Changes in soil macroinvertebrate communities following liming of acidified forested catchments in the Vosges Mountains (North-eastern France)

Apolline Auclerc [a,*], Johanne Nahmani [a], Delphine Aran [a], Virginie Baldy [b], Henry Callot [c], Charles Gers [d], Etienne Iorio [e], Emmanuel Lapied [f], Aurore Lassauce [a], Alain Pasquet [g], Jörg. Spelda [h], Jean-Pierre Rossi [i], François Guérold [a]

[a] Laboratoire des Interactions Ecotoxicologie Biodiversité Ecosystèmes (LIEBE), CNRS, UMR 7146, Université Paul Verlaine – METZ, Campus Bridoux, Avenue du général Delestraint, F-57070 Metz, France
[b] Université de Provence, IMEP, UMR CNRS 6116, Centre Saint-Charles – Case 4 3, Place Victor Hugo, 13331 Marseille cedex 03, France
[c] Musée Zoologique de l'Université et de la Ville de Strasbourg, 29 bd. de la Victoire, 67000 Strasbourg, France
[d] EcoLab, Université Paul Sabatier, Batiment 4R3 – b2 118 Route de Narbonne, 31062 Toulouse cedex 9, France
[e] ECO-MED-Pôle Entomologie, Tour Méditerranée, 65 av. Jules Cantini, 13298 Marseille Cedex 20, France
[f] Bioforsk Soil and Environment, Fredrik A. Dahls vei 20, N-1432 Ås, Norway
[g] UMR CNRS 7178 IPHC-DEPE-UdS, UHP-Nancy Université, BP 239-54506 Vandoeuvre les Nancy, France
[h] Bavarian State Collection of Zoology, Münchhausenstraße 21, 81247 Munich, Germany
[i] INRA, UMR CBGP (INRA/IRD/Cirad/Montpellier SupAgro), Campus international de Baillarguet, CS 30016, F-34988 Montferrier-sur-Lez cedex, France

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ABSTRACT

To counteract acidification of terrestrial ecosystems due to decades of acid atmospheric depositions two catchments were limed ($2.5 t ha^{-1}$) in fall 2003. Four years later, the effects of liming on soil macroinvertebrate community from both catchments were investigated by comparing the two limed catchments with two adjacent acidified control sites. During two seasons (fall and spring) and for each catchment, 21 samples of soil and litter-dwelling macroinvertebrates were extracted along a transect in order to evaluate the effect of liming on community structure. A canonical correspondence analysis (CCA) was used to evaluate which chemical soil factors could better explain the trends of structure changes of macroinvertebrate communities. Results showed that the taxonomic richness was not improved by liming. However, the total abundance was significantly lower for the two limed catchments as compared to control sites. Communities strongly differed as 42 taxa (52.2%) were different between the granite limed site and its adjacent control and 34 taxa (55.7%) on sandstone. The CCA revealed that liming affected soil communities mainly via changes in Ca concentration and soil pH which tended to favour some taxa such as Curculionidae while it exerted a negative effect on other zoological groups such as spiders that were preferentially found on control soils. These results tend to demonstrate that liming can be considered as a disturbance that have marked effects upon soil macro-invertebrate through species-dependant response to soil chemical changes.

1. Introduction

Since the onset of the industrial revolution, terrestrial and aquatic ecosystems have been exposed to severe deposition of acidifying compounds in numerous sensitive regions throughout the Northern Hemisphere (Campbell and Lee, 1996; Driscoll et al., 2001). The detrimental effects of acidification on terrestrial and aquatic biota and finally, on the benefits provided by ecosystems to human societies, have been well recognized in the 1970s as a major environmental problem. In recent decades,

international and national efforts (e.g. Clean Air Act in the USA and the Convention on Long-Range Transboundary Air Pollution in Europe, EMEP, 1999) have been performed to achieve reduction in emissions of acidifying compounds to the atmosphere and consequently rates of acidic deposition, especially of sulphur, have substantially declined in Europe and North America. While different studies have addressed signs of recovery of ecosystems following the reduction of acid depositions in several regions (Stoddard et al., 1999; Fölster and Wilander, 2002; Oulehle et al., 2006; Kirk et al., 2010) other studies have reported a significant delay in the recovery of ecosystems mainly due to the release of formerly stored SO_4^{2-} coupled with the leaching of Al and exchangeable base cations (Likens et al., 1996; Alewell et al., 2000; Prechtel et al., 2001; Graf Pannatier et al.,

* Corresponding author. Tel.: +33 03 87 84 21; fax: +33 03 87 84 23.
E-mail address: apolline.auclerc@umail.univ-metz.fr (A. Auclerc).

