, including the tree species pool, and site-specific sampling design

	Finland	Poland	Romania	Italy
Site description				
Latitude, longitude (°)	62.9, 29.9	52.8, 23.9	47.3, 26.0	43.2, 11.2
Area ^a (km ²)	1447	346	4.26	216
Altitude (m)	139.4±36.6	165.7±12.6	891.8±96.4	405.8±60.5
Date of sampling	2017/06/12–16	2017/05/05–10	2017/05/22–28	2017/04/10–16
MAT (°C)	2.0±0.3	6.9±0.1	5.5±0.5	13.4±0.3
MAP (mm)	632±6	597±4	692±25	738±43
Soil type ^{II}	Podzol	Cambisol/Luvisol	Eutric Cambisol	Cambisol
Sand (%) ^I	48.2±6.2	65.5±7.5	12.9±9.4	17.2±6.4
Silt (%) ^I	46.6±5.6	28.7±6.3	59.6±4.9	64.7±4.9
Clay (%) ^I	5.1±0.8	5.8±1.6	27.4±6.1	18.1±5.4
C (mg g ⁻¹ dry soil) ^{II}	37.8±11.5	28.4±5.3	49.2±16	50.4±13.4
N (mg g ⁻¹ dry soil) ^{II}	1.7±0.6	1.7±0.2	3.5±1	2.6±0.9
pH ^{II}	3.9±0.3	3.8±0.3	4.6±0.7	4.6±1.1
Bulk density (g cm ⁻³) ^{II}	1.03±0.09	1.02±0.07	0.93±0.06	0.88±0.07
Number of mono-specific plots	6	6	8	10
Number of mixed plots	3	14	8	9
Tree species pool				
(1) <i>Abies alba</i>			×	
(1) <i>Picea abies</i>	×	×	×	
(1) <i>Pinus sylvestris</i>	×	×		
(2) <i>Quercus ilex</i>				×
(3) <i>Acer pseudoplatanus</i>			×	
(3) <i>Betula pendula/pubescens</i>	×	×		
(3) <i>Carpinus betulus</i>		×		
(3) <i>Castanea sativa</i>				×
(3) <i>Fagus sylvatica</i>			×	
(3) <i>Ostrya carpinifolia</i>				×
(3) <i>Quercus petraea</i>				×
(3) <i>Quercus robur</i>		×		
(3) <i>Quercus cerris</i>				×

Soil measurements are from the first 10 cm of mineral soil. (1) Evergreen needle-leaf, (2) evergreen broad-leaf, (3) deciduous broadleaf

MAT mean annual temperature, MAP mean annual precipitation, from WorldClim

^aArea was obtained from the polygon area joining most distant plots within each country, using Google Earth

^IData from SoilForEUROPE project

^{II}Data from FunDivEUROPE project

230 further referred to as “*detrivore assemblage*” and “*predator*
231 *assemblage*”, respectively (taxa list in Table S2).

232 From these three matrices, we calculated several commu-
233 nity descriptors: taxonomic richness (S) Pielou’s evenness (J ;
234 Pielou 1966), and Hill _{$q=1$} ’ diversity (D_1). D_1 was obtained with
235 the formula:

$$236 D_q = \left(\sum_{i=1}^S p_i^q \right)^{\frac{1}{1-q}} \quad (1)$$

237

238 where S is the total number of taxa (i.e., fundamental taxo-
239 nomic units: broad groups or species depending on the
240 matrix), p the proportion of taxa i and q the “order” of the
241 diversity. The order q determines the diversity index sen-
242 sitivity to common and rare taxa with values of q below
243 or above one giving diversities highly sensitive to rare or
244 common taxa, respectively (Jost 2006). We choose $q = 1$ and
245 even though Eq. (1) is not defined when the diversity order
246 is one its limit exists and equals:

$$D_1 = \exp\left(-\sum_{i=1}^S p_i \ln p_i\right) = \exp(H) \quad (2)$$

This is the exponential of Shannon entropy which has the advantage of being relatively insensitive to rare or common taxa. All analyses were done using R software v.3.5.2 (R Core Team 2019) with the individual forest plots as replication units (i.e., the three samples per plot were pooled for calculations). Community descriptors were calculated with the diversity function of the vegan package (Oksanen et al. 2019).

257 Selection of predictor variables

The predictor variables used in this study are summarized in Table S3, and protocols of variable acquisition are detailed in Online Appendix 1. Tree richness was included in the analyses as a factor (one or three tree species), and we assessed the effect of tree functional type using the relative basal area of evergreen species across the three tree triplets. Other predictor variables (i.e., leaf litter traits, microenvironmental characteristics, and soil properties) were summarized by computing three Principal Components Analysis (PCA) ordinations (Fig. S2) with the *prcomp* function from the package *factoextra* (Kassambara 2019). The scores of the forest plots on the retained axes of each PCA were then used as synthetic environmental variables to further explain the structure and composition of macrofauna communities. Pearson correlation between all predictor variable is given in Figure S3.

Litter traits included the concentrations of cellulose, lignin, polyphenols, nitrogen, and calcium measured in freshly fallen leaf litter of all tree species for each country independently (i.e., we used country mean trait value for each tree species). PCA was computed with community weighted means of these traits (Garnier et al. 2004), using tree basal area over the three triplets as a measure of the relative proportion of each species. We kept the first PCA axis which accounted for 49.5% of overall variance and represented a “litter quality” gradient from low-quality associated with high concentrations of lignin and cellulose (negative scores) to high-quality associated with high nitrogen and polyphenol concentrations (positive scores) (Fig. S2A).

