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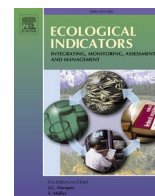
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Using plant litter decomposition as an indicator of ecosystem response to soil contamination

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ABSTRACT

The inventory and remediation of contaminated sites have emerged as top environmental priorities worldwide. A large body of evidence has accumulated to show how soil contamination affects biological communities and ecological processes. This knowledge has yet to be used for the development of indicators of soil quality that are meaningful to end-users and are easy to implement in soil quality assessment schemes. In this study, we used quantifiable measures of litter decomposition, a key biophysical process, as indicators of the ecological impact of soil contamination by trace metals and hydrocarbons. We conducted a litterbag experiment with coarse and fine mesh bags to compare highly vs. minimally contaminated sites within eight locations representative of a wide array of environmental conditions and types of pollution. Contrary to the common assumption that soil contamination hampers soil functions, idiosyncratic responses were detected for litter decomposition rate and decomposer activity metrics. A negative relationship between detritivore and microbial responses to soil contamination indicates that wherever the activity of one group of decomposers is reduced, increase in activity of the other group may ensure litter decomposition to proceed at rate similar or higher than baseline rate. This finding may indicate that compensatory dynamics in soil communities is important in determining ecosystem stability against chemical stressors. As litter decomposition may inform on the capacity of terrestrial ecosystems to cope with soil contamination, it may be a useful complement to chemical soil analyses in routine soil quality assessment schemes.

1. Introduction

Soil contamination is one of the world's biggest environmental problems faced by humanity (Montanarella et al., 2016; Rodríguez-Eugenio et al., 2018). Soil contamination arises wherever one or several chemical compounds are present in soil above levels thought to have undesired effects on humans and biota (Rodríguez-Eugenio et al., 2018). Threshold and guideline values for contaminant contents in soils are defined based on geogenic background concentrations and known toxicity for plants, animals and humans. This approach on environmental risk evaluation has inherent limitations owing to the cost of screening soil samples for all putative contaminants, uncertainties in contaminant bioavailability to biota (e.g., Scheifler et al., 2003), incomplete ecotoxicological database, and a lack of predictive

framework for emergent ecological effect of multiple contaminants (Critto et al., 2007). As the self-sustaining ability of terrestrial ecosystem and its ability to deliver services to human are integral part of soil ecosystem health (Bünemann et al., 2018), more holistic approach to soil contamination assessment is required if we are to design effective management strategies for contaminated sites (Palanisami et al., 2011; Niemeyer et al., 2012; Rodríguez-Eugenio et al., 2018).

Soil quality integrates various agronomic (e.g. soil fertility and sustainability) and ecological (e.g., biodiversity and respiration rate) endpoints, most of which are intricately linked to organic matter dynamics, directly or indirectly (Bardgett and van der Putten, 2014; Bünemann et al., 2018). Primary production and plant litter decomposition, two complementary processes, drive soil organic matter dynamics and, therefore, could be used to monitor the "heartbeat" of ecosystems. litter

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decomposition has become a popular way to assess ecological integrity of river ecosystems (Woodward et al., 2012; Gessner and Chauvet, 2002; Chauvet et al., 2016). Measures of litter decomposition have proven to be useful and necessary complements to structural indicators, such as point-in-time analyses of the state of the habitat or a community (Palmer and Febria, 2012; Chauvet et al., 2016). Although several lines of evidence indicate that human impact on soil ecosystems can affect litter decomposition (Coughtrey et al., 1979; Berg et al., 1991; Cotrufo et al., 1995; McEnroe and Helmisaari, 2001; Johnson and Beverley, 2004; Scheid et al., 2009; Lucisine et al., 2015), the conceptualization and design of a standard methodology for routine evaluation of soil quality have yet to be undertaken.

Numerical and per capita responses of litter decomposers to environmental stressors can trigger changes in the rate and pathways of litter decomposition, thus providing a strong rationale for the use of this ecosystem process in environmental risk assessment schemes (Gessner and Chauvet, 2002; Chauvet et al., 2016). Based on short-term laboratory ecotoxicological studies, exposure to high contaminant levels should be expected to be detrimental to soil biota, including main decomposer groups: heterotrophic microbes and invertebrate detritivores (Neuhauser et al., 1985; Giller et al., 1998; da Silva Souza et al., 2014; Liu et al., 2020). In the field, negative impacts of soil contamination may be hampered by low levels of contaminant bioavailability and local adaptation of soil biota (Donker and Bogert, 1997; Bruins et al., 2000; Haimi and Mätäsniemi, 2002; Hobbelen et al., 2006). This may thus explain why a number of studies reported unexpected high abundance or activity of microbial and invertebrate decomposers in highly contaminated sites (Haimi and Mätäsniemi, 2002; Hobbelen et al., 2006; Lucisine et al., 2015; Joimel et al., 2017; Huot et al., 2018).

In addition to direct toxic effects on decomposers, indirect effects of contaminants mediated by plants might play a role in determining how plant litter decomposition changes with soil contamination (e.g., Lucisine et al., 2015). Several studies have reported that contaminant accumulation in plants and subsequent physiological stress response can result in altered plant litter quality, with effects on individual performance and population size of soil decomposers (Berg et al., 1991; McEnroe and Helmisaari, 2001; Scheid et al., 2009; Lucisine et al., 2015). Moreover, reduction in litter turnover may result in thicker litter layer (Coughtrey et al., 1979; Mousseau et al., 2014), which may benefit in some ways to decomposers (Nahmani and Lavelle, 2002). The notion that soil contamination can influence plant litter decomposition in an unexpected fashion is well illustrated by findings of Bonzom et al. (2016) who reported a trend for faster decomposition of leaf litter as radionuclide contamination increased along a soil transect in the vicinity of Chernobyl nuclear power plant.

