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1 **Vegetation shapes aboveground invertebrates communities**
2 **more than soil properties and pollution: a preliminary**
3 **investigation on a metal contaminated site**

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17

18 **Declarations**

19 **Ethics approval and consent to participate**

20 This article does not describe any studies involving human participants performed by the authors. All
21 applicable international, national and/or institutional guidelines for the care and use of animals were followed.

22 **Consent for publication**

23 Not applicable.

24 **Availability of data and materials**

25 Lists of plant and invertebrate species are available on the repository dat@osu ([https://dataosu.obs-](https://dataosu.obs-besancon.fr/)
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27 **Competing interests**

28 The authors declare that they have no conflict of interest.

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35 **Authors' contributions**

36 SO, major contributor in writing the original draft of the manuscript, analyzed and interpreted the data on
37 plant and invertebrate inventory and their spatial distribution. FM performed the invertebrate inventory,
38 whereas TC performed the plant inventory. RS and FR conceptualized this study and acquired the funding. CF,
39 RS and FR supervised the study. All authors read and approved the final manuscript.

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52 **Abstract**

53 Pollution with trace metals (TM) has been shown to affect diversity and/or composition of plant and animal
54 communities. While ecotoxicological studies have estimated the impact of TM contamination on plant and
55 animal communities separately, ecological studies have widely demonstrated that vegetation is an important
56 factor shaping invertebrate communities. It is supposed that changes in invertebrate communities under TM
57 contamination would be explained by both direct impact of TM on invertebrate organisms and indirect effects
58 due to changes in plant communities. However, no study has clearly investigated which would more
59 importantly shape invertebrate communities under TM contamination. Here, we hypothesized that invertebrate
60 communities under TM contamination would be affected more importantly by plant communities which
61 constitute their habitat and/or food than by direct impact of TM. Our analysis showed that diversity and
62 community identity of flying invertebrates were explained only by plant diversity which was not affected by
63 TM contamination. Diversity of ground-dwelling (GD) invertebrates in spring was explained more importantly
64 by plant diversity (27% of variation) than by soil characteristics including TM concentrations (8%), whereas
65 their community identity was evenly explained by plant diversity and soil characteristics (2-7%). In autumn,
66 diversity of GD invertebrates was only explained by plant diversity (12%), and their identity was only
67 explained by soil characteristics (8%). We conclude that vegetation shapes invertebrate communities more
68 importantly than direct effects of TM on invertebrates. Vegetation should be taken into account when
69 addressing the impacts of environmental contamination on animal communities.

70

71 **Keywords**

72 Alpha diversity; beta diversity; plant-invertebrate interaction; community composition; trace metals.

73

74 **1 Introduction**

75 Trace metals (TM) are naturally occurring elements, whose concentrations in the environment can be
76 dramatically increased by various anthropogenic activities, which can deeply impact wildlife (Eisler, 2000;
77 Nordberg et al., 2014). Although technical and regulatory improvements have considerably reduced the
78 emission of some TM, legacy TM contamination persists in nature because TM are non-degradable chemicals.
79 The emission of other elements such as antimony failed to be drastically reduced (He et al., 2019) and emerging
80 elements (e.g. rare earth elements) are increasingly emitted into the environment in relation to their use in new
81 technologies (Gwenzi et al., 2018). Altogether, TM persist in nature and continue to affect ecosystems (EMEP,
82 2013). Harmful effects of TM contaminations are observed at several biological levels (Walker et al., 2012).
83 At community level, diversity indices have commonly been used as indicators for estimating pollutants' effects
84 on plants and invertebrates (Zvereva et al., 2008; Zvereva and Kozlov, 2012, 2010). Ecosystems undergoing
85 strong disturbances display many negative responses, one of which being the decrease of biodiversity (Odum,
86 1985). In terrestrial ecosystems, it has been frequently reported that diversity of plants was negatively affected
87 by soil TM contamination (Bes et al., 2010; Dazy et al., 2009; Ginocchio, 2000; Vidic et al., 2006). Change in
88 the composition of plant community (i.e. change in identities and/or abundances of plant species in a
89 community) along a gradient of TM soil contamination has also been reported (Strandberg et al., 2006).
90 However, responses of the diversity and composition of plant community to soil TM contamination vary
91 according to TM and vegetation types (Zvereva et al., 2008). A similar framework has been highlighted in
92 biodiversity and composition of terrestrial invertebrate communities under TM contamination. Some studies
93 have stressed negative correlations between diversity of invertebrates and soil TM contamination (Paoletti et
94 al., 1988; Read et al., 1987; Spurgeon and Hopkin, 1996), whereas others have focused on changes in
95 invertebrate community structure and composition rather than in diversity indices (Babin-Fenske and Anand,
96 2011; Migliorini et al., 2004; Nahmani and Lavelle, 2002). Both ground-dwelling and flying invertebrates
97 might be impacted by metal environmental contamination because either or both larval and adult stages can be
98 exposed through direct cutaneous contact with contaminated substrates and/or through contaminated food
99 consumption (Hopkin, 1989).

100 While impacts of metal contamination on biodiversity have widely been studied separately in both plants
101 and invertebrates, interactions between plants and animals are suggested as one of key factors in influencing
102 the responses of communities to environmental TM contamination (Bol'shakov et al., 2001; Eeva et al., 2012;

103 Storm et al., 1993). In fact, some results have nuanced the potential relationships between plant and
104 invertebrates diversity in sites contaminated by TM suggesting a critical role of direct effects of environmental
105 contamination (Brändle et al., 2001; Read et al., 1998), while other works have suggested possible effects of
106 vegetation on composition of invertebrate communities under TM contamination (Grelle et al., 2000; Nahmani
107 and Rossi, 2003). However, no study, to our knowledge, has specifically attempted to disentangle the relative
108 importance of plant community *versus* soil TM contamination in shaping invertebrate communities. In contrast,
109 ecological studies have clearly shown that vegetation is an important factor shaping above- and below-ground
110 invertebrate composition and structure of assemblages in grassland (Brose, 2003; Haddad et al., 2001; Knops
111 et al., 1999; Scherber et al., 2010; Siemann, 1998) and woodland (Fraser et al., 2007; Humphrey et al., 1999;
112 Scherber et al., 2014; Sobek et al., 2009) ecosystems. Although potential underlying mechanisms are still
113 debated (Borer et al., 2012; Haddad et al., 2009), diversified plant communities could provide a variety of
114 resources for a greater number of herbivore species (Hutchinson, 1959), shelters from predators and/or more
115 stable prey availability for predators, supporting their higher diversity and abundance (Root, 1973). Given the
116 determinant influence of vegetation on invertebrate communities, we hypothesized that diversity and
117 composition of invertebrate community under soil TM contamination would be more importantly explained by
118 changes in vegetation as indirect effects of soil TM contamination than by direct effects of TM on invertebrate
119 organisms.

120 In the present study, the potential effects of TM soil contamination and diversity of plants on diversity and
121 composition of invertebrate communities were assessed in a smelter-impacted area in northern France, using
122 diversity of taxa (i.e. alpha diversity) and its variation (i.e. beta diversity) at local level. We specifically aimed
123 at disentangling and quantifying the relative importance of soil contamination and of plant community features
124 on invertebrate community characteristics. We first explored (i) the relationship between plant diversity, soil
125 TM concentration and some soil properties known to influence TM bioavailability and toxicity in order to
126 identify potential changes in vegetation determined by soil TM contamination. We then analyzed (ii) the effects
127 of plant diversity on diversity and identity of invertebrates in communities independently from TM
128 contamination and soil properties and (iii) the effects of TM contamination and soil properties on invertebrate
129 communities independently from plant diversity in order to quantitatively compare their respective effects.

130 **2 Materials and methods:**

131 **2.1 Study sites**

132 This study was carried out in the surroundings of the former lead (Pb) and zinc (Zn) smelter named
133 “Metaleurop Nord” located in Northern France (Noyelles Godault, Hauts-de-France, France). The smelter was
134 in activity from 1894 to 2003 and was the only producer of primary Pb in France. Its pyro-metallurgic process
135 had generated large quantities of dust containing many metals. For instance, about 1.0 ton of cadmium (Cd),
136 16.9 tons of Pb and 31.6 tons of Zn were released in 2002, despite the implementation of technical
137 improvements during the 1970s (DRIRE, 2003). An area of approximately 120 km² around the smelter is still
138 affected by dust emission released from Metaleurop Nord and from another large Zn smelter named “Umicore”
139 close to Metaleurop Nord (Douay et al., 2008). Several studies have revealed high soil TM contamination in
140 the surrounding soils. For instance, concentrations in agricultural top soils are as high as 21 mg kg⁻¹ of dry soil
141 for Cd, 1132 mg kg⁻¹ for Pb, and 2167 mg kg⁻¹ for Zn (Sterckeman et al., 2002), whereas concentrations of
142 these metals reached up to 67, 4890 and 2685 mg kg⁻¹, respectively, in the upper organic layers of grasslands
143 around the smelter (Sterckeman et al., 2000). In the study of Fritsch et al. (2010), total concentrations of the
144 three metals in soils sampled from wooded patches reached up to 236, 7331 and 7264 mg kg⁻¹ of dry soil,
145 respectively.

146 The present study was undertaken on six sites of 25 ha (500m x 500m) in the surroundings of Metaleurop
147 Nord. The area is a densely urbanized zone mixed with arable lands (ploughed fields mostly, grassland), forest
148 and planted woods, and shrublands in derelict lands. Five sites among the six ones were located within an area
149 of 40 km² (5 x 8 km) including the smelter in its center (50°25'42 N and 3°00'55 E). The other site was located
150 about 10 km northeast of the former smelter and is considered as a control site due to its relatively low soil TM
151 contamination: 0.9 - 2.4, 43 - 200, 89-278 mg kg⁻¹ of dry soil for Cd, Pb, and Zn, respectively (Fritsch et al.,
152 2010), which are similar to the regional reference values (Sterckeman et al., 2007). Field inventory of plants
153 and invertebrates was built some points within six sites chosen along a gradient of TM soil concentrations
154 (Table 1).

155 **2.2 Field inventory of plants and invertebrates**

156 Our sampling method for plants, flying and ground-dwelling invertebrates are summarized in Figure 1 and
157 described below.