The microenvironmental variables included forest floor mass, biomass of understory vegetation and volume of coarse deadwood debris per unit ground area, and the leaf area index of canopy trees as a proxy of canopy closure. Here, to include enough variance in microhabitat and microclimate properties, we kept the first two PCA axes, explaining 38.2% and 26% of the overall variance, respectively. The first axis corresponded to a switch from plots with a high understory vegetation biomass (negative scores), to plots

with most of the soil covered by a thick forest floor (positive scores), and is for simplicity further referred to as “forest floor mass”. The second axis reflected “canopy openness”, with closed canopy plots having negative scores on this axis (Fig. S2B).

Soil characteristics in the top 10 cm of mineral horizon included bulk density, pH (determined in a CaCl₂ solution), clay content, carbon content, and C/N ratio. We kept the first axis which explained 52.5% of the overall variance and represented a gradient of “soil quality”, with sites having negative scores being characterized by more compact, acidic and C-poor soils (Fig. S2C).

Statistical analysis

To test the effect of tree stand properties and environmental variables on the whole macrofauna, detritivore, and predator community composition, we calculated the Bray–Curtis dissimilarity matrix of the three matrices and performed a partial distance-based Redundancy Analysis (dbRDA; Legendre and Anderson 1999) with *capscale* function of the *vegan* package, and including the country as a random factor with the argument condition (Borcard et al. 2018). The significance of the predictor variable and of the ordination along each axis was assessed using permutation tests (*anova* function of the *stats* package, R Core Team 2019), constraining the permutation within countries (4999 permutations, how function in *permutest* package; Besag and Clifford 1989).

Since macrofauna communities are concomitantly influenced by many environmental factors, themselves driven by tree species richness and functional type, we modeled the response of each community descriptor first with a model (M1) including only tree species richness and functional type as co-variable, and then with a complete model (M2) including also microenvironment variable. Thus, H1 and H2 are validated if a significant effect of tree species richness and evergreen proportion are detected in M1, respectively. If these effects are no longer supported in M2 and are replaced by significant effects of the other co-variables, this gives further insights into the mechanisms through which tree species richness and evergreen proportion affect macrofauna communities. On the other hand, similar results in M1 and M2 would suggest that tree species richness or evergreen proportion effects are mediated by mechanisms others than those covered by our co-variables. Finally, the fact of finding significant effects only for microenvironmental variables in M2, would imply that macrofauna communities are influenced by microenvironment independently of tree species richness and evergreen proportion. H3 was tested by comparing the results of both models obtained for detritivore and predator assemblages separately.

We applied a MultiModel Inference (MMI) approach (Burnham et al. 2002) allowing to quantify for the relative

347 importance of each co-variable and constructed the two con-
348 secutive models as below:

$$349 Y \sim \text{Tree SR} + \text{Evergreen \%} + 1|\text{Country} \quad (\text{M1})$$

$$350 Y \sim \text{Tree SR} + \text{Evergreen \%} + \text{Litter quality} + \text{FF mass} + \text{Canopy openness} + \text{Soil quality} + 1|\text{Country} \quad (\text{M2})$$

352 where Y is one of the 15 response variables (i.e., taxonomic
353 richness, Hill_{q=1} diversity, evenness, abundance, and bio-
354 mass calculated separately for the whole macrofauna and
355 detritivore and predator assemblages). The list of terms
356 preceded by the “~” are the explanatory variables (with
357 Tree SR = tree species richness; Evergreen % = percentage
358 of evergreen basal area; litter quality = PC1 of litter traits;
359 FF mass = PC1 of microenvironmental variables; canopy
360 openness = PC2 of microenvironmental variables; soil qual-
361 ity = PC1 of soil properties; PC refereeing to the plot score
362 on the axes of PCA of environmental variables as defined in
363 the previous section), and “1|Country” refers to the belong-
364 ing to countries included as random factor. We used Gener-
365 alized Linear Mixed Models with the *glmmTMB* function of
366 the *glmmTMB* package (Magnusson et al. 2019) and checked
367 for residual normality and homoscedasticity. Abundance
368 data were $\log(1+x)$ transformed since including an argu-
369 ment to model residuals distributions in the function (Pois-
370 son or negative binomial family) was not sufficient to meet
371 model assumptions (Ives 2015). In both model steps (M1
372 and M2), best models were selected based on the Akaike
373 Information Criterion for small sample size (AICc, *dredge*
374 function in the *MuMIN* package), keeping all models within
375 $\Delta\text{AICc} < 6$ (Harrison et al. 2018). Predictor estimates were
376 obtained by averaging their value across the models in which
377 the predictor appeared to avoid estimate value shrinkage
378 towards zero (Harrison et al. 2018). Estimates were stand-
379 arized (β_{st} scale-standardization) to allow cross model
380 comparisons of predictor effects. To quantify to what extent
381 including microenvironmental variables improve community
382 descriptors modeling, we compared the best model obtained
383 from the reduced (M1) and complete (M2) model. These
384 two best models were compared on the basis of the addi-
385 tional variance explained by fixed effects (R^2_{m}) and by fixed
386 and random effects (R^2_{c} ; Nakagawa and Schielzeth 2013),
387 and AICc. Additionally to this first analysis across the four
388 sites (continental scale), we performed the same analytical
389 procedure with the complete model (M2) in each country
390 individually (regional scale) to investigate to what extent the
391 observed effects could depend on the geographic context (as
392 in de Wandeler et al. 2018). Abundance data were $\log(1+x)$
393 transformed as well as detritivore and predator biomass data
394 to reach model assumptions. The analysis was not feasible
395 for detritivore assemblage in Finland because of the large
396 proportion of empty sites (eight out of nine plots).