Based on previous studies, variable effects of soil contamination on plant litter decomposition should be expected. Systematic quantitative assessment of litter decomposition in inventoried contaminated sites is thus likely to provide useful indications of why inconsistent responses arise and where contamination impairs soil ecosystem functioning the most. As a proof-of-concept, we conducted a large-scale litterbag experiment to compare rates of leaf litter decomposition and levels of decomposer activities in contaminated vs. minimally disturbed sites. Litterbags were filled with leaf litter taken from a single site to isolate decomposer-mediated effects of soil contamination on decomposition and to eliminate confounding effect of litter quality (Woodward et al., 2012; Chauvet et al., 2016). We selected sites impacted by multiple persistent contaminants (mainly trace metals; TMs) originating from past anthropogenic activities (past industrial or mining activities) or geogenic processes, across France. Our selection of sites encompassed a broad spectrum of natural environmental settings, and types and levels of contaminants in soils so as to capture the full range of possible responses of plant litter decomposition to contamination. A set of complementary indicator metrics were used to describe how fast plant litter disappeared from litterbags and to disentangle the roles of micro- and macro-decomposers in mediating effects of soil contamination on

decomposition. Our work was guided by the following predictions: (1) contamination effect on litter decomposition will be predominantly negative (i.e. reduction of litter decomposition rate), (2) the nature and level of soil contamination and soil edaphic factors are important to explain spatial variation in contamination effect size, (3) micro- and macro-decomposers may display variable responses to soil contamination.

2. Material and methods

2.1. Study sites

A spatially-replicated litterbag experiment was carried out in eight areas (A-H) broadly distributed across France, that span a wide range of climatic and geologic conditions, and anthropogenic influences (Table 1; Fig. 1). Soil contamination originated from heavy industrial (A, B, C, and E) and mining (F, G, and H) waste discharge except in area D wherein serpentine rock outcrops support naturally TM-rich soil. Zn, Pb, Cd and Sb were prevalent TMs in the contaminated sites in areas A, C, E and G. Cu, Ni and Mo were also found in large amounts in area E. TMs occurred at lower levels in areas B, D, F and H. Cr and Ni were the main contaminants in the naturally contaminated soil in area D. In area H, soil contamination was predominantly mediated by As. In addition to TMs, PAH were well above baseline levels in areas B and C and was a major contaminant in area E.

We adopted a paired-site design intended to minimize local-scale (i.e. within areas) variation in climate and soil factors other than the contamination level. In each area, a heavily contaminated site was paired and compared with a nearby reference site that was not exposed to contaminant discharge. To tease apart effects of the type vs. level of soil contamination on soil ecosystem functioning, we selected a third site with intermediate levels of soil contamination wherever possible and appropriate (areas A, B, E, G; Table 1; Table A.1.). Twenty sites were thus surveyed as part of the present study. The precise locations where litterbags were incubated were determined to minimize difference in topography, geology, topsoil structure and vegetation type between reference and contaminated sites within each area. All sites were covered by woody vegetation left unmanaged for at least 5 years before the study was launched.

2.2. Soil properties

We performed soil analyses in the 20 study sites to quantify contaminant contents and some general physical and chemical soil properties thought to influence plant litter decomposition. During the litterbag experiment, on May 2013, superficial soil (A horizon) was collected in each site from twelve sub-sampling points distributed evenly, where litterbags had been deployed. Soil cores were pooled and mixed thoroughly to obtain representative samples per site of ca. 1 kg fresh soil mass. Soil samples were sieved to remove particles >2 mm and were shipped to LAS-INRA for physical and chemical analyses following national standards (COFRAC n°1-1380; NF EN ISO/CEI 17025:2005). Soil contamination level was determined based on the contents of 11 TMs (As, Cd, Co, Cu, Cr, Mo, Ni, Pb, Sb, Zn, Tl) and 16 US-EPA PAH (naphthalene, acenaphthene, fluorene, phenanthrene, anthracene, fluoranthene, pyrene, benzo(a)anthracene, chrysene, benzo(b)fluoranthene, benzo(k)fluoranthene, benzo(a)pyrene, dibenzo(ah)anthracene, benzo(ghi)perylene, indeno(123,cd)pyrene, acenaphthylene). Sites were also compared based on soil texture, i.e. the dry mass fraction of clay (<2 µm), silt (2–50 µm) and sand (50–2000 µm), and chemical parameters including pH, Cation Exchange Capacity (CEC), and total contents of organic carbon, nitrogen, phosphorus (Table A.2).

2.3. Standardization of soil contaminant contents

Soil contaminant contents were standardized to normal baseline

Table 1
General characteristics of the study areas sorted by latitude (see Fig. 1)

Area	A	B	C	D	E	F	G	H
Longitude °E	3.02	5.98	6.13	6.65	4.63	3.98	3.65	2.33
Latitude °N	50.46	49.21	48.76	48.05	45.54	44.11	43.94	43.34
Altitude (m a.s.L.)	36	231	199	613	225	263	183	347
Mean temperature (°C) ^a	11.0	10.4	11.3	8.5	12.3	14.3	14.1	14.3
Precipitation (mm) ^a	576	779	746	1296	549	1199	910	1199
Contaminants ^b	Cd, Pb, Sb, Zn, Cu	PAH, Sb, Pb, Zn, Cd, Sb	Pb, Zn, Cd, Sb, Tl, Mo, Cu, PAH, Cr	Cr, Ni, Co	Mo, Pb, Cu, Zn, Sb, Cd, Cr, Ni, PAH, Co	Pb, Sb, As	Cd, Zn, Pb, Sb, Tl, As	As, Sb
Origin of soil contamination	deposition of smelter dusts	restored coking plant site	settling pond filled with steel plant waste	serpentine outcrop	steel slag disposal site	old ore mining site	old ore mining site	old ore mining site
Number of sites	3	3	2	2	3	2	3	2
Vegetation type	eutrophic alluvial forest	afforesting grassland	meso-hydrophilic deciduous forest	beech-fir mixed forest	eutrophic alluvial forest	acidic pine-chesnut forest	thermophilic forest	chesnut forest

Footnote:

^a Climatic data were obtained from permanent weather monitoring stations (source: MétéoFrance) situated close (<15 km) to the study sites. Values recorded daily were used to calculate mean temperature and cumulative precipitation over the first ten months of 2013, i.e. during the litterbag experiment.