158 Vegetation survey was realized from 4th June to 5th September 2012 on many woody habitats (natural forests,
159 tree plantations such as poplar groves, or copses and hedgerows in natural or cultivated lands and urban parks)
160 of each site. Vascular plant taxa were identified separately in three different strata: tree stratum (woody species
161 > 8 m high), shrub stratum (woody species < 8 m high), and herbaceous stratum. Plants were identified in the
162 field at species level following Dudman and Richards (1997) and Lambinon et al. (2004). Cover-abundance
163 was visually estimated as vertically projected area for each species following Braun-Blanquet et al. (1952). In
164 total, 236 plant taxa were listed in the three strata: 25 species in tree stratum; 42 species in shrub stratum and
165 193 species in herbaceous stratum (N.B. some plant taxa were observed in several strata).

166 Inventory of invertebrates was carried in spring (April) and in autumn (September and October) 2012 on
167 some of woody patches where soils had been sampled and analyzed in previous studies (Fritsch et al., 2010)
168 by using two types of trapping: pitfall traps and yellow pan traps. It is important to note that this sampling
169 aimed at providing a snapshot of invertebrate communities rather than a full description of invertebrate
170 communities, which would have required a longer sampling period.

171 The pitfall trap is one of the most frequently used methods for sampling epigeic invertebrates such as ground
172 beetles, rove beetles, wandering spiders, and ants (Leather, 2005). Three 800ml polypropylene beakers with
173 neither roof nor preservative fluid were set at 15m intervals between each of them in woody patches where
174 plants were present in all the three strata, constituting and hereinafter referred to as a “trap line”. From two to
175 eight trap lines were set per season (i.e. spring and autumn) on each of the six study sites (i.e. 36 trap lines
176 were used in spring and 32 in autumn, Table 1).

177 The yellow pan trap is frequently used for sampling flying insects. Trapping color plays a determinant role
178 in the effectiveness with which different insect groups are caught, but yellow color is most efficient for catching
179 a wide range of phytophagous insects and their predators or parasitoids (Kirk, 1984). One to three yellow pan
180 traps with soap mixed water were set on the ground on each of the six study sites and for each season in woody
181 patches where plants were present in all the three strata (i.e. 12 yellow pan traps were used in spring and 12 in
182 autumn, Table 1).

183 Locations of the two types of traps were geo-referenced. Both pitfall and yellow pan traps were checked
184 every morning for three consecutive days, and then removed from the field. Captured invertebrates were stored
185 in ethanol or in freezer at -20°C and then identified in laboratory at the finest possible taxonomic level by

186 morphological characteristics. The main references used for invertebrate determination were Coulon (2003),
187 Forel and Leplat (2001), Jeannel, (1941) and Trautner and Geigenmueller (1987).

188 Fauna captured by pitfall and yellow pan traps were considered as “ground-dwelling (GD)” and “flying”
189 invertebrates, respectively. Collembolans were removed from our inventory. Most of the individuals were
190 identified at family level (GD 74% and flying 78%), but other were identified at order (GD 24% and flying
191 21%) or class levels (GD 2% and flying 1%) (cf. Supporting Information SI Spreadsheet file). Twenty-four
192 taxa at different taxonomic levels (three classes, three orders and 18 families) were listed in the GD
193 invertebrates, while 78 taxa (one class, four order and 73 families) were listed in flying invertebrates. All
194 invertebrates were captured as adult stage. It is worth to note that larva of some families occur in aquatic
195 habitats: five families of Diptera larvae (Chironomidae, Limoniidae, Psychodidae, Simuliidae, and
196 Sciomyzidae) which mainly occur in aquatic habitats, and seven families of Diptera larvae (Ceratopogonidae,
197 Tipulidae, Dolichopodidae, Empididae, Phoridae, Syrphidae, and Scathophagidae) which could occur in
198 aquatic/semi-aquatic habitats.

199 **2.3 Data preparation**

200 2.3.1 *Diversity index choice*

201 In this study, richness, Simpson’s diversity index, Simpson’s evenness and abundance were used to estimate
202 alpha diversity. Richness (S : number of different taxa) and Simpson’s diversity index ($D: 1/\sum P_i^2$, where P_i is
203 the proportional abundance of taxa i) were used to contrasting total number of taxa (richness) to number of
204 abundant taxa at habitat patch level (Jost, 2006). Simpson’s evenness ($E: D/S$) was calculated and used as
205 another variable with reference to the proportion of dominant taxa among all taxa. Abundance of all taxa (N)
206 was also added as another information about the community. The four indices are hereinafter referred to as
207 “alpha diversity”.

208 Spatial variation in composition among communities (i.e. beta diversity) was estimated by using the total
209 variance of the site-by-taxa community data (Legendre et al., 2005; Legendre and De Cáceres, 2013). The beta
210 diversity can be partitioned into two matrices representing “replacement” and “richness difference” (Borcard
211 et al., 2018), and each matrix can be analyzed in relation to explanatory environmental variables (Legendre
212 and De Cáceres, 2013). For all types of plant strata and of invertebrates, dissimilarity matrices for beta diversity
213 were built from presence-absence of each taxon in communities because binary dissimilarity coefficients

214 produce more relevant results than quantitative indices when taxa are largely different among communities
215 (Legendre, 2014). The two matrices for replacement and richness difference were hereinafter referred to as
216 “beta diversity”.

217 2.3.2 *Calculation of diversity indices and matrices.*

218 Alpha and beta diversity of invertebrates were based upon individuals captured by 68 trap lines for GD
219 invertebrates and 24 yellow pan traps for flying invertebrates. Diversity of plants were measured for each
220 stratum (tree, shrub and herb) based on cover-abundance (m^2) of each species present in an area of $1000 m^2$
221 around trap lines or yellow pan traps. As pitfalls and yellow pan traps were not precisely set at the same
222 locations, alpha and beta diversity of plants were measured for each type of invertebrate traps. These areas are
223 hereinafter referred to as “buffers”. The observations for invertebrates were carried out by "buffer". Each buffer
224 shows inventory for three strata of plants and an inventory for invertebrates, as well as parameters of soil
225 properties and soil metal concentrations in soils (cf. below). The number of buffers in each season and site is
226 indicated in Table 1. As the plant inventory was done once between June and September, their presence and
227 relative cover-abundance were considered to be similar at the two seasons for further statistical analysis.

228 Both alpha diversity and beta diversity were calculated at species level for plants. Calculation of diversity
229 for invertebrates was carried out at family level. Invertebrates which could not be identified at family level
230 were also integrated into this calculation of diversity indices using their abundance at a taxonomic level as fine
231 as possible (i.e. order or class) (cf. SI Spreadsheet file). Dissimilarity matrix for beta diversity was built using
232 the Jaccard dissimilarity coefficient and partitioned into matrices for replacement and richness difference,
233 hereinafter referred to as “replacement” and “richness difference”, respectively.

234 2.3.3 *Soil data*

235 Soil properties and soil TM concentrations were referred to Fritsch et al. (2010). As concentrations of Cd,
236 Pb and Zn in soils were highly correlated (Pearson’s $r > 0.9$, p-value of correlation test < 0.001), it is not
237 possible to disentangle their individual effects. Only Pb concentration in soil was used as a proxy of soil TM
238 contamination in our statistical analyses. Soil pH and organic carbon content ($g\ kg^{-1}$) in soil, considered as a
239 proxy of the organic matter (OM) content in soils, were used as soil properties importantly related to metal
240 bioavailability (Bradham et al., 2006; Giller et al., 1998; Visioli et al., 2013). Soil pH was also positively
241 correlated with soil TM concentrations (Spearman’s $\rho > 0.6$, p-value of correlation test < 0.001 for the three

242 TM). For each buffer, we used soil TM contamination and soil properties of the nearest soil sampling point
243 from the given buffer (i.e. no more than 50 m). Trace metal soil contamination (as represented by Pb soil
244 concentrations), OM content and pH were hereinafter referred to as “Pb”, “pH”, and “OM”, respectively, and
245 linked to each buffer.

246 **2.4 Statistical Analysis**

247 *2.4.1 Data transformation*

248 Lead concentrations and OM, as well as abundance (i.e. total cover-abundance of plants or total number of
249 individual invertebrates), were logarithmically transformed because of their skewed distributions. Alpha
250 diversity and the soil variables were then scaled to zero mean and to unit variance for each variable because of
251 their different unit.

252 *2.4.2 Relationships between plant diversity and soil properties*

253 Before assessing the effects of plant diversity on invertebrate communities, the relationship between plant
254 diversity, soil TM contamination and soil properties was explored. Both alpha diversity indices and beta
255 diversity matrices for plants were calculated in vegetation patches near soil sampling points of Fritsch et al.
256 (2010). The analysis used vegetation around 17 soil sampling points, where plants were available for all three
257 strata.

258 A redundancy analysis (RDA) was executed for the alpha diversity in relation to soil TM contamination and
259 soil properties. A forward selection of significant explanatory variables was carried out (Borcard et al., 2018).
260 Proportion of variance explained by the selected explanatory variables was indicated by an adjusted R^2 (R^2_{adj})
261 (Peres-Neto et al., 2006). Relationships between plant beta diversity, soil TM contamination and soil properties
262 were assessed by using the distance-based RDA (dbRDA) (Legendre, 2014). Briefly, a principal coordinate
263 analysis (PCoA) was carried out for each dissimilarity matrix after square-rooted transformation. Their
264 principal coordinates were used as response variables and a forward selection of significant explanatory
265 variables was carried out, and R^2_{adj} was measured. Furthermore, species presence-absence data were *a*
266 *posteriori* projected on the ordination plot using weighted averages (Borcard et al., 2018), which shows how
267 occurrence of species in communities is affected by the environmental factors analyzed.

268 2.4.3 Relationships between diversity of invertebrates, diversity of plants and soil properties

269 The partial RDA (pRDA) and the variation partitioning was applied for invertebrate alpha diversity, using
270 soil TM contamination, soil properties and plant alpha diversity as explanatory variables (Borcard et al., 2018).
271 The pRDA for plant diversity was executed as follows: after RDA for invertebrate alpha diversity data in
272 relation to soil TM contamination and soil properties, the residual variation of this RDA (i.e. variation of
273 invertebrate diversity data non-explained by soil properties) was handled by another RDA in relation with plant
274 alpha diversity. This was *vice versa* for the pRDA in relation to soil properties. Variation explained by selected
275 variables of each explanatory matrix, as well as variation explained jointly by them, were shown using Venn
276 diagram. If one of the two explanatory matrices was not significantly related to the response matrix, ordinal
277 RDA was carried out. The partial dbRDA was applied for invertebrate beta diversity, using soil TM
278 contamination and soil properties and plant alpha diversity as explanatory variables. Invertebrate presence-
279 absence data were then *a posteriori* projected on the ordination obtained.