Results

We collected a total of 2951 soil invertebrates belonging
to 16 broad groups, with an average of 237.6 ± 98.9 indi-

viduals per square meter in Finland, 246.1 ± 106 in Poland,
 300 ± 111.8 in Romania, and 204.1 ± 76.4 in Italy. Among
the identified specimens, roughly one sixth of all individu-
als collected (504 individuals) were detritivores assigned
to 14 species of Lumbricidae, 10 of Isopoda, and 20 of
Diplopoda, and a bit more than one fourth (803 individuals)
were predators assigned to 90 species of Araneae and 49 of
Chilopoda. Nine detritivore species were singletons (1 indi-
vidual sampled), and 3 doubletons (2 individuals sampled),
while 55 singletons and 25 doubletons predator species were
recorded. Macrofauna individuals were sampled in every
plots, but detritivore species (Lumbricidae, Isopoda, Diplop-
oda) were absent in nine plots, mainly in Finland (absent in
eight over nine plots).

Community composition

At a coarse level of taxonomic resolution, whole macro-
fauna communities were organized along the first axis of
the dbRDA (Fig. 1), which explained 38.4% of overall vari-
ance ($p < 0.001$, Table S4) and was mainly driven by litter
quality, evergreen proportion, and forest floor mass. Plots
with negative scores on the first axis were characterized
by high understory biomass, thin forest floor layer, high
litter chemical quality, and low evergreen proportion, and
they supported high abundance of earthworms of all three
ecological types (i.e., endogeic, epigeic, and anecic). Plots
with positive scores were dominated by evergreen tree spe-
cies, presented a thick forest floor layer, a high amount of
coarse deadwood debris, and harbored a relatively high
abundance of predators (Araneae, Chilopoda, predatory
Coleoptera, Opiliones). The second axis explained 23.4%
of overall variance ($p = 0.075$) and highlighted the effect of
soil quality on macrofauna communities. Plots with positive
scores were characterized by low clay and carbon content,
lower pH associated with evergreen tree dominance, and
harbored comparatively higher densities of rhizophagous
Coleoptera, Diptera larvae, and Diplopoda. The same anal-
ysis on detritivore and predator assemblages did not reveal
any significant ordination (dbRDA_{Detritivore} axis 1 $p = 0.13$,
dbRDA_{Predator} Axis 1 $p = 0.06$, Fig. S4, Table S4), meaning
that the predictors considered in our study did not signifi-
cantly explain community composition at the finer level of
taxonomic resolution.

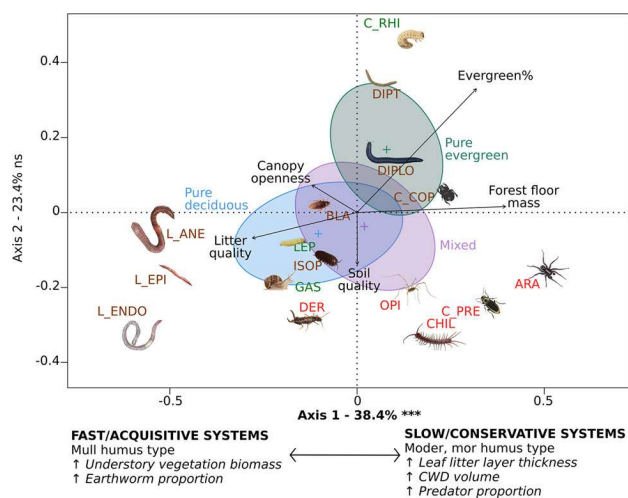


Fig. 1 dbRDA biplot of the whole macrofauna community. *ARA* Araneae, *C_PRE* Coleoptera Predaceous, *C_RHI* Coleoptera Rhizophagous, *GAS* Gasteropoda, *CHIL* Chilopoda, *L* Lumbricidae, *EPI* Epigeic, *ANE* Anecic, *ENDO* Endogeic, *DIPLO* Diplopoda, *ISOP* Isopoda, *OPI* Opilionidae, *DER* Dermaptera, *BLA* Blattaria, *LEP* Lepidoptera Larvae, *DIPT* Diptera Larvae, *CWD* coarse deadwood debris. Name colors represent predaceous (red), saprophagous (brown), and herbivorous (light green) groups. Solid black arrows represent significant predictor variables after permutational ANOVA. Explained variance (%) and level of significance of each axis is shown in the axis title. Ellipses correspond to forest systems levels: pure deciduous (light blue), mixed (purple), and pure evergreen (dark green) stands. Illustration credit www.lesbullesdemo.fr