^b The most important contaminants found at highly contaminated sites are listed in descending order of “standardized” content (see Fig.2). Only contaminants whose contents were more than two times higher than normal background values are displayed.

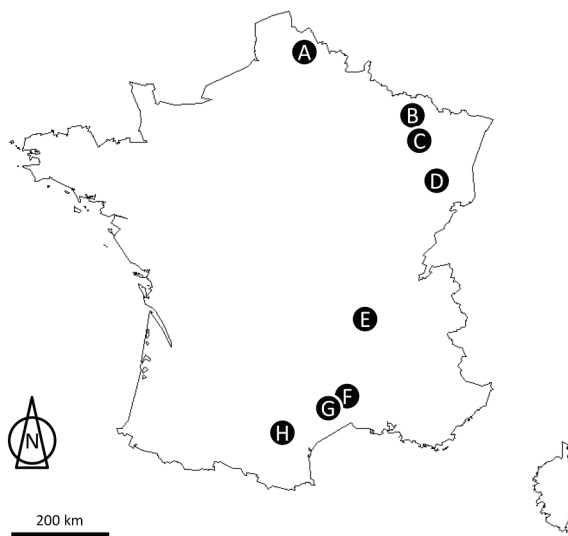


Fig 1. Location of the study areas within France

concentrations so as to enhance comparability of the results among contaminants and sites. We used empirically-derived background concentrations in least polluted sites in France as reference values (e.g., Saby et al., 2009; Appendix B; Table B.1). As PAH analysis yielded many values below lower limits of quantification (Table A.1), the summed content of all the 16 PAHs were used in further analyses. This choice did not introduce major bias since there were strong positive correlations among all PAH compounds (mean Pearson correlation: $r = 0.82$).

Profile plots were constructed to represent standardized contents of soil contaminants by area and site (Fig. 2). The data showed a good agreement between observed and expected differences between reference and contaminated sites. However, in two areas, the site selected for intermediate level of soil contamination was quite similar to the highly contaminated site (area E) or reference site (area B). The misclassified sites in area E and B were therefore specified a posteriori as another highly contaminated site and reference site, respectively, in statistical analyses.

2.4. Litterbag experiment

A total of 360 litterbags (L × W:20 × 12 cm and height: 3 cm) were deployed across the 20 study sites on January 2013. Litter

decomposition rate was assessed in coarse ($n = 180$) and fine ($n = 180$) mesh bags made of 5-mm square garden mesh netting and 0.5-mm nylon mesh net, respectively. This design helps tease apart the role of macro-detrivore (deviation between coarse and fine mesh bags) vs. microbial (measured in fine mesh bags) activities in mediating variations in total litter decomposition (assessed in coarse mesh bags) (Handa et al., 2014; Lecerf, 2017). Litterbags were filled with pre-weighed (3.5 and 2.5 g air-dried mass for coarse and fine mesh bags, respectively) batches of abscised leaves of birch (*Betula pendula* Roth.). The leaf species was chosen because all sites were colonized by birch trees. The leaves were collected in one place located several kilometers apart from main urban and industrial areas (49.062°N, 6.501°E) during fall of 2012, in a large net suspended horizontally ca. 1 m above the soil. As initial litter chemistry ($C = 0.46 \text{ g.g}^{-1}$; $N = 0.007 \text{ g.g}^{-1}$; $P = 0.003 \text{ g.g}^{-1}$; lignin = 0.15 g.g^{-1}) was kept invariant across litterbags, cross-site variation in litter decomposition metrics were solely driven by soil properties.

Each site received nine litterbags of each mesh size arranged in three blocks (=replicates). Litterbags were laid on soil surface after the site litter layer was removed. They were secured by the mean of bamboo sticks driven into the soil through the mesh bags' corners. Due to logistical constraints, litterbags were deployed in each area on different days (<6-day differences). At each deployment occasion, extra leaf-bags were transported to the field and then returned to the laboratory to obtain accurate estimate of initial litter mass corrected for mass loss due to handling. Three coarse mesh bags and three fine mesh bags, one from each replicate block, were harvested after 3, 6 and 9 months of exposure in the field. These bags were randomly picked and stored in plastic zip-lock bags kept in cool boxes during transportation to the laboratory.

2.5. Determination of litter decay rate and decomposer activity levels

Leaf fragments recovered from each litterbag were gently brushed to remove exogenous particles and visible animals. Leaf samples were frozen-dried and weighed to the nearest 0.01 g and the remaining mass was expressed as a ratio of final to initial dry mass. A first-order kinetic model was fitted to trajectories of litter mass remaining through time in order to estimate litter decay rates in coarse mesh (k_c) and fine mesh (k_f) bags for each site (Adair et al., 2010; Appendix C; Fig. C.1; Table C.1). The ratio of k_f -to- k_c values was used to calculate the percent contribution of litter fragmentation to decomposition (%F as proposed by Lecerf, 2017; Equation C.3; Table C.1), as a surrogate of macro-detrivore activity (Handa et al., 2014).