280 All statistical analyses and graphics were performed by the statistical software R (ver. 3.6.1; R Development
281 Core Team). PCA, PCoA and RDA were handled with the “vegan” package. The function “forward.sel” of the
282 package “adespatial” was used for forward selection. The functions “beta.div.comp” and “dbRDA.D” from
283 Legendre (2014) were used for building replacement and richness difference dissimilarity matrices and for
284 carrying out accurate significance test for dbRDA, respectively.

285 **3 Results and Discussion**

286 **3.1 Plant alpha and beta diversity in relation with soil TM contamination and soil properties**

287 Alpha diversity of plants was not significantly explained by soil TM contamination or soil properties,
288 whatever the plant stratum was. Beta diversity was significantly but weakly explained by soil properties:
289 replacement of tree and herbaceous strata was explained by pH ($R^2_{\text{adj}} = 0.052$ and 0.030 , respectively), whereas
290 replacement of shrub stratum was explained by Pb ($R^2_{\text{adj}} = 0.055$, for detail see Supporting Information SI
291 Figure 1). Richness difference was not significantly explained by soil TM contamination or soil properties in
292 all plant strata.

293 According to the ecological indicator value of Landolt et al. (2010) mainly based on plants of the Alpine
294 region, almost all plant species present in low and high metal contaminated buffers show tolerance to soil metal
295 content, referring predominantly to serpentine tolerance (i.e. the tolerance to nickel and chromium), and

296 preference for neutral acidity of soil (Supporting Information SI Figure 1 and SI Table 1). However, most
297 woody patches in our study area showed a high degree of soil anthropization (human density is more than 1000
298 people per km², Douay et al., 2009). Indeed, some *Salix* sp. and *Populus* sp. specimens, considered as plants
299 for phytoremediation of heavy metal-contaminated soils (Pulford and Watson, 2003), were observed in
300 vegetation patches with both high and low pH, as well as in patches with high or low soil contamination levels
301 (SI Table 1) (N.B. Concentrations of Pb in soil were used as a proxy of soil TM contamination and does not
302 mean influence of Pb.) This could mean that a large proportion of vegetation cover in our study area has been
303 maintained and/or modified by human management. Thus, effects of soil properties on diversity of vegetation
304 could be biased by anthropogenic factors in our study area. Nonetheless, our results suggest that diversity
305 indices of vegetation can be considered to be virtually independent of soil properties.

306 **3.2 Alpha and beta diversity for ground-dwelling (GD) invertebrates in relation with vegetation and** 307 **with soil TM contamination and soil properties.**

308 GD invertebrate diversity was more influenced by plant diversity than by soil TM contamination and/or soil
309 properties, but significant relationships varied between season, beta and alpha diversity of invertebrates, and
310 plant strata (Table 2).

311 In spring, alpha diversity was significantly explained by Simpson's index and abundance of herbs, Pb and
312 OM ($R^2_{\text{adj}} = 0.423$). Among the 42.3% of variance, 26.7% was explained only by Simpson's index and
313 abundance of herbs, 8.0% of variance was explained by Pb and OM, and 7.7% were shared by both plant
314 diversity and soil variables (Figure 2a). Controlling for soil variables, richness and abundance of GD
315 invertebrates were negatively correlated with abundance of herbs, whereas evenness was positively correlated
316 with abundance of herbs (Figure 2b). Moreover, Simpson's index of GD invertebrates was negatively
317 correlated with Simpson's index of herbs (Figure 2b). On the other hand, controlling for alpha diversity of
318 plants, Simpson's index and, to a lesser extent, richness of GD invertebrates were positively correlated with
319 Pb (Figure 2c). Evenness was positively correlated with OM, whereas abundance was negatively correlated
320 with OM (Figure 2c). Replacement was significantly but weakly explained by both pH and Simpson's index
321 of shrubs ($R^2_{\text{adj}} = 0.068$). Among the 6.8% of variance, 2.6% were explained by pH, 2.3% by Simpson's index
322 of shrubs, and 1.9% were shared by them (Figure 3a). Coleoptera were observed in buffers of both high and
323 low pH or Simpson's index of shrubs. Chilopoda, Opiliones and Glomeridae were present mostly in buffers
324 with low pH, whereas Araneae and Opiliones were observed in buffers with high Simpson's index of shrubs

325 (Supporting Information SI Figure 2 and SI Table 2). Richness difference was significantly explained by the
326 abundance of herbs as well as by Pb and OM ($R^2_{\text{adj}} = 0.198$). Among the 19.8% of variance, 7.2% were
327 explained by herb N, 4.0 % were explained by Pb and OM, and 8.7% were shared by them (Figure 3b). Apart
328 from Coleoptera, Arachnida and Glomeridae were present mostly in buffers with high Pb, whereas numerous
329 taxa such as Chilopoda, Arachnida, Glomeridae, and Polydesmidae were observed in low abundance of herbs
330 (SI Figure 1 and SI Table 2).

331 In autumn, alpha diversity for GD invertebrates was significantly explained by richness of trees ($R^2_{\text{adj}} =$
332 0.125) but not by soil properties. Evenness was positively correlated with richness of trees, whereas richness,
333 Simpson's index, and abundance of GD invertebrates were negatively correlated with richness of trees (Figure
334 4). Replacement was significantly explained by OM and pH, and abundance of shrubs ($R^2_{\text{adj}} = 0.151$). The two
335 soil properties explained themselves 8.3% of variance, and the rest of the variance (7.3%) was shared with
336 abundance of shrubs (Figure 5). Opiliones, Polydesmidae, Julidae, Isopoda and Formicidae were observed in
337 buffers with high OM and/or high pH (Supporting Information SI Figure 3 and SI Table 3). On the other hand,
338 richness difference was significantly explained by plant diversity richness of trees ($R^2_{\text{adj}} = 0.112$), but not by
339 soil properties. Many GD taxa were observed in low richness of trees, such as Araneae, Opiliones, Glomeridae,
340 Polydesmidae, Julidae, Chilopoda, Formicidae, and Coleoptera (SI Figure 3 and SI Table 3).

341 Our results demonstrate that both alpha and beta diversity of GD invertebrate communities are more
342 explained by plant diversity than by soil TM contamination or some soil properties. The influence of plant
343 diversity, however, largely varied according to plant strata, diversity indices, and seasons. It has been widely
344 reported in both grassland and woodlands that richness and abundance of aboveground invertebrates are
345 positively correlated with richness and abundance of herb layer plants (e.g. Borer et al., 2012; Haddad et al.,
346 2009). Rzanny et al. (2013) and Hertzog et al. (2016) showed more important and direct effects of plant biomass
347 than plant richness on predator arthropods like Carabidae, Staphylinidae or Araneae. Negative correlations we
348 observed between diversity of herbs and GD invertebrates in spring are not in agreement with these studies,
349 Koricheva et al., (2000) observed negative correlation between plant diversity and density of carabid beetles
350 and spiders in an experimental grassland study, though. Moreover, negative effects by grass richness on
351 diversity of predator arthropods was observed in the study of Hertzog et al. (2016), which could be due to low
352 nutritious values of grasses than other plants cascading to communities of herbivores and carnivore (Denno
353 and Fagan, 2003). Communities of arthropod predators strongly depend on plant functional groups and such

354 functional groups were not integrated in our study. Another possible reason is trappability bias due to herb
355 cover. Pitfall traps are effective for capturing highly mobile invertebrates (Uetz and Unzicker, 1976), but their
356 trappability depends on the soil surface, more or less suitable for their movement, and on invertebrates'
357 movement behavior. Complex structure of layer vegetation around pitfall traps could have affected trappability
358 of pitfall traps (Greenslade, 1964; Melbourne, 1999). In autumn, alpha diversity of GD invertebrates was
359 influenced by tree. In the literature, Schuldt et al. (2011) demonstrated that spider richness and abundance was
360 negatively correlated with tree species richness in forests, which concurs with our result. Meanwhile, influence
361 by herb was not observed in autumn. We suppose that effects of herbs could not be statistically deduced due to
362 low abundance of GD invertebrates in autumn (SI Spreadsheet file). Low abundance of GD invertebrates in
363 autumn could be due to their lower activity in this season. In fact, Grelle et al. (2000) observed higher density
364 of myriapods and isopods in spring than in autumn in metal contaminated sites and speculated seasonal change
365 in activity of these invertebrates. Niemelä et al. (1992) also reported higher abundance of carabid beetles in
366 spring than in autumn in woody sites, due to seasonal change of temperature. Moreover, seasonal variation in
367 activity of GD invertebrates could also be attributed to change in height of vegetation, as demonstrated in the
368 study of Hertzog et al. (2017) in an experimental grassland. Prather and Kaspari (2019) also showed that
369 activity of GD invertebrates increased in sites with vegetation clipping. In our study, cover-abundance was
370 used as a proxy to the abundance of plants but height of herbs was not considered. However, herbs had grown
371 from spring and became higher in autumn, which could reduce activity of GD invertebrates.