this effect disappeared in M2, where total biomass instead decreased with forest floor mass and increased with canopy openness (Fig. 2). In this case, the best complete model showed a lower AICc ($\Delta AICc = -9.5$) and higher proportion of explained variance ($\Delta R^2m = +0.08\%$, $\Delta R^2c = +0.24\%$; Fig. 2, Table S5). Most significant effects detected at the continental scale were also detected in at least 1 country (14 effects out of 23; Table S6). Only the negative effect of canopy openness on broad group Hill_{q=1} diversity and the negative effect of evergreen proportion and broad group evenness only appeared at the continental scale. On the other hand, some factors that were not significant at the continental scale showed significant effects at the regional scale in one or two countries. Regarding detritivore species assemblages, the proportion of variance explained by fixed effects was low, ranging from 4% (*J*) to 23% (biomass). Including the country as a random factor substantially increased the explained variance to 68% (*J*) and 79% (abundance), except for taxa Hill_{q=1} diversity which only reached 24% of total explained variance in both models. In M1, none of the community metrics were affected by tree species richness, while evergreen proportion negatively affected all of them (Fig. 2, Table S5). However, most of these effects were replaced in M2 by the effect of microenvironmental variables, which produced a better model with substantially lower AICc and higher explained variance. Detritivore richness marginally increased with canopy openness, while detritivore Hill_{q=1} diversity increased with litter quality (std.est. = 0.33, $p = 0.029$). Evergreen proportion was retained as the best predictor of detritivore evenness in both models (M1: std. est. = -0.22, $p = 0.012$; M2: std. est. = -0.21, $p = 0.033$; Fig. 2, Table S5). Forest floor mass was negatively correlated with abundance and biomass (ab: std. est. = -0.08, $p = 0.013$; m: std. est. = -0.17, $p < 0.001$; Fig. 2, Table S5), while the opposite pattern was found with canopy openness (ab: std. est. = 0.15, $p = 0.023$; m: std. est. = 0.22, $p = 0.02$; Fig. 2, Table S5). Five out of the eight significant relationships found at the continental scale were also observed at the regional scale, but the effect of forest floor mass and canopy openness on detritivore abundance and biomass mainly occurred at the continental scale. In Poland, tree SR increased detritivore Hill_{q=1} diversity, and evergreen proportion reduced detritivore biomass and marginally abundance.

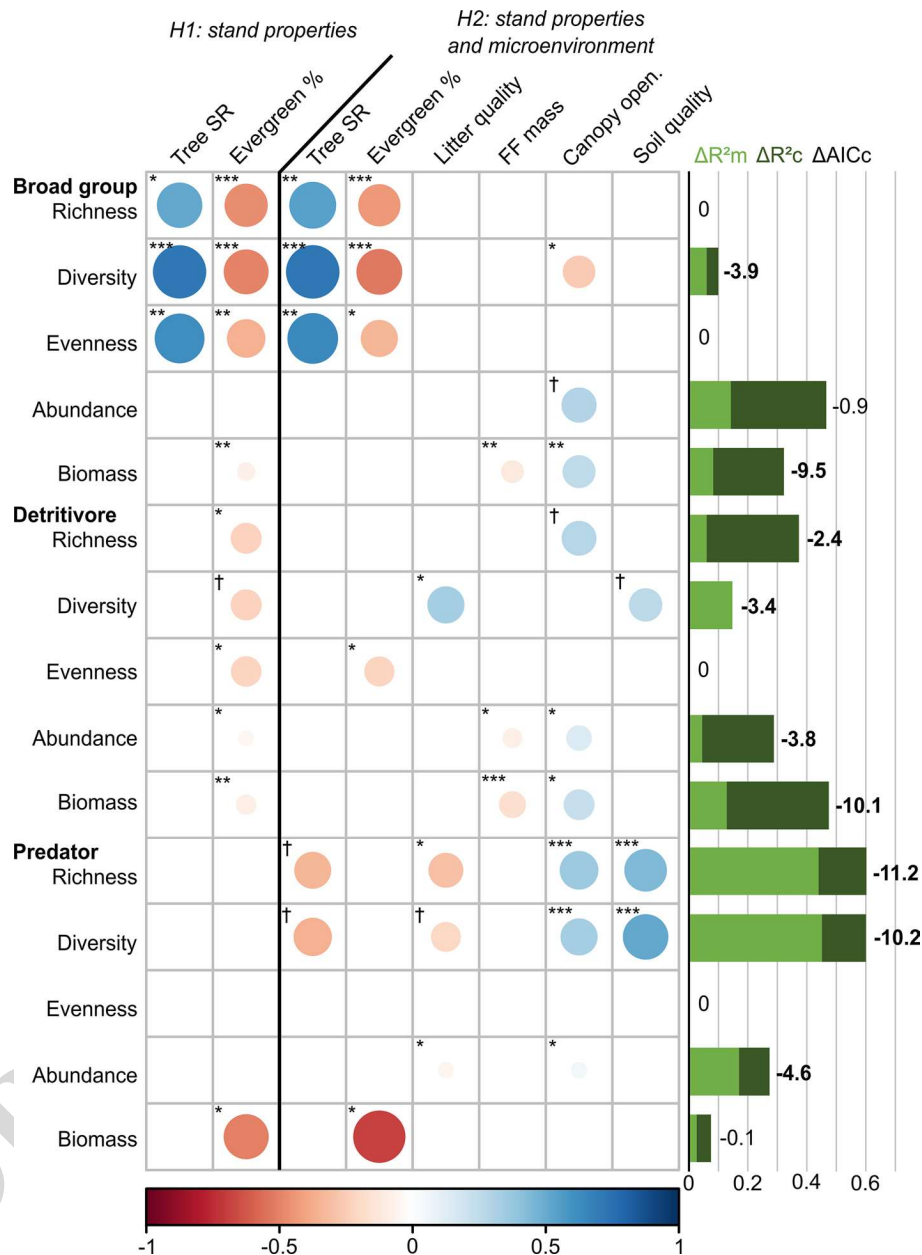
Most descriptors of predator assemblages were well explained by fixed factor, except for evenness, with R^2m ranging from 9% (biomass) to 45% (*D*₁). The random factor accounted for a very small part of predator richness, diversity, or evenness, but consistently increased explained variance for abundance and biomass. Most of community metrics were better predicted in the complete model. Predator species richness and (marginally) Hill's diversity decreased with litter quality (*S*: std. est. = -0.29, $p = 0.012$; *D*₁: std. est. = -0.21, $p = 0.059$) and strongly increased with canopy