The leaf litter recovered from fine mesh bags at the three sampling occasions was finely grounded (<0.2 mm) and an aliquot (3.5 mg) from

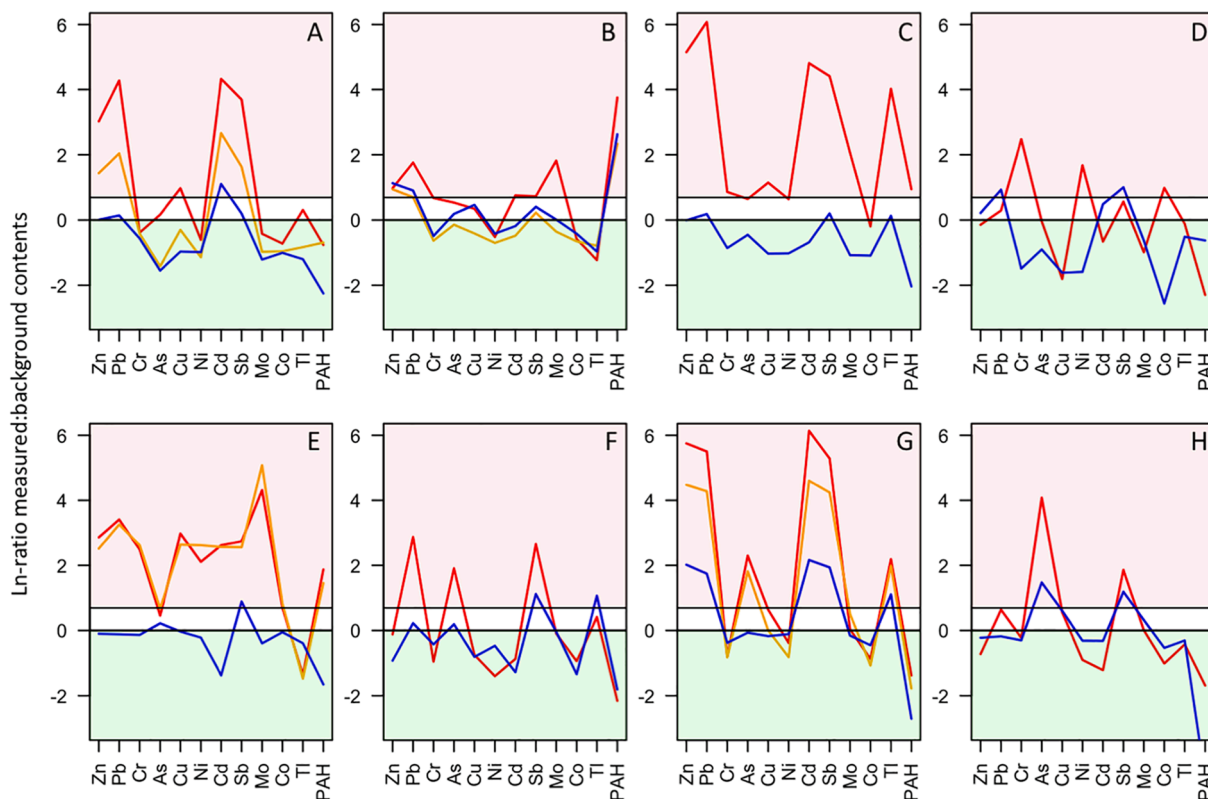


Fig. 2. Profile plots showing levels of 12 contaminants (x-axis) in 20 sites across 8 study areas in France. In each area (labelled A–H), a highly contaminated site (red line) was compared to a minimally-contaminated site (blue line). Orange lines in panels A, B, E and G represent sites selected a priori to represent intermediate levels of soil contamination. Values displayed on y-axes are log-ratios of soil contaminant contents vs. reference background values (Table B.1). The green-filled area below the line $y = 0$ highlights contaminant contents lower than background values and the red-filled area above the line $y = \ln(2)$ highlights contaminant contents exceeding twofold background values.

each bag was analyzed for nitrogen content using a Carlo-Erba NA 2100 elemental analyzer. As pattern of N content through time was well approximated by a zero-order kinetic model, the rate of litter N enrichment (dN) was calculated for each site as the slope of the regression line for litter N vs. days (Appendix D; Fig. D.1; Table D.1). dN was used as a proxy of microbial decomposer activity in litterbags, as we found a strong relationship between dN and proxies of microbial biomass assessed through real-time PCR quantification (Fig. D.2).

2.6. Data analyses

Effect of soil contamination on decomposition metrics was visualized by the mean of scatter plot with x-axis and y-axis representing reference and contaminated site, respectively, and each point representing a pair of sites. The difference of contaminated vs. reference site was used as a measure of contamination effect size.

To test if soil contamination had a consistent effect on process rates (k and dN), linear mixed-effects models were fitted to log-transformed litter mass or untransformed litter N content. Log-transformation was needed to linearize the exponential equation linking litter mass remaining and time. Spatial components (blocks nested in areas) of the sampling design were specified as random factors. As “block” accounted for little variation in the dataset, final models retained only “area” as a random factor (Zuur et al., 2009). The category of site (reference vs. contaminated) and number of days litterbags had spent in the field were specified as fixed effects. The two-way interaction allowed us to determine whether soil contamination had a consistent effect on the rate of litter mass loss or N enrichment. The model for log-transformed litter mass also included litterbag mesh size (coarse vs. fine) alone and in interaction with “site category” and “time” as fixed terms. The three-way

interaction in the model was an appropriate way to test for the effect of soil contamination on macro-detrivore activity, as the decomposition in coarse mesh bags was never slower than that in fine mesh bags.