372 Change in species composition due to different sensitivity to metal contamination among taxa could be one
373 explanation for the relationship between diversity of plants and invertebrate communities. For example,
374 Glomeridae and Polydesmidae are considered to be tolerant to metal pollution due to their high abundance in
375 polluted sites (Read et al., 1998). Abundance of staphylinid beetle was positively correlated with soil Zn content
376 in northern France (Nahmani and Lavelle, 2002). Ants are also considered to be relatively tolerant to metal
377 pollution (Eeva et al., 2004). Isopods have been well documented in the literature as suitable indicators for
378 metals pollution due to their capacity to accumulate and immobilize metals at high levels in their body (e.g.
379 Blanuša et al., 2002; Hopkin, 1990; Hopkin et al., 1993; Hopkin and Martin, 1982; Hussein et al., 2006).
380 Isopods also have several mechanisms for adaptation to metal contaminated habitats, such as avoidance for
381 metal contaminated food and excretion of inner metals (Donker et al., 1996; Drobne, 1997; Odendaal and
382 Reinecke, 1999; Zidar et al., 2004). These taxa mentioned above were observed in buffers with high soil TM

383 contamination and/or low pH in our study (SI Spreadsheet; SI Table 2; SI Table 3). Likewise, change in
384 composition of GD invertebrates along the gradients of vegetation could explain our results. Our results
385 actually showed that shrub diversity explained replacement in GD invertebrate communities. A diversified
386 plant community can provide a variety of resources for herbivore species, which then support prey availability
387 for predators (Hutchinson, 1959; Root, 1973). Schuldt et al. (2008) and Vehviläinen et al. (2008) also argued
388 that the abundance of predatory arthropods like spiders, ants or carabids strongly depends on the presence of
389 specific trees due to several factors such as favorable microclimates, prey abundance or foraging efficiency
390 enhanced by those trees. In our study, phytophagous Curculionidae, saprophagous Aphodiidae, and zoophagous
391 Silphidae, Lampyridae, Staphylinidae, as well as Araneae and Opiliones, were observed in buffers with high
392 Simpson's index of shrubs, whereas saprophagous Forficulidae and polyphagous Elateridae were observed
393 with low Simpson's index of shrubs (diet category on the basis of Jeannel (1941) and Mora (2002); SI Table
394 2). Furthermore, other abiotic factors also can determine the composition of GD invertebrates, such as
395 temperature, soil moisture, and quality of humus (Koivula et al., 1999; Niemelä et al., 1992; Perner and Malt,
396 2003; Zimmer et al., 2000; Zimmer and Topp, 2000). Soil pH is also one of the factors determining the
397 composition of GD invertebrates even in unpolluted sites (Schuldt et al., 2011). Communities of GD
398 invertebrates could be indirectly shaped by vegetation that controls these parameters, rather than directly by
399 soil TM contamination and/or soil properties.

400 **3.3 Alpha and beta diversity of flying invertebrates in relation to soil properties and vegetation**

401 Flying invertebrate diversity was influenced by plants but not by soil properties. Only beta diversity, but not
402 alpha diversity, was significantly explained by plant diversity of different strata (Table 2).

403 In spring, replacement was significantly but weakly explained by richness of shrubs ($R^2_{adj} = 0.062$). Many
404 taxa were observed in buffers with either high or low richness of shrubs. Moreover, considering the diet of
405 flying invertebrates taxonomic groups according to Jeannel, (1941) and Mora (2002), predator or parasitoid
406 flying invertebrates were more observed in buffers with low richness of shrubs than in buffers with high
407 richness of shrubs (Supporting Information SI Figure 4 and SI Table 4). In autumn, Richness difference was
408 significantly explained by Simpson's index of trees, evenness of shrubs, and abundance of herbs ($R^2_{adj} = 0.523$).
409 Many types of diet categories (e.g. zoophagous, saprophagous, phytophagous, opophagous) were observed in
410 buffers where plant diversity indices were high (SI Figure 4 and SI Table 4).

411 In a recent meta-analysis (Zvereva and Kozlov, 2010), a decrease in population density of epigeic arthropods
412 (e.g. Aranea, Formicidae, Carabidae and Staphylinidae) with increased air pollution (thus not only by TM) was
413 observed, while the density of other arthropod groups, including flying invertebrates, increased. The same
414 meta-analysis also demonstrated that responses of population density to pollution were negative for Arachnida
415 and Coleoptera but positive for Lepidoptera and Hemiptera. Responses to pollutions are likely to differ between
416 ground-dwelling and flying invertebrates.

417 On the contrary, plant diversity only influenced the composition of flying invertebrates. Based on data about
418 flowering period of woody plants by Landolt et al. (2010), spring was the main flowering period of many trees
419 and shrubs in our study area. Availability of young leaves and flowers of shrubs might mostly draw attention
420 of phytophagous and/or nectarivorous invertebrates. In autumn, diversity indices of many strata were related
421 to beta diversity. Tree species richness in woodland system positively affects richness, diversity and/or
422 abundance of flying invertebrate families like Hymenoptera (Fraser et al., 2007; Sperber et al., 2004) or Diptera
423 (Scherber et al., 2014) due to an increased heterogeneity of structures and availability of resources. Hirao et al.
424 (2009) also showed that lepidopteran community was vertically stratified, which suggests that more vertically
425 diversified habitats might support a more diversified flying invertebrate community. Seasonal difference of
426 diversity of flying invertebrates could be explained, at least partly, by flowering seasons of plants. Furthermore,
427 trapping efficiency by pan traps could also vary among seasons. Rodriguez-Saona et al. (2012) actually
428 demonstrated seasonal change in color preference coinciding with blooming season in blunt-nosed and sharp-
429 nosed leafhoppers (Hemiptera: Cicadellidae). Our results strongly suggest that vegetation shapes the
430 composition of flying invertebrates while environmental metal pollution of soils did not significantly act as a
431 filter.

432 **3.4. Limitations of the study**

433 With limited duration of invertebrate field investigation, invertebrate community data in this study cannot
434 be considered as a reliable estimation of true diversity and composition of invertebrate communities. Thus our
435 study should be considered as a snapshot evaluation of the separate and combined influences of vegetation,
436 soil characteristics and TM contaminants on invertebrate communities. Another drawback in our results is the
437 variable degree of taxonomic resolution (cf. SI Spreadsheet file), which might have prevented us to find further
438 relationships between invertebrate communities and plant communities or soil contamination or properties.

439 **4 Conclusion**

440 This study sheds light on the effects of plant diversity on diversity and composition of aboveground
441 invertebrate community in a site contaminated by TM. Our results overall indicated that plant diversity shapes
442 community of flying invertebrates and is also a factor controlling both diversity and composition of ground-
443 dwelling invertebrates more importantly than TM contamination and other soil properties do. Although
444 underlying mechanisms about complex correlations between diversity of invertebrates and both diversity of
445 plants and soil properties remain an issue for further studies, our results suggest that soil TM contamination
446 and soil properties did not independently and substantially impact invertebrate communities. This study is, to
447 our knowledge, the first one on a metal polluted ecosystem to actually disentangle the relative importance of
448 two major parameters likely to shape invertebrate communities, plant communities and soil contamination and
449 properties. This will pave the road to the evaluation of contaminant impacts on terrestrial invertebrate
450 community dynamics, and to further insights into pollutant induced community tolerance.

451

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464 **Supporting information**

465 SI Figure 1: Biplots of distance-based redundancy analysis on replacement of plants of tree, shrub, and
466 herbaceous strata.

467 SI Figure 2: Biplots of partial distance-based redundancy analysis on beta diversity matrices of ground-
468 dwelling invertebrates in spring.

469 SI Figure 3: Biplots of partial distance-based redundancy analysis on beta diversity matrices of ground-
470 dwelling invertebrates in autumn.

471 SI Figure 4: Biplots of distance-based redundancy analysis on beta diversity matrices of flying invertebrates in
472 spring and autumn.

473

474 SI Table 1: Plant species observed in buffer with high and low values of soil properties and some of their life
475 history traits.

476 SI Table 2: Ground-dwelling invertebrates observed in buffers with high and low selected soil properties or
477 plant diversity indices in spring.

478 SI Table 3: Ground-dwelling invertebrates observed in buffers with high and low selected soil properties or
479 plant diversity indices in autumn.