442 Community structure

443 When all macrofauna was considered, the proportion of
 444 explained variance by fixed effects (R^2m) in the full model
 445 (M2) varied from 14% (abundance) to 44% (Hill_{q=1} diver-
 446 sity *D*₁). Accounting for random effects (R^2c) increased the
 447 proportion of explained variance to 24% (evenness *J*) and
 448 to 76% (biomass), indicating a strong variability between
 449 countries. Broad group richness, Hill_{q=1} diversity and even-
 450 ness were well predicted in the reduced model (M1), while
 451 biomass, and to a lesser extent abundance, were better pre-
 452 dicted in the complete model (M2). Broad group richness,
 453 Hill_{q=1} diversity and evenness were higher in mixed than in
 454 monospecific stands (M1, *S*: std. est. = 0.51, $p = 0.013$; *D*₁:
 455 std. est. = 0.72, $p < 0.001$; *J*: std. est. = 0.62, $p < 0.01$, Fig. 2,
 456 Fig. S5–S6), and at the same time decreased with the propor-
 457 tion of evergreen trees (M1, *S*: std. est. = -0.46, $p < 0.001$;
 458 *D*₁: std. est. = -0.50, $p < 0.001$; *J*: std. est. = -0.36, $p < 0.01$,
 459 Fig. 2, Fig. S5–S6). There were no consequent changes
 460 between M1 and M2 in the proportion of explained vari-
 461 ance or AICc, except for broad groups *D*₁ that also decreased
 462 with canopy openness ($\Delta AICc = -9.5$, $\Delta R^2m = +0.06\%$,
 463 $\Delta R^2c = +0.04\%$; Fig. 2, Table S5). Broad group abundance
 464 was poorly predicted regardless of the model, while bio-
 465 mass decreased with evergreen proportion in M1. However,

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Fig. 2 Standardized estimates and explained variance from Multimodel Inference. Circle size and colour intensity are proportional to the effects strength, red colour show for negative effect, blue colour show positive effect). The level of significance of the effect is indicated (†, *, **, ***: p value $< 0.1, < 0.05, < 0.01, < 0.001$). Non-significant variable estimates are not shown but are reported in Table S5. The bar graph on the right indicates the change in the proportion of variance explained by fixed effects (R^2_m , light green) and fixed plus random effects (ΔR^2_c , dark green), as well as the difference in AICc (ΔAIC_c , number) between the most parsimonious models from each of the two hypotheses. *Tree SR* tree species richness, *FF mass* forest floor mass, *Canopy open.* canopy openness



519 openness (S : std.est. = 0.36, $p < 0.001$; D_1 : std.est. = 0.33,
 520 $p < 0.001$) and soil quality (S : std.est. = 0.45, $p < 0.001$;
 521 D_1 : std.est. = 0.51, $p < 0.001$). Here, changes in the proportion
 522 of explained variance and AICc were very high (S :
 523 $\Delta R^2_m = +0.44\%$, $\Delta R^2_c = +0.16\%$, $\Delta AIC_c = -11.2$; S :
 524 $\Delta R^2_m = +0.45\%$, $\Delta R^2_c = +0.15\%$, $\Delta AIC_c = -10.2$; Fig. 2,
 525 Table S5). Predator abundance weakly decreased with litter
 526 quality and weakly increased with canopy openness, while
 527 biomass strongly decreased with evergreen proportion in
 528 both the reduced and complete models. Nine of the 11 sig-
 529 nificant effects detected at the continental scale were also
 530 present at the regional scale. Tree SR decreased predator
 531 abundance in Finland but increased their biomass in Poland.
 532 Canopy openness negatively affected predator assemblage

533 evenness in both Poland and Italy, while litter quality
 534 decreased predator biomass in Finland and Poland. Finally,
 535 soil quality had a negative effect on predator abundance and
 536 biomass in Finland, while FF mass increased predator abun-
 537 dance in Poland.

Discussion

538
 539 The results of our study show the effect of tree richness
 540 and functional type (i.e., stand evergreen proportion) on
 541 soil macrofauna communities and highlight the underly-
 542 ing mechanisms. Interestingly, we found that forest stands
 543 with a low evergreen tree proportion supported macrofauna

544 communities with a higher number of broad groups that
 545 were also more diverse and evenly represented. In contrast,
 546 at a species-level taxonomic resolution, the effects of tree
 547 species richness and functional type were less pronounced.
 548 Instead, litter quality, microhabitat and microclimate became
 549 important drivers of both detritivore and predator assem-
 550 blage structure, with trophic cascade effects potentially
 551 occurring between these two trophic groups. The majority
 552 of the effects observed at the continental scale were also
 553 present in at least one country, giving further support to
 554 our results (Table S6). Some effects idiosyncratically dis-
 555 appeared or appeared at the regional scale due to changes
 556 in sample size, or narrower environmental and community
 557 variable gradients as reported for earthworms in European
 558 forests (de Wandeler et al. 2018). In our study, considering
 559 this regional scale provided no additional insights into the
 560 links between macrofauna communities and their environ-
 561 ment, and this will therefore not be discussed further.