To assess whether soil contamination elicited heterogeneous response of litter decomposition (e.g., occurrence of both neutral, negative and positive effects), the complete dataset was broken down into subsets to compare contaminated and reference sites within each pair of sites. Comparisons were performed using separate general least square models with the same fixed-effects structure as for the mixed-effect models used for the trend tests described above (Zuur et al., 2009). P -values from each comparison were then combined according to the Fisher’s method (Fisher, 1932).

Bivariate relationships were examined using the Pearson correlation (r) test. Multivariate regression analysis was performed using Partial-Least Squares (PLS) regressions (Carrascal et al., 2009) to gain a better mechanistic understanding of how soil factors influenced cross-site variability of decomposition metrics.

All statistical analyses were performed using R (R Core Team, 2017). Statistical models were fitted with the library “nlme” and PLS regression with the library “pls”. Model assumptions were assessed graphically and, whenever appropriate, data transformation (i.e. log) was applied to alleviate deviation from model assumptions.

3. Results

3.1. Soil contaminant contents

Across all sites, the highest contents of topsoil (A horizon) contaminants were 39.3 g.g^{-1} for Zn, 21.4 g.g^{-1} for Pb, 1.19 g.g^{-1} for Cr, 1.95 g.g^{-1} for As, 661 mg.g^{-1} for Cu, 606 mg.g^{-1} for Ni, 281 mg.g^{-1} for Cd,

198 mg.g⁻¹ for Sb, 252 mg.g⁻¹ for Mo, 48.8 mg.g⁻¹ for Co, 66.3 mg.g⁻¹ for Tl and 66.3 mg.g⁻¹ for total PAH (Table A.1). None of these maxima were recorded at reference sites where contaminant contents were generally substantially lower than in sites selected for the presence of soil contamination (Fig. 2). Minimal values were <50 mg.g⁻¹ for Zn and Pb, <20 mg.g⁻¹ for Cr, <10 mg.g⁻¹ for As, Cu and Ni, <2 mg.g⁻¹ for Cd, Sb, Mo, Co and Tl and <5 mg.g⁻¹ for total PAH (Table A.1).

Profile plots show that, across all study areas, soil contamination was of different nature and levels (Fig. 2). Zn, Pb, Cd and Sb were prevalent TMs in the contaminated sites in areas A, C, E and G. Cu, Ni and Mo were also found in large amounts in area E. TMs occurred at lower levels in areas B, D, F and H. Cr and Ni were the main contaminants in the naturally contaminated soil in area D. In area H, soil contamination was predominantly mediated by As. In addition to TMs, PAH were well above baseline levels in areas B and C whereas this was a major contaminant in area E (Fig. 2). Results from soil contaminant analysis performed as part of this study were thus consistent with expected differences between reference and contaminated sites. However, in two areas, the site selected for intermediate level of soil contamination was quite similar to the highly contaminated site (area E) or reference site (area B). We thus considered the two misclassified sites as another highly contaminated site (area E) and reference site (area B) in further analyses (cf. Fig. 3).

3.2. Litter decomposition

First-order and zero-order kinetic models approximated well the trajectories of litter mass loss and nitrogen enrichment through time, respectively (Fig. C.1; Fig. D.1). Litter decay rate was greater in coarse (mean $k_c = 0.0033$ day⁻¹; sd = 0.0010) than in fine (mean $k_f = 0.0022$ day⁻¹; sd = 0.0004) mesh bags (Fig. 3a, b; Table C.1). Percent litter fragmentation (%F) was up to 20% and 37% at reference sites and contaminated sites, respectively (Fig. 3c). k_c was more tightly correlated with %F (Pearson correlation coefficient: $r = 0.79$, $P < 0.0001$) than k_f ($r = 0.25$, $P = 0.28$) and dN ($r = 0.45$, $P = 0.0457$). These results indicate that macro-detrivore activity was potentially important in mediating effects of soil contamination on litter decay rate in coarse mesh bags.

No consistent effect of soil contamination on litter decomposition was detected based on visual inspection of plots in Fig. 3 and the results from trend tests ($P > 0.1$; Table 2). Heterogeneity tests further reveal that variable ecosystem responses to contaminants happen. This was significant for k_c ($P = 0.0173$) and %F ($P = 0.0236$) and marginally-significant for dN ($P = 0.0567$). These results primarily lie in the fact that both positive and negative responses (i.e. points above and below the 1:1 line, respectively) occurred across all site pairs (Fig. 3). Additionally, more than half of the data points clusters tightly around the 1:1 line in Fig. 3a, indicating that k_c in reference and contaminated sites were often alike. In area A, k_c and %F were substantially higher at the contaminated sites than the reference site whereas the converse hold true in area E (Fig. 3a,c). Weaker effects of soil contamination on k_c and %F were observed in other study areas, with the exception of %F in area D where contamination was associated with a 3-fold increase in detritivore activity (Fig. 3c). Soil contamination did not strongly reduce dN which was similar or slightly higher (areas C and E) in contaminated than in reference sites (Fig. 3d).

Data points on Fig. 3c and d displayed distinct patterns, suggesting that soil contamination affected micro- and macro-decomposers in a different manner. Indeed, the differences in %F and dN between contaminated and reference sites were related to each other through a negative relationship ($r = -0.78$, $P = 0.0026$; Fig. 4). Furthermore, no data point occurs in the lower left-hand quadrant of the plot in Fig. 4, indicating that contamination may reduce either microbial or macro-detrivore activity but not both at the same time.