480 SI Table 4: Flying invertebrates observed in buffers with high and low plant diversity indices in the two seasons.

481

482 SI Spreadsheet file: Taxonomic resolution of invertebrates.

483

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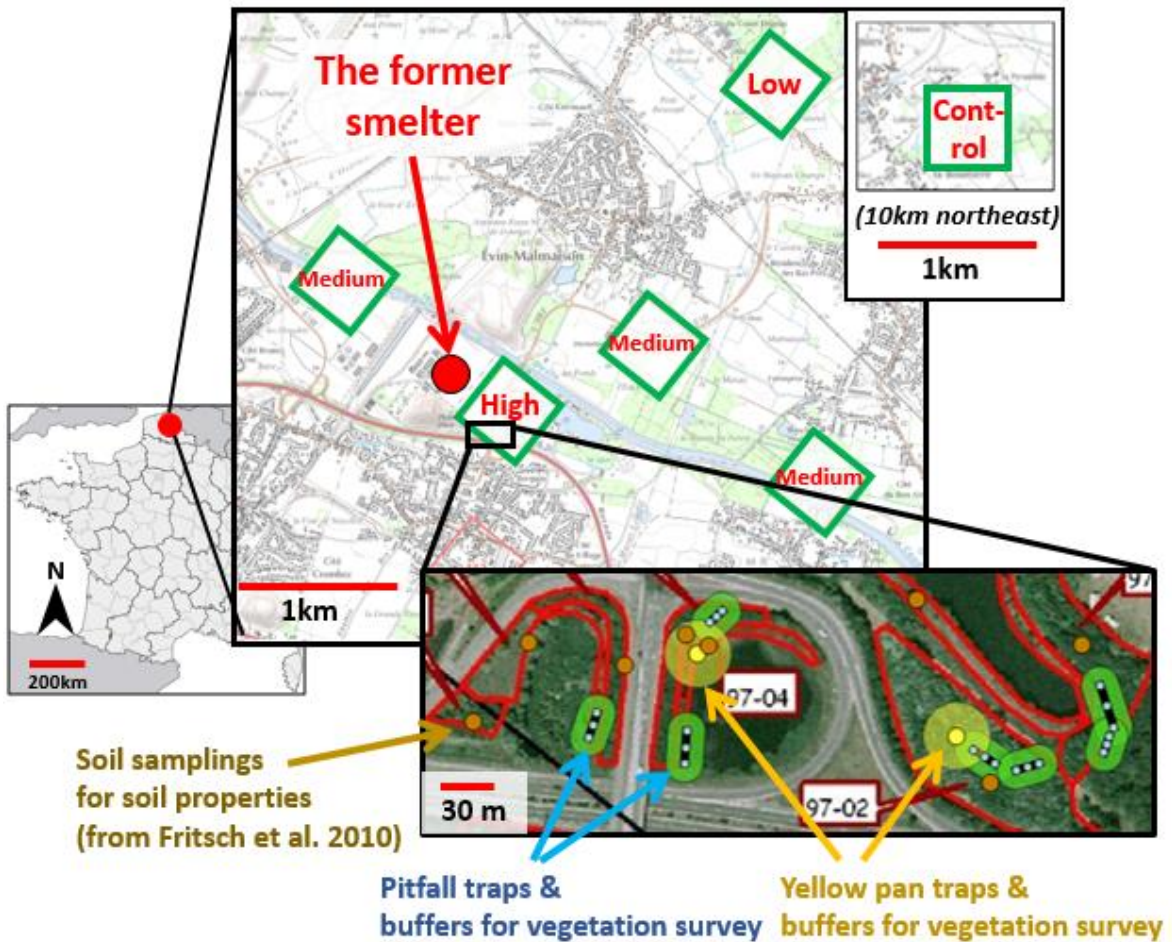
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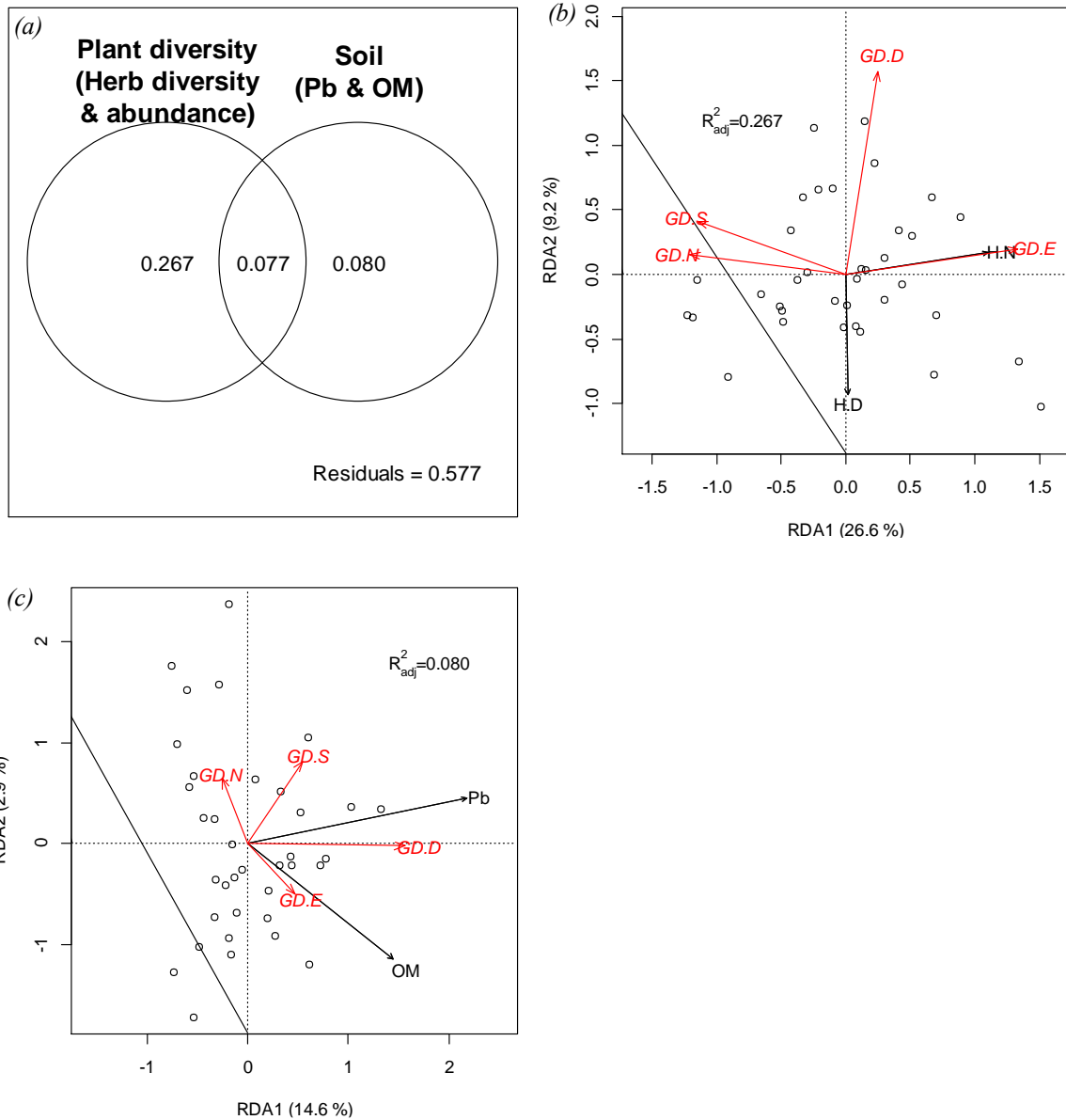
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730 *Figure 1: Maps of the study area. Three upper maps show the position of the former smelter Metaleurop nord*
 731 *(red circle) and of the six study sites (green border boxes with their contamination level in red letters). Lower*
 732 *right map shows sampling strategy for plants and invertebrates. Three pitfall traps were set in line (black line*
 733 *with three blue points) in woody patches and each trap line was considered as one sampling point for ground-*
 734 *dwelling invertebrates. Vegetation in a buffer of 1000m² around a trap line (green oval) was linked to the given*
 735 *trap line. Similarly, yellow pan traps (yellow points) were set in woody patches and vegetation in a buffer of*
 736 *1000m² around a trap (yellow circles) was linked to the given pan trap. Soil properties of given woody patches*
 737 *(red polygons with brown point indicating soil sample, from Fritsch et al. 2010) were attributed to each trap*
 738 *line and pan trap.*



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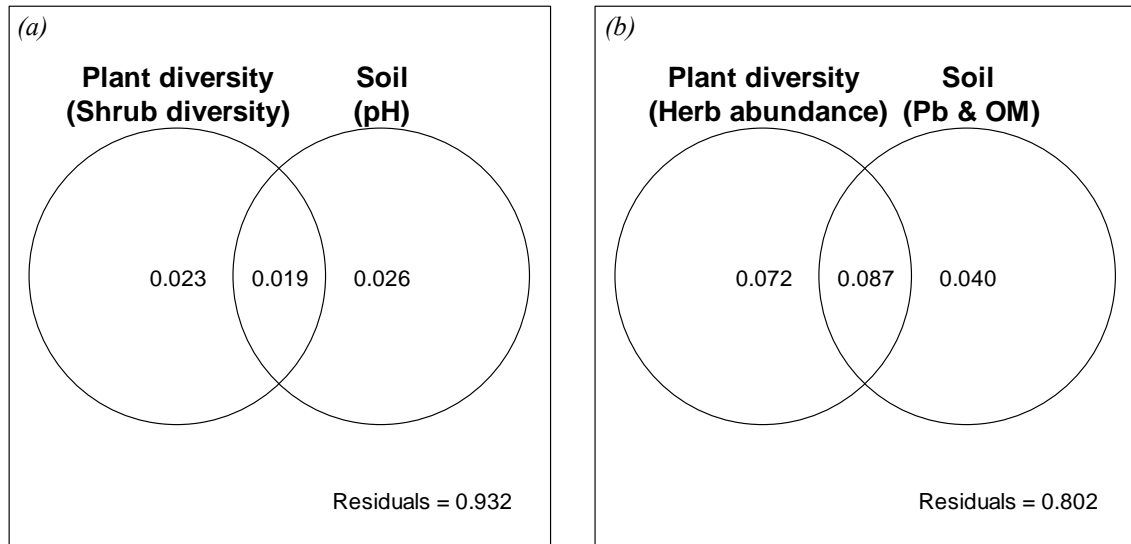
740 *Figure 2: Results of partial redundancy analysis (pRDA) on alpha diversity indices for ground-dwelling (GD)*
 741 *invertebrates in spring. (a) Venn diagram represents variance explained by diversity of plants and soil*
 742 *properties. (b) Biplot of pRDA on invertebrate diversity explained only by plant diversity indices. (c) Biplot of*
 743 *pRDA on invertebrate diversity explained only by soils properties. GD.D, GD.E, GD.N, GD.S: Simpson's*
 744 *diversity index, Simpson's evenness, abundance and richness of GD invertebrates, respectively. H.D, H.N:*
 745 *Simpson's diversity index and abundance of herbaceous stratum, respectively.*



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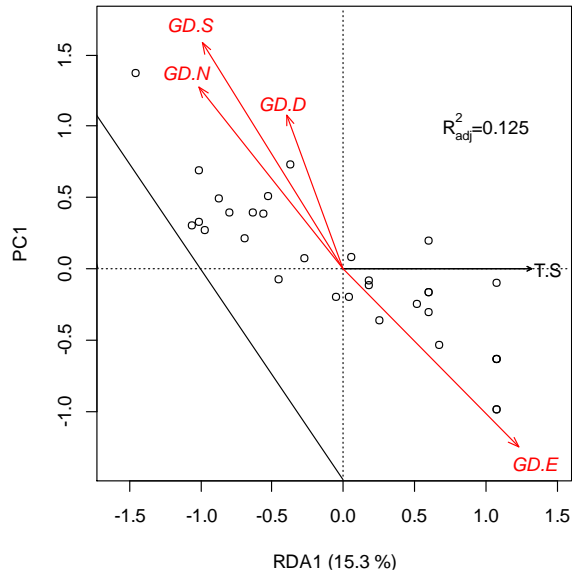
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748 *Figure 3: Results of partial distance-based redundancy analysis on beta diversity matrices for GD*
749 *invertebrates in spring. Venn diagrams represent variance explained by diversity for plants and soil properties*
750 *for replacement of GD invertebrates in (a) and for richness difference of GD invertebrates in (b).*



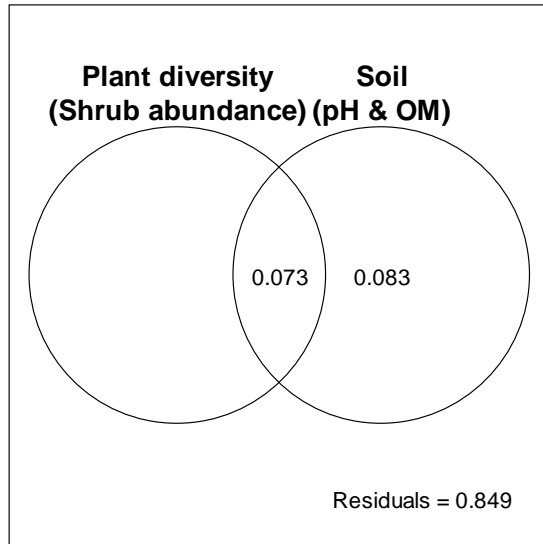
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752 Figure 4: Biplot of redundancy analysis (RDA) on alpha diversity indices for GD invertebrates in autumn.
753 GD.D, GD.E, GD.N, GD.S: Simpson's diversity index, Simpson's evenness, abundance and richness of GD
754 invertebrates, respectively. TS: tree stratum richness.