562 **Main axes of variability in soil macrofauna** 563 **communities**

564 The results of our redundancy analysis show that as much
 565 as 38.4% of the total variability in macrofauna communi-
 566 ties, when described at a coarse taxonomic resolution, was
 567 explained by an opposition between two extremes of a gra-
 568 dient from pure deciduous to pure evergreen stands. This
 569 gradient is consistent with the classification of ecosystems
 570 along a productivity gradient (Wardle 2004), soil process
 571 domains (Desie et al. 2019), or the distinction between dif-
 572 ferent humus types ranging from mull, i.e., “fast turnover”
 573 and “acquisitive strategy”, to moder and mor, i.e., “slow
 574 turnover” and “conservative strategy” (Ponge 2003; Zanella
 575 et al. 2011).

576 In fast cycling systems, deciduous trees provide high-
 577 quality litter and canopy openness over the year, allow-
 578 ing the establishment of an important understory vegeta-
 579 tion, which produces litter rich in important nutrients such
 580 as calcium and nitrogen (Reich et al. 2005; Gilliam 2007;
 581 Augusto et al. 2015). This results in both a higher earthworm
 582 proportion in macrofauna communities and more diverse
 583 detritivore assemblages in general (Reich et al. 2005). Being
 584 more abundant and diverse, macrodetritivores are expected
 585 to further accelerate litter burial and decomposition, thus
 586 reducing the litter layer thickness at the soil surface (Hedde
 587 et al. 2010; Coulis et al. 2016). Conversely, the decrease in
 588 earthworm relative abundance and detritivore diversity in
 589 evergreen dominated forests is a long known pattern that
 590 can be explained by the poor quality of litter inputs as well
 591 as the more acidic conditions of the forest floor (Reich et al.
 592 2005; Ammer et al. 2006; Schelfhout et al. 2017). Such a
 593 decrease in macrodetritivore abundance is expected to be
 594 associated to lower bacterial activity, thicker forest floor

layer, and the promotion of other groups of smaller detriti-
 595 vores such as Collembola (Scheu et al. 2003). This probably
 596 also explains the observed increase in predator relative abun-
 597 dance in stands with higher evergreen proportion, as this
 598 group could benefit simultaneously from the higher diversity
 599 and amount of microhabitats, and from the increased avail-
 600 ability of mesofauna prey (Arpin et al. 1986; Kaspari and
 601 Yanoviak 2009).
 602

603 **Tree diversity and functional type direct** 604 **versus indirect effects**

605 In line with our first hypothesis, both our reduced and com-
 606 plete model showed a strong positive effect of tree species
 607 richness and a negative effect of evergreen proportion on
 608 the richness, diversity, and evenness of macrofauna broad
 609 groups. This is globally congruent with the results of other
 610 studies that described a higher diversity of soil organisms
 611 at a broad taxonomic level in mixed compared to pure ever-
 612 green forests (Scheu et al. 2003; Salamon et al. 2008). As
 613 mentioned previously, many environmental factors can dif-
 614 fer between mixed and pure forests, including litter quality
 615 and trait diversity, microhabitat heterogeneity and quantity,
 616 canopy openness and soil quality (Scherer-Lorenzen et al.
 617 2005), and most of them could indirectly explain tree effects
 618 on soil macrofauna communities. However, when included
 619 in a more detailed statistical model, none of the microenvi-
 620 ronmental variables considered in our study were found to
 621 explain macrofauna community metrics at a broad level of
 622 taxonomic resolution, apart from canopy openness which
 623 had a weak negative effect on Hill_{q=1} diversity. This suggests
 624 that tree species richness and evergreen proportion effects on
 625 macrofauna broad groups could be related to other micro-
 626 environmental variables not included in our analysis, such
 627 as litter trait diversity or microhabitat heterogeneity. This
 628 would be in line with other studies that have emphasized
 629 the importance of litter chemical and physical trait variation,
 630 which may both determine resource diversity for detritivores
 631 and microhabitat quantity and diversity for invertebrates in
 632 general (Hansen and Coleman 1998).

633 At a finer level of taxonomic resolution, tree species
 634 richness no longer had a detectable effect on detritivore nor
 635 predator community descriptors, as indicated by our reduced
 636 model. Concomitantly, the negative effect of evergreen pro-
 637 portion on detritivore and predator assemblages produced
 638 by the reduced model was not retained in the complete
 639 model, except for detritivore evenness and predator biomass.
 640 Instead, our results revealed rather an indirect effect via
 641 resource quality, habitat volume, and microclimate. The lack
 642 of tree species richness effect on macrofauna assemblages at
 643 this level of taxonomic resolution, is congruent with simi-
 644 lar studies focusing on earthworms or on detritivorous and
 645 predatory beetles (Schwarz et al. 2015; Chamagne et al.