Partial Least Square regression models were fitted to the data to examine how soil properties influenced litter decomposition and to elucidate drivers of heterogeneous responses to contamination. Values

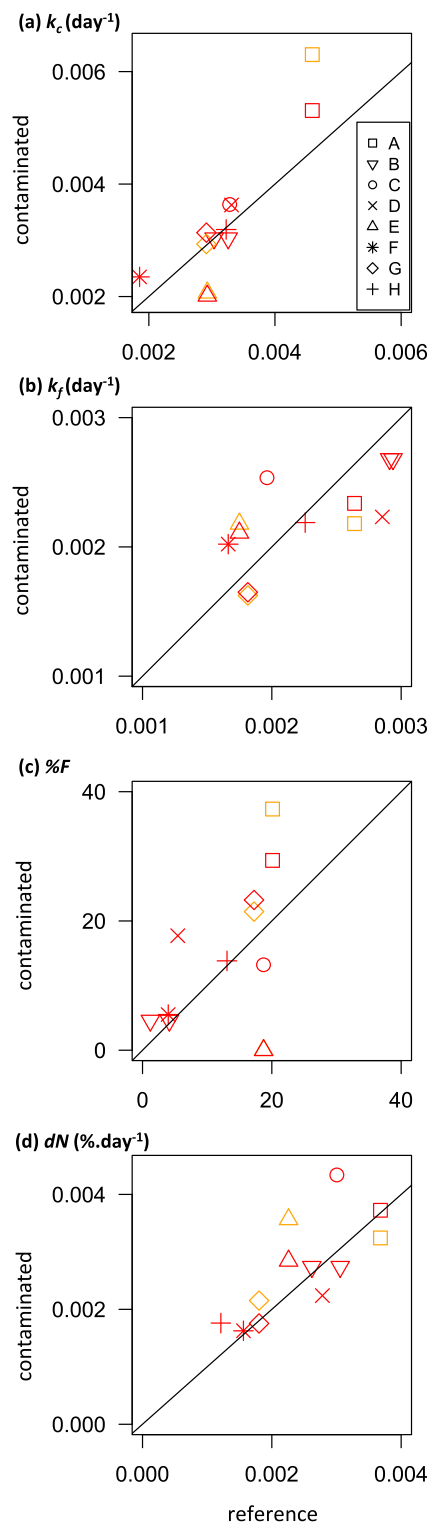


Fig. 3. Leaf litter decay rates in coarse (a) and fine (b) mesh bags, and detritivore (c) and microbial (d) activities assessed by the mean of the percent contribution of litter fragmentation to decomposition and litter N enrichment rate in leaf litter, respectively. Each symbol represents a pair of sites positioned according to values assessed in a reference (x-axis) and a contaminated (y-axis) site. The shape and color of points indicate the study area and modality of contamination level (high = red and intermediate = orange), respectively. Contamination effect size is proportional with the vertical distance between individual points and the 1:1 line.

Table 2
Results of statistical analyses assessing the effect of soil contamination on plant litter decomposition.

Hypothesis	Trend test		Heterogeneity test	
	F	P	χ^2	P
Change in litter decay rate (k_c)	0.6	0.4472	30.1	0.0173
Change in macro-detritivore activity (%F)	2.6	0.1093	29.1	0.0236
Change in litter N enrichment rate (dN)	1.5	0.2291	25.8	0.0567

Footnote: Trend test was performed using linear mixed-effects models and heterogeneity test was performed following Fisher (1932) (see Materials and Methods).

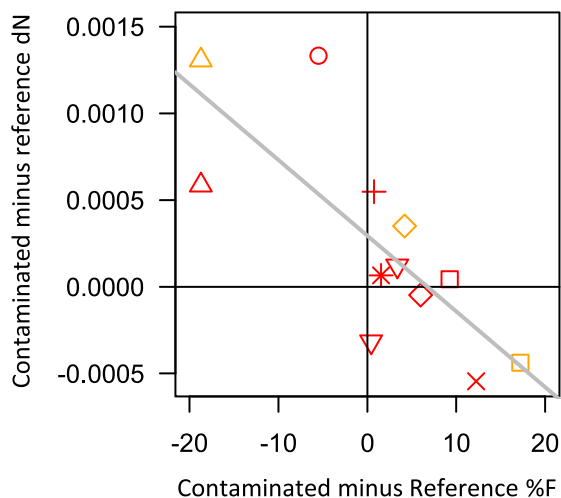


Fig. 4. Response to soil contamination (i.e. difference between contaminated and reference sites) of a proxy of micro-decomposer activity (dN, y-axis) vs. a proxy of macro-decomposer activity (%F, x-axis). The grey line shows a significant negative relationship. The shape and color of points indicate the study area and modality of contamination level, respectively (see Fig. 3).

of R^2X and R^2Y indicate that less than half of the variance encapsulated into data of soil properties was needed to explain 70% or more of the variance of response variables (Table 3). A few soil contaminants had significant effects on litter decay rate and/or decomposer activity metrics. Mo, Sb, and As were negatively associated with k_c (Mo: $t = -2.7$, $P = 0.014$), k_f (Sb: $t = -2.1$, $P = 0.05$) and dN (As: $t = -3.7$, $P = 0.002$), respectively. A significant positive association was also found between dN and PAH ($t = 2.3$, $P = 0.033$). It is worth noting here that none of the response variables were significantly related to Zn and Pb ($P > 0.286$; Table 3), two major contaminants in many case study areas (Fig. 2; Table A.1).