755

756 Figure 5: Results of partial distance-based redundancy analysis on replacement of GD invertebrates in autumn.
757 Venn diagram represents variance explained by diversity for plants and soil properties. (N.B. There is no value
758 in the circle for plant diversity because all variance explained by plant diversity was shared with variance
759 explained by soil parameters.)



760

Values <0 not shown

761 *Table 1. Summary for soil physico-chemical properties, numbers of encaptured specimens and determined taxa of ground-dwelling (GD) and flying invertebrates for the six*
 762 *sites.*

	TE2	103	117	097	171	043
Soil contamination level	Control ^a	Low	Moderate	High	Moderate	Moderate
[Cd] _{soil} (mg kg ⁻¹) ^b	0.9 - 2.4	1.5 - 6.0	3.6 - 17.8	15.3 - 236.5	4.9 - 14.5	1.3 - 42.7
Min - Max (Median)	(1.4)	(4.3)	(9.1)	(48.3)	(7.5)	(15.2)
[Pb] _{soil} (mg kg ⁻¹) ^b	43.3 - 199.8	237.5 - 333.0	244.7 - 859.8	658.5 - 6809.4	287.6 - 2063.3	105.0 - 1028.9
Min - Max (Median)	(107.4)	(267.2)	(512.0)	(1295.3)	(584.0)	(323.1)
[Zn] _{soil} (mg kg ⁻¹) ^b	89.3 - 277.7	114.4 - 407.5	302.8 - 958.5	1069.3 - 7263.5	487.2 - 2451.5	153.9 - 1549.6
Min - Max (Median)	(168.8)	(352.7)	(555.8)	(1874.7)	(1362.7)	(512.8)
pH ^b	4.5 - 7.2	4.6 - 6.9	7.3 - 8.1	7.9 - 8.2	7.7 - 8.3	6.2 - 8.3
Min - Max (Median)	(5.9)	(5.6)	(7.9)	(8.0)	(8.0)	(7.0)
OM (g kg ⁻¹) ^b	26.1 - 186.0	47.7 - 96.3	34.3 - 77.3	31.5 - 110.9	35.0 - 223.0	28.5 - 125.4
Min - Max (Median)	(52.6)	(54.8)	(60.5)	(50.5)	(95.8)	(57.9)
Number of buffers ^c for GD invertebrates (spring / autumn)	14 (7 / 7)	15 (8 / 7)	6 (2 / 4)	9 (7 / 2)	14 (7 / 7)	10 (5 / 5)
Number of enraptured GD invertebrates by buffer (Min - Max)	1 - 19	8 - 199	6 - 25	1 - 106	1 - 15	3 - 77
Number of determined taxa of GD invertebrates by buffer (Min - Max)	1 - 5	2 - 10	2 - 5	1 - 10	1 - 7	2 - 9
Number of buffers ^c for flying invertebrates (spring / autumn)	4 (1 / 3)	5 (3 / 2)	3 (1 / 2)	4 (2 / 2)	4 (3 / 1)	4 (2 / 2)
Number of enraptured flying invertebrates by buffer (Min - Max)	11 - 179	31 - 220	34 - 311	82 - 313	39 - 168	108 - 325
Number of determined taxa of flying invertebrates by buffer (Min - Max)	10 - 38	10 - 31	13 - 29	18 - 23	16 - 27	22 - 31

763 a: TM concentrations as close as possible to background concentrations.

764 b: Values from Fritsch et al. (2010)

765 c: Buffers where plants of all strata were present.

766 Table 2. Plant diversity and soil properties significantly influencing alpha and beta diversity of ground-
 767 dwelling (GD) and flying invertebrates.

Type of invertebrates	Season	Type of diversity	Significant influence	
			Plant stratum	Soil properties
GD invertebrates	Spring	<i>Alpha</i>	Herb	Pb, OM
		<i>Beta</i>	Shrub & herb	pH
	Autumn	<i>Alpha</i>	Tree	-
		<i>Beta</i>	Tree & shrub	Pb
Flying invertebrates	Spring	<i>Alpha</i>	-	-
		<i>Beta</i>	Shrub	-
	Autumn	<i>Alpha</i>	-	-
		<i>Beta</i>	Tree, shrub & herb	-

768

Supporting Information for:

Vegetation shapes diversity and composition of aboveground invertebrates more than soil properties and pollution: a preliminary investigation on a metal contaminated site

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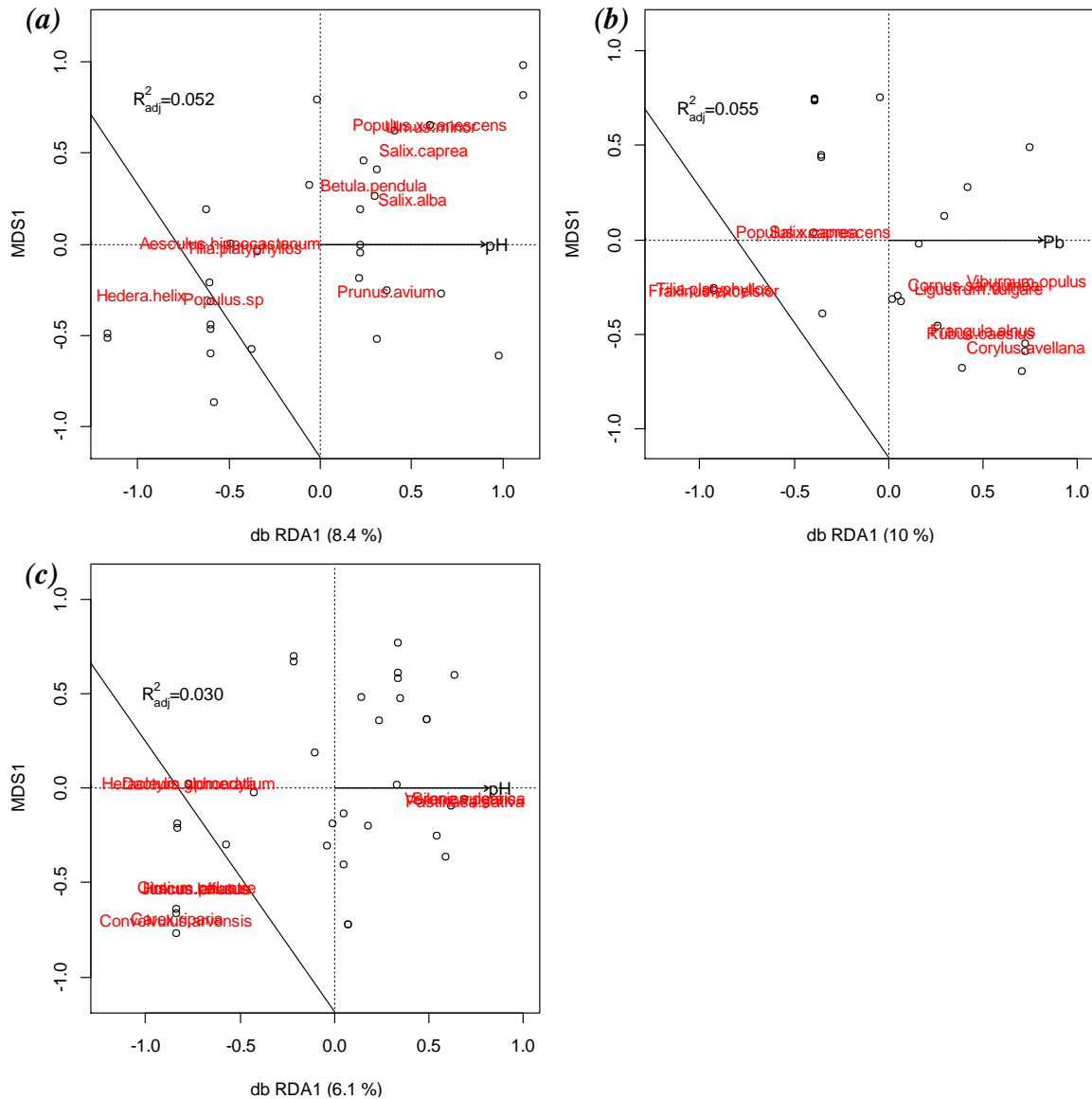
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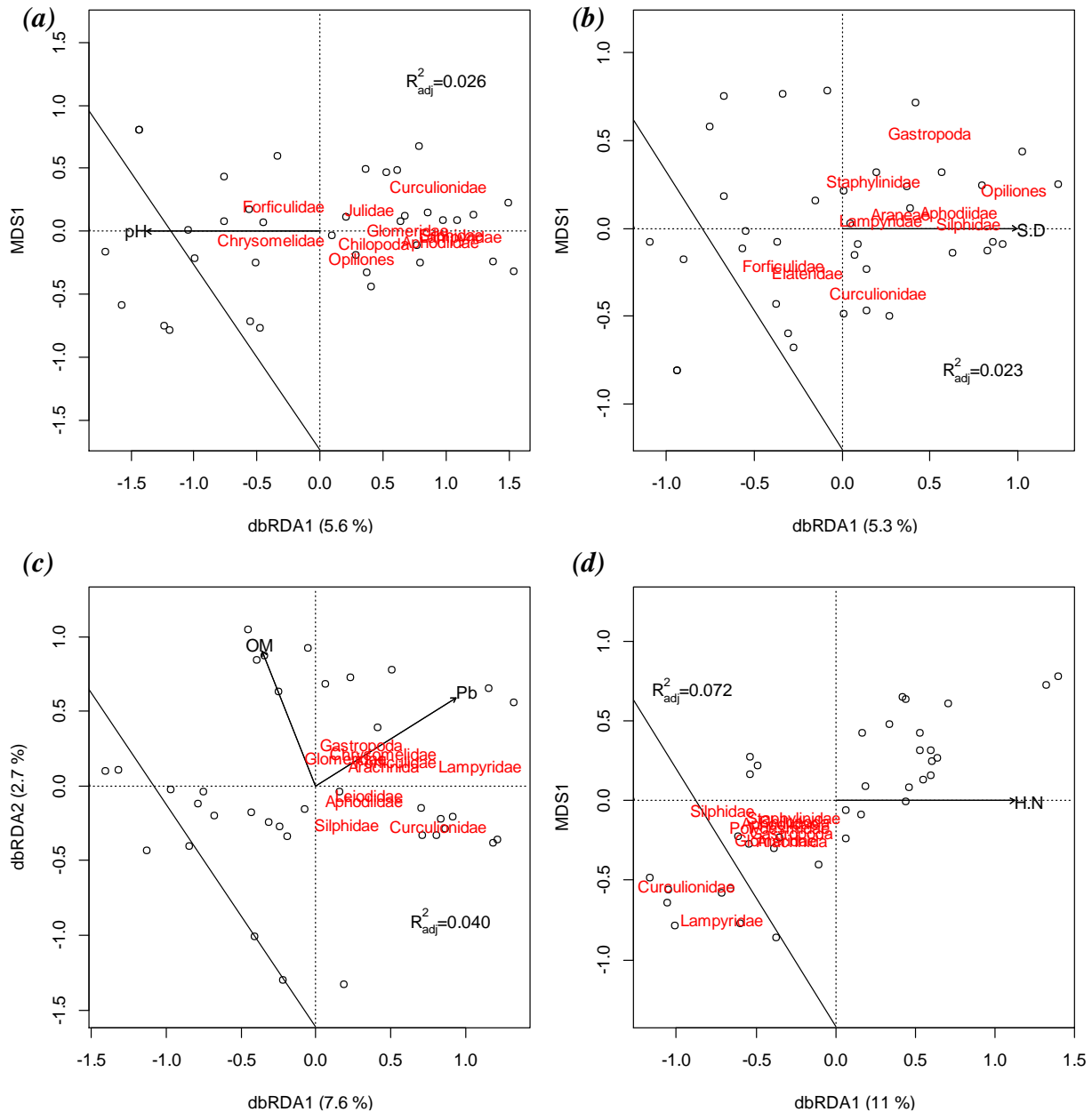
Both authors contributed equally to supervising this work