2016; De Wandeler et al. 2018). Other studies did report a positive effect of tree species richness on spiders, saproxylic beetles, or earthworm richness, but differences in sampling protocols and study design can probably explain these apparently contradictory results (Chamagne et al. 2016; Ampoorter et al. 2019). Here, we also have to consider that our design only included two levels of tree species richness (monocultures and three-species mixtures), which is different from a true species richness gradient. This might have impeded the detection of a tree richness effect, if it occurs at another level of the diversity gradient. The negative effect of evergreen proportion on detritivore evenness was consistent regardless of the model, suggesting a significant importance of diversity of litter traits or microhabitat, as already discussed for broad group diversity. The negative response of predator biomass to evergreen proportion, which was also highlighted by both modeling approaches, and the simultaneous lack of effect on their abundance, indicates that evergreen trees drive the predator assemblages towards smaller body-sized taxa in less productive stands (Skłodowski 2002). This supports the previously discussed idea that soil fauna communities in evergreen-dominated stands are dominated by small detritivores (Collembola and Acari), representing a preferred prey for small body-sized predators (Arpin et al. 1986; Scheu et al. 2003).

Detritivore and predator communities also showed a strong response to canopy openness, with increased detritivore abundance and biomass and predator richness and diversity in more open forests. This can first be explained by the direct controls exerted by canopy openness on forest ground insolation, water availability, and temperature conditions (Prescott 2002), as well as their expected effects on ectotherm activity and on animals' ability to access resources (Turner et al. 1987; Kaspari et al. 2000; Salmon et al. 2008). Secondly, canopy openness increase light and water availability for understory plants, which can result in higher plant cover and diversity (Thomas et al. 1999). Detritivores will thus benefit from the nutrient-rich herbaceous plant leaf litter and roots, which may constitute an important and high-quality source of organic matter (Lavelle and Spain 2001; Gilliam 2007; Henneron et al. 2015). Finally, predators may also rely on understory vegetation which determines to a large extent the characteristics and heterogeneity of their microhabitat (Pakeman and Stockan 2014).

690 Detritivore versus predator responses

691 A surprising result of our study is the fact that predator
692 assemblages seem to be more sensitive to soil quality than
693 detritivores. This predator response to soil quality may first
694 be attributed to the fact that roughly half of them belonged
695 to Chilopoda in our samples (Table S2), a group which
696 is known to have at least partly endogeic behavior and is

therefore sensitive to soil properties, notably soil pH and
organic matter content (Blackburn et al. 2002). Conversely,
the absence of detritivore response may be explained by
three mechanisms. First, it is possible that other soil and
forest floor properties not included here, such as forest
floor pH or litter phosphorus content, may be more important
for detritivore communities (De Wandeler et al. 2016).
Secondly, detritivore assemblages were composed of both
endogeic groups (endogeic Lumbricidae) and epigeic groups
(epigeic Lumbricidae, Diplopoda, and Isopoda). Epigeic
taxa may show weaker response to soil characteristics than
endogeic taxa which may have resulted in the absence of
response (Scheu and Falca 2000; Henneron et al. 2015; De
Wandeler et al. 2016). Finally, soil characteristics and plot
scores on the first PCA axis were strongly country specific
(Table 1), and it is possible that by including country as a
random factor in the models, captured part of soil characteristics
variations was obscured. This is supported by the smaller
proportion of variance explained by fixed compared to
random effects (14 vs 50% on average) for detritivore
assemblage descriptors, which is notably due to the very low
abundance of these organisms in Finland.

In addition to the direct and indirect effects of tree richness and functional type on macrofauna communities, trophic cascades may also have occurred between detritivore and predator assemblages, particularly because Lumbricidae, and to a lesser extent Diplopoda and Isopoda, represent potentially important preys for Chilopoda and Araneae (Scheu and Falca 2000). First, higher detritivore abundance and biomass in response to increased canopy openness may have enhanced predator diversity and richness through higher resource availability (Abrams 1995). Secondly, increased detritivore diversity in response to litter quality may have resulted in a more heterogeneous resource for predators, potentially decreasing prey-finding probability for the more specialized species (Root 1973), and resulting in the observed less rich, diverse and abundant predator assemblages. These mechanisms stress the importance of including trophic interactions when modeling soil macrofauna distribution in forests (Scheu et al. 2003; Salamon et al. 2008). To this end, it would also be interesting to include in future studies other sampling methods, such as pitfall traps, that could be more effective at sampling large, mobile predators such as Carabidae that may feed on large Lumbricidae.

Importance of taxonomic resolution

Given that the effect of tree species richness and evergreen proportion was detectable on whole macrofauna communities described at a low taxonomic resolution but no longer on detritivore or predator assemblages identified at the species level deserves particular attention.

748 Mixed deciduous-evergreen stands, with their intermedi-
 749 ate position between two forest type extremes (“fast” pure
 750 deciduous, versus “slow” pure evergreen systems) may
 751 provide the necessary conditions for the co-existence of
 752 a high number of broad groups with contrasting ecologi-
 753 cal requirements (Fig. 1). This can also be explained by
 754 the fact, as mentioned previously, that mixed deciduous-
 755 evergreen forests produce a litter layer with larger chemi-
 756 cal and physical trait variation, thus increasing resource
 757 diversity for detritivores and microhabitat features for
 758 invertebrates in general (Schuldt et al. 2008). The same
 759 does not apply when considering individual detritivore
 760 or predator species, because their narrower environmen-
 761 tal preferences limit them to a more restricted part of
 762 the environmental gradient. This can explain why, at the
 763 species level, detritivores and predators were more sensi-
 764 tive to resources, habitat, and microclimate conditions
 765 than to tree species diversity and functional type (Fig.
 766 S4; Kaspari 2001).