PLS regression models identified total P content in soils as an important predictor of total litter decomposition rate (k_c : $t = 3.0$, $P = 0.007$) and proxies for microbial activity (k_f : $t = 2.9$, $P = 0.009$; dN: $t = 2.9$, $P = 0.008$). In addition, soil texture explained variations in k_c (% Silt: $t = 2.5$; $P = 0.021$) and %F (%Sand: $t = -2.2$, $P = 0.038$). These results suggest that phosphorus enhanced microbial process rates and fine-textured soil promoted detritivore-mediated decomposition. As contaminated and reference soils were not always strictly equivalent in terms of Pt content and soil texture (Appendix A; Table A.2; Fig. A.1), it was important to ascertain that soil heterogeneity did not affect our evaluation of soil contamination effects on plant litter decomposition. Differences in soil Pt content, %Silt and %Sand between contaminated and reference sites ranged from -0.08 to $+0.08$ g.kg $^{-1}$, -270 to $+380$ g.kg $^{-1}$ and -397 to $+348$ g.kg $^{-1}$, respectively. However, these differences within site pairs did not correlate with differences in decomposition metrics between reference and contaminated sites (k_c vs. %Silt: $r = 0.19$, $P = 0.546$; k_c vs. Pt: $r = -0.18$, $P = 0.565$; k_f vs. Pt: $r = 0.446$, $P = 0.146$;

%F vs. %Sand: $r = -0.25$, $P = 0.426$; dN vs. Pt: $r = 0.45$, $P = 0.14$). This indicates that uncontrolled variability of Pt content, %Silt and %Sand did not confound the effects of soil contaminant on plant litter decomposition reported here.

4. Discussion

Our study indicates that direct evaluation of a soil ecosystem function, such as plant litter decomposition, can provide complementary information to quantitative analyses of soil contaminants and their interpretation based on basic toxicology principles. Indeed, extremely high levels of contaminants in several study sites did not result in consistently reduced litter decomposition rates and decomposer activities. Weak or neutral contamination effects conceivably arise due to low contaminant bioavailability for, and putative adaptation of life, in historically-contaminated sites (Donker and Bogert, 1997; Bruins et al., 2000; Haimi and Mätäsniemi, 2002; Hobbelen et al., 2006; Lemmel et al., 2019). However, these mechanisms, along with monotonic dose-response models routinely used to infer biological effect of contaminants, fall short of telling us why litter decomposition rate and decomposer activities were sometimes higher at contaminated sites. Apparent positive effect of soil contamination on litter decomposition rate has been previously reported by Bonzom et al. (2016) whose study focused on radionuclide-rich soils in the Chernobyl area. Furthermore, Lucisine et al. (2015) did not detect any difference in the capacity of soils to decompose plant litter but they found that a dominant tree species produced more degradable leaf litter when growing at a contaminated site than at uncontaminated sites. Collectively, results from the present and previous studies indicate that soil contamination can sometimes enhance turnover rate of plant litter.

Ecological mechanisms can explain why plant litter decomposition was sometimes enhanced in litterbags set on contaminated soils. Soil contamination is likely to act as an environmental filter that sorts individuals and species according to functional traits (Liang et al., 2015). It remains unclear why decomposers adapted to life in contaminated soils should exert a stronger control on plant litter decomposition than decomposers from uncontaminated soils. One explanation may be that individuals require more energy, and thus consume more detritus, to overcome the metabolic cost of toxic exposure (e.g., Donker and Bogert, 1997). Contaminants may also alter species coexistence patterns; for instance, Giller et al. (1998) proposed that intermediate contamination levels can favor microbial diversity in soil through release of competitive exclusion. Positive diversity-decomposition relationships (Srivastava et al., 2009) may then mediate faster decomposition at contaminated sites. Extending this hypothesis to soil fauna (Hedde et al., 2012) provides an explanation to why soil contamination had greater positive effect on litter decomposition rate and detritivore activity in the moderately than highly contaminated sites in area A (Fig. 3). As proliferation of macrodetritivores in severely contaminated soils has been reported by other investigators (Lucisine et al., 2015; Huot et al., 2018), this should be expected to produce an acceleration of litter decomposition in these situations, too.

Interestingly, proxies for micro- and macro-decomposer activities displayed opposite responses to soil contamination. This provides a rationale for expecting weak or neutral effects of soil contamination on litter decomposition rate since negative response of one decomposer group might be compensated by positive response of the other group. Thus, soil contamination elicited coordinated responses of diverse biota, which was likely to confer resistance to soil ecosystem functioning. Our finding clearly illustrates that achieving a comprehensive assessment of soil quality requires complementary indicators of ecosystem structure (i.e., biological communities) and processes to be used in combination. It also raises fundamental questions about why micro- and macro-decomposer activities displayed opposite responses. It is plausible that compensatory dynamics arose from contamination-induced release of antagonistic interactions between microbial decomposers and

Table 3

Summary of Partial Least Squares (PLS) regression outputs. Separate analyses were performed to determine how each of the four tested metrics (k_c , k_f , %F and dN) was influenced by soil physical and chemical properties.

Variables	k_c (log)		k_f (log)		%F (sqrt)		dN	
	t_{19}	P	t_{19}	P	t_{19}	P	t_{19}	P
ncomp	2		3		2		2	
R ² X	39.3		45.3		39.7		40.8	
R ² Y	74.1		86.2		72.4		70.2	
Zn (log)					+1.1	0.286		
Pb (log)								
Cr (log)							+1.2	0.264
As (log)	-1.5	0.158					-3.7	0.002*
Cu (log)								
Ni (log)	-1.3	0.213	-1.0	0.309	-1.4	0.192		
Cd (log)	+2.0	0.061			+1.3	0.210	+1.1	0.302
Sb (log)			-2.1	0.050*	+1.5	0.146	-1.3	0.210
Mo (log)	-2.7	0.014*			-2.0	0.057		
Co (log)								
Tl (log)	-1.1	0.280						
PAH (log)			+2.0	0.057	-1.9	0.072	+2.3	0.033*
%Clay			-1.5	0.152	+1.3	0.226		
%Silt	+2.5	0.021*	+1.5	0.160	+2.1	0.054		
%Sand	-1.9	0.069			-2.2	0.038*		
pH (log)	+1.1	0.295					+2.1	0.051
CEC (log)	+1.0	0.327					+1.8	0.088
Corg (log)			+1.8	0.086	-1.8	0.090		
Nt (log)								
Pt (log)	+3.0	0.007*	+2.9	0.009*			+2.9	0.008*

Footnotes: ncomp is the number of PLS components retained in the model. R²X and R²Y indicate percent variances of the explanatory and dependent variables, respectively, accounted in models.