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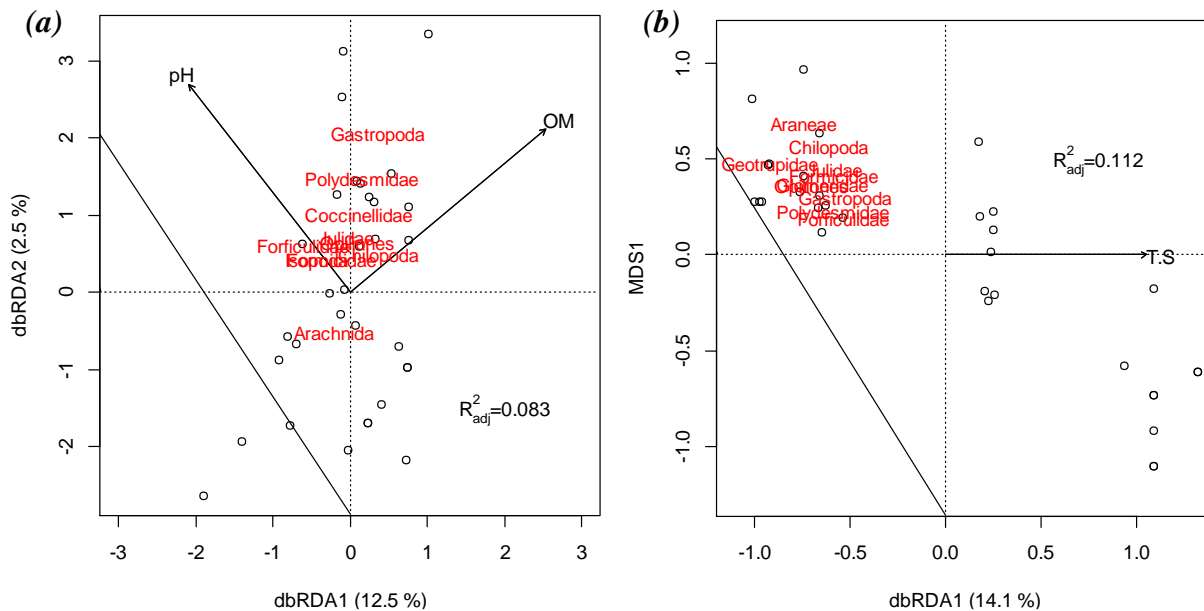
Supporting Information SI Figure 1	Page S1
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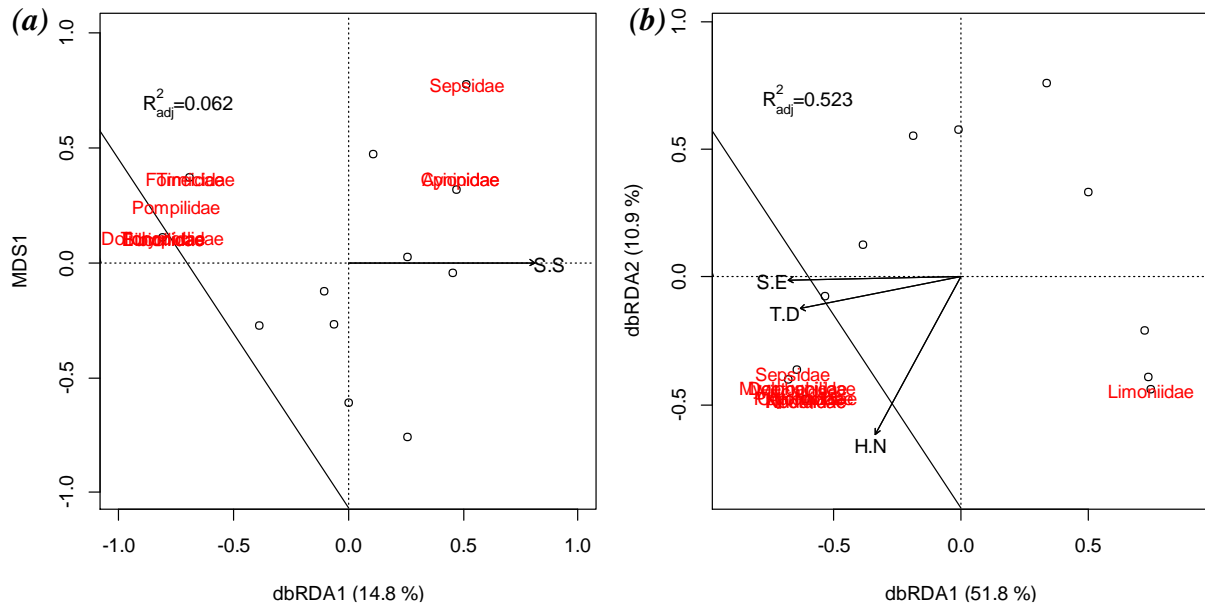
Supporting Information SI Figure 1: Biplots of distance-based redundancy analysis on replacement of plants of tree (a), shrub (b), and herbaceous (c) strata. The x axis represents the first (and the only) canonical axis and the y axis represent the first unconstrained axis. Vegetation is represented by points and selected soil property variables are represented by arrows (pH: soil pH; Pb: soil Pb concentrations). Species whose occurrence in buffers was related to selected soil properties or TM concentrations were a posteriori projected as weighted averages (in red). Adjusted R^2 (R^2_{adj}) is mentioned in each plot.



Supporting Information SI Figure 2: Biplots of partial distance-based redundancy analysis on beta diversity matrices of ground-dwelling invertebrates in spring. Replacement explained by only soils properties (a) and explained by only plant diversity indices (b). Richness difference in spring explained by only soils properties (c), and by only plant diversity indices (d). The x axis represents the first canonical axis, and the y axis represents the second canonical axis (c) or the first unconstrained axis (a, b and d). Buffers are represented by points and the selected variables are represented by arrows (pH: soil pH; Pb: soil Pb concentrations; OM, soil organic matter content; SD: Simpson diversity for shrubs; HN: abundance of herbs). Species whose occurrence in buffers was related to selected soil properties or TM concentrations were a posteriori projected as weighted averages (in red). Adjusted R^2 (R^2_{adj}) is mentioned in each plot.



Supporting Information SI Figure 3: Biplots of partial distance-based redundancy analysis on beta diversity matrices of ground-dwelling invertebrates in autumn. Replacement explained by only soils properties (a), and richness difference explained by plant diversity indices (b). The x axis represents the first canonical axis, and the y axis represents the second canonical axis (a) or the first unconstrained axis (b). Buffers are represented by points and the selected variables are represented by arrows (pH: soil pH; OM, soil organic matter content; TS: richness of trees). Species whose occurrence in buffers was related to selected soil properties or TM concentrations were a posteriori projected as weighted averages (in red). Adjusted R^2 (R^2_{adj}) is mentioned in each plot.



Supporting Information SI Figure 4: Biplots of distance-based redundancy analysis on replacement of flying invertebrates in spring (a) and on richness difference in autumn (b) explained by plant diversity indices. The x axis represents the first canonical axis, and the y axis represents the second canonical axis (b) or the first unconstrained axis (a). Buffers are represented by points and the selected variables are represented by arrows (SS: richness of shrubs; TD: Simpson diversity for trees; SE: Simpson's evenness for shrubs; HN: abundance of herbs). Species whose occurrence in buffers was related to selected soil properties or TM concentrations were a posteriori projected as weighted averages (in red). Adjusted R^2 (R^2_{adj}) is mentioned in each plot.

Supporting Information SI Table 1: Plant species observed in buffer with high and low values of soil properties and some of their life history traits (metal tolerance, pH tolerance and flowering months) from Landolt et al. (2010). Reaction characterizes the content of free H-ions in the soils, from 1 (extremely acid) to 5 (alkaline, high pH), and x signifies a very large range of variation. Certain tolerance to metals in the soil, referring predominantly to serpentine tolerance, i.e. the tolerance to nickel and chromium, is represented by 'X' and empty cells signifies no particular studies for a given species.