767 The differences in response patterns highlighted by
 768 the use of different levels of taxonomic resolution also
 769 illustrate some important methodological issues. Indeed,
 770 approaches at low taxonomic resolution are often favored
 771 in studies of soil macrofauna, especially because they
 772 allow to bypass the taxonomic impediment that exists for
 773 many groups of soil invertebrates (Decaëns et al. 2010).
 774 The use of broad taxonomic levels makes it possible
 775 to consider the whole macrofauna community without
 776 reducing datasets to the best-known groups for which
 777 species-level identifications are possible. Taxa of higher
 778 rank also have wider geographic distributions, making
 779 comparisons easier between geographically distant sites.
 780 In our case, where sites harbor contrasting macrofauna
 781 species pools, the multiple pedoclimatic changes along
 782 latitude may be the major drivers of soil communities (De
 783 Wandeler et al. 2018). This is supported by the fact that
 784 the proportion of variance explained by random effects is
 785 larger when using species than when using broad group
 786 as fundamental taxonomic units (Table S5), as well as the
 787 small effect of the included predictor variables on detriti-
 788 vore and predator assemblage composition in the dbRDA
 789 analysis (Table S4, Fig. S4). Finally, datasets constructed
 790 at coarse levels of taxonomic resolution also by definition
 791 have fewer zeros than those constructed at species level,
 792 thus increasing the robustness and statistical power of
 793 analyses (Harrison et al. 2018). However, a corollary of
 794 this is that they are also potentially less efficient at detect-
 795 ing subtle community responses to ecological gradients
 796 since the distributions of higher rank taxa along these
 797 gradients are wider than those of the species that consti-
 798 tute them (Kaspari 2001). This stresses the importance of
 799 investigating community responses at different levels of
 800 taxonomic resolution.

Conclusion

801 Our study highlights the complexity of the direct and indi-
 802 rect mechanisms underlying the relationships between
 803 tree species richness and composition and macrofauna
 804 communities. Mixed forest stands supported richer, more
 805 diverse and even macrofauna communities, at a broad
 806 level of taxonomic resolution. Compared to mixed stands,
 807 pure deciduous stands favored Lumbricidae and other
 808 macrodetritivore groups, while evergreen forests were
 809 dominated by predator taxa. Combined, these two results
 810 suggest that mixed forest stands offer resource, microhabi-
 811 tat, microclimate, and soil conditions suitable for a wide
 812 range of organisms of contrasting lifestyles. Future stud-
 813 ies should incorporate if possible quantitative description
 814 of changes in litter or fine root trait diversity and habi-
 815 tat heterogeneity, as they can be of importance for soil
 816 macrofauna. Macrofauna response to tree species richness
 817 and functional type was detectable almost only at a coarse
 818 level of taxonomic resolution, while macrofauna species
 819 rather responded to microenvironmental variables. This
 820 highlights the importance of combining different levels
 821 of taxonomic resolution to elucidate in a comprehensive
 822 way the complex tree-macrofauna relationships in forest
 823 ecosystems. 824

Supplementary Information The online version contains supplemen-
 825 tary material available at <https://doi.org/10.1007/s00442-021-04931-w>. 826

Acknowledgements This research was part of the SoilForEUROPE
 827 project funded through the 2015–2016 BiodivERsA COFUND call
 828 for research proposals, with the national funders Agence Nationale
 829 de la Recherche (ANR, France), Belgian Science Policy Office (BEL-
 830 SPO, Belgium), Deutsche Forschungsgemeinschaft (DFG, Germany),
 831 Research Foundation Flanders (FWO, Belgium), and The Swedish
 832 Research Council (FORMAS, Sweden). We thank the site managers
 833 Leena Finér with the Finnish Forest Research Institute (Metla), Bog-
 834 dan Jaroszewicz with the University of Warsaw, Olivier Bouriaud with
 835 the Forest Research and Management Institute (ICAS), and Filippo
 836 Bussotti with University of Florence and associates, as well as the
 837 SoilForEUROPE consortium for their assistance with the soil sampling
 838 campaign (project website: <https://websie.cefe.cnrs.fr/soilforeurope/>).
 839 The authors thank Sylvain Coq, Alexandru Milcu, Marion Blache and
 840 Fiona Cornet for their precious help during the sampling campaign and
 841 lab analysis and Morgane Arietta Ganault for illustrations. We thank
 842 the two anonymous reviewers whose constructive comments improved
 843 the manuscript. This work was possible thanks to the grant awarded
 844 to Pierre Ganault from the “Ecole Doctorale GAIA” of the University
 845 of Montpellier. 846

Author contribution statement SH, BM, JN, TD participated in
 847 designing the sampling campaign, JW, LMG, LPDS, JN, SH, JFD, BM,
 848 TD participated in the sampling campaign, PG, JFD, EI, AP, CM and
 849 TD did the species identification and laboratory analysis, PG analyzed
 850 the data, PG and TD wrote the manuscript, all co-authors contributed
 851 in the writing of the manuscript. 852

Data availability The datasets generated during and/or analyzed during
 853 the current study will be used for a data paper and then uploaded to the
 854

855 FunDivEUROPE data platform <https://fundiv.befdata.biow.uni-leipzig.de/data>.
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