Log-transformation indicated in parentheses was applied to some variables to meet assumption of linearity and normal distribution. t- and P-values provide information on the sign and significance of the effect of soil variables in each model. For the sake of readability, results are not displayed when $t < 1$ (and hence $P \gg 0.05$) Asterisks indicate significant predictor assuming a type I error rate of 0.05.

invertebrate detritivores, as the latter occupy a higher trophic level than the former and hence feed on them (Moore et al., 2004).

Case study areas wherein total decomposition rate differed the least between contaminated and reference sites included contaminations of industrial (areas B and C), mining (areas G and H) and geogenic (area D) origins (see the cluster of data points on the 1:1 line in Fig. 3a). In addition, total decomposition rate did not respond to variable levels of soil contamination in a consistent and coherent manner. Lastly, we did not find that contamination effect size increases with contamination levels in areas A and G. There are thus multiple lines of evidence that heterogenous responses of litter decomposition to soil contamination cannot be ascribed solely to the origin and level of soil contamination. However, our study was not intended to quantify dose–response relationships and further investigations should re-examine the match between chemical and ecological indicators of soil contamination based on bioavailable fractions rather than total contents of contaminants (e.g., Hobbelen et al., 2006). This endeavour may be hampered by the fact that bioavailability is challenging to determine accurately in the field and methods that can be routinely applied (i.e. CaCl₂ extraction of metals or cyclodextrin extraction of PAH from soil matrix) may not reflect the genuine extent of toxic exposure of biota (Scheffler et al., 2003).

Results from regression analyses showed variable ecological effects of some contaminants depending on whether the indicator metric related to micro- or macro-decomposers (Table 3). This can be explained by fundamental physiological and ecological differences between heterotrophic microbes and invertebrate detritivores, as also pointed out by the fact that they responded to natural variability (i.e. soil Pt and texture) in a different manner. More complex mechanisms are suggested by the lack of systematic agreement between the two metrics for microbial activity (k_f and dN). For instance, soil As content had a significant effect on dN , but not on k_f , indicating that arsenic might affect more nitrogen than carbon dynamics in soil ecosystems. However, as trends reported for contaminant effects in Table 3 were not often significant,

the results should be interpreted with great caution. Due to the multi-contaminated nature of most studied sites, contaminant contents varied in a coordinated manner and, hence, impacts of each individual contaminant cannot be evaluated accurately.

A range of ecological factors governs plant litter decomposition (Berg and McClaugherty, 2008) and, therefore, controlling natural variability is essential to develop sensitive and robust indicators (Gessner and Chauvet, 2002). The standardized protocols applied here used a specified reference leaf species so as to control for effects of litter quality, a chief driver of local and regional variability of litter decomposition rate (Cornwell et al., 2008). As leaf litter enclosed in mesh-bags represents a dominant type but not the diversity of on-site plant litter, results have only a comparative value and they have limited relevance for soil organic matter budget. Other potential confounding factors, such as climatic and edaphic parameters, are more difficult to control a priori, notably when reference condition is inferred based on minimally impacted sites. Here, it was not possible to ensure that all potentially important drivers of litter decomposition (i.e., soil Pt content and texture) did not differ between reference and contaminated sites. However, these differences did not explain patterns of apparent effects on soil contamination on litter decomposition, demonstrating that careful analysis of decomposition results can yield meaningful ecosystem assessment.

5. Conclusion

In our study, litter decomposition did not satisfy the criterion of consistent response to stress required for ecological indicators (Dale and Beyeler, 2001). It therefore could not replace soil chemical analyses as a mean to investigate where soil contamination occurs and what types of chemicals are present. However, litter decomposition proved useful to reveal inconsistent ecosystem responses to soil contamination potentially arising from compensatory dynamics. It would be worth elucidating the role of other ecologically meaningful patterns, such as non-

monotonic dose–response and ecological contingency, in driving apparent context-dependent changes of soil ecosystem functioning. Irrespective of the direction of change in litter decomposition rate, deviations from reference condition indicate that the capacity of soil to decompose and recycle organic matter is compromised. Assuming that the severity of ecological impact scales positively with absolute change in process rate (Gessner and Chauvet, 2002), plant litter decomposition may help prioritize sites where to concentrate efforts of evaluation and remediation of ecological impacts of soil contamination. However, translating results from decomposition studies into effective management strategies requires that we gain a deeper mechanistic understanding of why soil contamination affects plant litter decomposition in so many ways.

Author contributions

AL, AC, FG, MD, HR and FMD designed the study and performed the field and laboratory works. AL, AC and FMD analyzed the data and wrote the paper. All authors provided suggestions and comments and had read and approved the submitted version of the manuscript.

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CRedit authorship contribution statement

Antoine Lecerf: Conceptualization, Methodology, Validation, Formal analysis, Writing - review & editing. **Aurélien Cebron:** Investigation, Methodology, Resources, Writing - review & editing. **Franck Gilbert:** Conceptualization, Methodology, Validation, Formal analysis, Writing - review & editing. **Michael Danger:** Conceptualization, Methodology, Validation, Formal analysis, Writing - review & editing. **Hélène Roussel:** Conceptualization, Methodology, Validation, Writing - review & editing, Project administration, Funding acquisition, Supervision. **Florence Maunoury-Danger:** Conceptualization, Methodology, Validation, Formal analysis, Writing - review & editing, Project administration, Funding acquisition, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A to D. Supplementary data

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