Taxa			Soil properties		Soil indicators	
Stratum	Species	Family	pH _[soil]	Pb _[soil]	Reaction	Heavy metal tolerance
Tree	<i>Hedera helix</i>	<i>Araliaceae</i>	Low		3	X
	<i>Tilia platyphyllos</i>	<i>Tiliaceae</i>	Low		4	X
	<i>Aesculus hippocastanum</i>	<i>Hippocastanaceae</i>	Low		4	X
	<i>Salix caprea</i>	<i>Salicaceae</i>	High		3	X
	<i>Betula pendula</i>	<i>Betulaceae</i>	High		x	X
	<i>Salix alba</i>	<i>Salicaceae</i>	High		4	
	<i>Populus x canescens</i>	<i>Salicaceae</i>	High		4	
	<i>Ulmus minor</i>	<i>Ulmaceae</i>	High		4	
Shrub	<i>Tilia platyphyllos</i>	<i>Tiliaceae</i>		Low	4	X
	<i>Fraxinus excelsior</i>	<i>Oleaceae</i>		Low	4	X
	<i>Salix caprea</i>	<i>Salicaceae</i>		Low	3	X
	<i>Populus x canescens</i>	<i>Salicaceae</i>		Low	4	
	<i>Cornus sanguinea</i>	<i>Cornaceae</i>		High	4	X
	<i>Frangula alnus</i>	<i>Rhamnaceae</i>		High	3	X
	<i>Ligustrum vulgare</i>	<i>Oleaceae</i>		High	4	X
	<i>Rubus caesius</i>	<i>Rosaceae</i>		High	4	X
	<i>Viburnum opulus</i>	<i>Caprifoliaceae</i>		High	3	X
	<i>Corylus avellana</i>	<i>Betulaceae</i>		High	3	X
Herb	<i>Cirsium palustre</i>	<i>Asteraceae</i>	Low		3	X
	<i>Holcus lanatus</i>	<i>Poaceae</i>	Low		3	X
	<i>Juncus effusus</i>	<i>Juncaceae</i>	Low		2	X
	<i>Carex riparia</i>	<i>Cyperaceae</i>	Low		4	
	<i>Convolvulus arvensis</i>	<i>Convolvulaceae</i>	Low		4	X
	<i>Dactylis glomerata</i>	<i>Poaceae</i>	Low		3	X
	<i>Heracleum sphondylium</i>	<i>Apiaceae</i>	Low		3	
	<i>Pastinaca sativa</i>	<i>Apiaceae</i>	High		4	X
	<i>Silene vulgaris</i>	<i>Caryophyllaceae</i>	High		3	X
	<i>Veronica persica</i>	<i>Scrophulariaceae</i>	High		4	X

Supporting Information SI Table 2: Ground-dwelling invertebrate families observed in buffers with high and low selected soil properties or plant diversity indices in spring and their diet from Jeannel (1941) and Mora (2002).

Beta diversity	Variables influencing beta diversity		Taxa	Diet
Replacement	Soil properties	High pH	<i>Chrysomelidae</i> (Coleoptera)	phytophagous
			<i>Forficulidae</i> (Dermaptera)	saprophagous
		Low pH	<i>Curculionidae</i> (Coleoptera)	phytophagous
			<i>Chilopoda</i> (Myriapoda)	zoophagous
			<i>Lampyridae</i> (Coleoptera)	zoophagous
			<i>Silphidae</i> (Coleoptera)	zoophagous
			<i>Opiliones</i> (Spider)	zoosaprophage
			<i>Aphodiinae</i> (Coleoptera)	saprophagous
			<i>Julidae</i> (Diplopoda)	saprophagous
			<i>Glomeridae</i> (Diplopoda)	saprophagous
	Plant diversity	High shrub Simpson's diversity	<i>Curculionidae</i> (Coleoptera)	phytophagous
			<i>Gastropoda</i>	phytophagous
			<i>Silphidae</i> (Coleoptera)	zoophagous
			<i>Lampyridae</i> (Coleoptera)	zoophagous
			<i>Staphylinidae</i> (Coleoptera)	zoophagous
			<i>Araneae</i> (Spider)	zoophagous
		<i>Opiliones</i> (Spider)	zoosaprophagous	
		<i>Aphodiidae</i> (Coleoptera)	saprophagous	
	Low shrub Simpson's diversity		<i>Forficulidae</i> (Dermaptera)	saprophagous
			<i>Elateridae</i> (Coleoptera)	mixed

(Continuous)

Beta diversity	Variables influencing beta diversity		Taxa	Diet
Richness Difference	Soil properties	High Pb	<i>Chrysomelidae</i> (<i>Coleoptera</i>)	phytophagous
			<i>Gastropoda</i>	phytophagous
			<i>Lampyridae</i> (<i>Coleoptera</i>)	zoophagous
			<i>Arachnida</i> (<i>Spider</i>)	zoophagous
			<i>Forficulidae</i> (<i>Dermaptera</i>)	saprophagous
			<i>Glomeridae</i> (<i>Diplopoda</i>)	saprophagous
		High Pb & low OM	<i>Curculionidae</i> (<i>Coleoptera</i>)	phytophagous
			<i>Lampyridae</i> (<i>Coleoptera</i>)	zoophagous
		Low OM	<i>Silphidae</i> (<i>Coleoptera</i>)	zoophagous
			<i>Leiodidae</i> (<i>Coleoptera</i>)	saprophagous
		<i>Aphodiidae</i> (<i>Coleoptera</i>)	saprophagous	
	Plant diversity	Low herb abundance	<i>Curculionidae</i> (<i>Coleoptera</i>)	phytophagous
			<i>Gastropoda</i>	phytophagous
			<i>Lampyridae</i> (<i>Coleoptera</i>)	zoophagous
			<i>Silphidae</i> (<i>Coleoptera</i>)	zoophagous
			<i>Staphylinidae</i> (<i>Coleoptera</i>)	zoophagous
			<i>Chilopoda</i> (<i>Myriapoda</i>)	zoophagous
			<i>Arachnida</i> (<i>Spider</i>)	zoophagous
			<i>Glomeridae</i> (<i>Diplopoda</i>)	saprophagous
			<i>Aphodiidae</i> (<i>Coleoptera</i>)	saprophagous
			<i>Polydesmidae</i> (<i>Diplopoda</i>)	saprophagous

Supporting Information SI Table 3: Ground-dwelling invertebrates observed in buffers with high and low selected soil properties or plant diversity indices in autumn and their diet from Jeannel (1941) and Mora (2002).

Beta diversity	Variables influencing beta diversity		Taxa	Diet
Replacement	Soil properties	High pH & High OM	<i>Gastropoda</i>	phytophagous
			<i>Coccinellidae</i> (<i>Coleoptera</i>)	zoophagous
			<i>Opiliones</i> (<i>Spider</i>)	zoosaprophage
			<i>Polydesmidae</i> (<i>Diplopoda</i>)	saprophagous
			<i>Julidae</i> (<i>Diplopoda</i>)	saprophagous
		Low pH & low OM	<i>Arachnida</i> (<i>Spider</i>)	mixed
		High pH	<i>Formicidae</i> (<i>Hymenoptera</i>)	omnivorous
			<i>Forficulidae</i> (<i>Dermaptera</i>)	saprophagous
			<i>Isopoda</i>	saprophagous
	Plant diversity	(No variable)		
Richness Difference	Soil properties	(No variable)		
	Plant diversity	Low tree richness	<i>Gastropoda</i>	phytophagous
			<i>Formicidae</i> (<i>Hymenoptera</i>)	omnivorous
			<i>Chilopoda</i> (<i>Myriapoda</i>)	zoophagous
			<i>Araneae</i> (<i>Spider</i>)	zoophagous
			<i>Opiliones</i> (<i>Spider</i>)	zoo-saprophagous
			<i>Geotrupidae</i> (<i>Coleoptera</i>)	saprophagous
			<i>Forficulidae</i> (<i>Dermaptera</i>)	saprophagous
			<i>Glomeridae</i> (<i>Diplopoda</i>)	saprophagous
			<i>Polydesmidae</i> (<i>Diplopoda</i>)	saprophagous
			<i>Julidae</i> (<i>Diplopoda</i>)	saprophagous

Supporting Information SI Table 4: Flying invertebrates observed in buffers with high and low selected soil properties or plant diversity indices and their diet in larvae and in adult from Jeannel (1941) and Mora (2002).

Beta diversity	Variables influencing beta diversity	Taxa	Diet (larvae)	Diet (adult)	
Replacement in spring	Soil properties	No variable			
	Plant diversity	High shrub richness	<i>Apionidae</i> (Coleoptera) <i>Cynipidae</i> (Hymenoptera) <i>Sepsidae</i> (Diptera)	phytophagous endophytrophagous saprophagous	phytophagous ? saprophagous
		Low shrub richness	<i>Torymidae</i> (Hymenoptera) <i>Tineidae</i> (Lepidoptera) <i>Bibionidae</i> (Diptera) <i>Formicidae</i> (Hymenoptera) <i>Dolichopodidae</i> (Diptera) <i>Pompilidae</i> (Hymenoptera) <i>Eucoilidae</i> (Hymenoptera)	phytophagous saprophagous saprophagous omnivorous zoophagous zoophagous parasitoid	mixed nectarivorous none omnivorous zoophagous zoophagous ?
Richness Difference in autumn	Soil properties	No variable			
	Plant diversity	High tree Simpson's diversity, shrub evenness & herb abundance	<i>Noctuidae</i> (Lepidoptera) <i>Delphacidae</i> (Hemiptera) <i>Chloropidae</i> (Diptera) <i>Agromyzidae</i> (Diptera) <i>Apionidae</i> (Coleoptera) <i>Mycetophilidae</i> (Diptera) <i>Milichiidae</i> (Diptera) <i>Psychodidae</i> (Diptera) <i>Nitidulidae</i> (Coleoptera) <i>Sepsidae</i> (Diptera) <i>Forficulidae</i> (Dermaptera) <i>Pompilidae</i> (Hymenoptera) <i>Carabidae</i> (Coleoptera)	phyllophagous opophagous endophytrophagous endophytrophagous phytophagous mycetophagous zoosaprophagous saprophagous saprophagous saprophagous saprophagous zoophagous zoophagous	nectarivorous opophagous nectarivorous phytophagous phytophagous ? zoosaprophagous none saprophagous saprophagous saprophagous zoophagous zoophagous
		Low shrub evenness	<i>Limoniidae</i> (Diptera)	mixed	none

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