2005). In strongly acidified areas, the base cation depletion inducing the pH decrease will only be reversible in the very long term. In addition, acidification is now reported across other large areas of the world, such as China (Larssen et al., 1999; Tang et al., 2001; Zhao et al., 2009) and India (Aggarwal et al., 2001). This demonstrates that acidification still represents an important worldwide ecological threat to ecosystems.

In order to improve Ca and Mg supply in soils and to reduce acidification, liming is a common practice in European forests and it has been intensely used since the early 1980s (Huettl and Zoettl, 1993; Pawlowski, 1997; Hüttl and Schneider, 1998; Formanek and Vranova, 2002; Lundström et al., 2003; Schaaf and Hüttl, 2006; Löfgren et al., 2009). It is clear that the main goal of this type of management is primarily to prevent forest dieback and/or restore forest health in adult stands and finally to improve the vitality of trees (i.e. the production of wood biomass in nutrient-poor forest ecosystems). As this mitigation strategy is applied to large forest areas, ecological consequences of calcareous amendments are thus of critical importance and studies on the effects of liming on trees (Huettl and Zoettl, 1993; Hüttl and Schneider, 1998; Huber et al., 2006; Røsberg et al., 2006) and several soil biota have been previously performed (Bååth et al., 1980; Hågvar and Amundsen, 1981; De Goede and Dekker, 1993; Rittner and Roth, 1995; Deleporte and Tillier, 1999; Geissen and Brümmer, 1999). Soil fauna indeed contributes to the structure and functioning of terrestrial ecosystems, including cycling of nutrients, soil carbon storage, and maintenance of soil structure (Brussaard, 1998; Jones and Bradford, 2001). Available studies suggested that liming effect might be dependant of time scale i.e. trends may change in time. For instance, in soils under sugar maple forests, Chagnon et al. (2001) found that liming caused a decrease in abundance and dominance of certain epigeic and endogeic collembolan species. The evidence for positive effect of liming, on the abundance, biomass and species richness of earthworm has been showed by several studies (Robinson et al., 1992; Edwards and Bohlen, 1996; Deleporte and Tillier, 1999; Davidson et al., 2004; Potthoff et al., 2008; Ampoorter et al., 2011). The effect of lime addition on spider populations depends on study sites (Buckton and Ormerod, 1996; Korenko et al., 2008). However, surprisingly few investigations on the liming effects on large or event complete range of taxa have been performed. The absence of integrative studies on the whole macroinvertebrate community may partly be responsible for the lack of a consistent concept about liming effects on soil organisms.

Despite the strong decrease of acid atmospheric depositions observed during the two last decades (van der Heijden et al., 2011), anthropogenic acidification still represents a major threat to forest (Dambrine et al., 1995, 1998) and surface waters (Guérold et al., 2000; Angéli et al., 2009) in the Vosges Mountains (Northeastern, France). To avoid forest decline and for the first time in France, two whole catchments (one lying on sandstone and one on granite), have been limed in fall 2003. In this context, the main objective of the present study was to evaluate the medium-term effects of liming on the composition and structure of soil macroinvertebrate communities. To this end, we compared the responses of communities of limed and unlimed adjacent control catchments. Specifically, we hypothesize that lime application should have induced an increase of abundance, species diversity, richness of soil and litter-dwelling macroinvertebrates. The response was implemented on two types of bedrock to evaluate to what extent the effects of liming on soil macroinvertebrate communities depend on the nature of the substratum. Finally, we assessed which chemical soil factor(s) could better explain change(s) in macroinvertebrate assemblages four years after liming.

2. Materials and methods

2.1. Study sites

The study was carried out in the Vosges Mountains (North Eastern, France). Average yearly rainfall and air temperature are 1400 mm and 7 °C respectively at the elevation of 800 m a.s.l. Two acidified catchments were limed in fall 2003, one lying on triasic sandstone SL (SiO_2: 92.7%) (123 ha, elevation: 800 m, 48°27′44.8″N; 07°05′49.7″E) and the other one underlain by hercynian granite GL (SiO_2: 72%) (124 ha; elevation: 1000 m, 47°57′22.9″N; 06°52′55.6″E). Two adjacent acidified catchments were chosen as control: SA lying on sandstone (222.2 ha, 800 m, 48°26′37.4″N; 07°05′25.3″E) and GA lying on granite (124 ha, 1000 m, 47°57′39.5″N; 06°53′05.1″E) (Fig. 1).

The catchments are all forested with a mixture of white spruce (*Abies alba*), Norway spruce (*Picea abies*), about 180 years old and beech (*Fagus sylvatica*), about 30 years old, with a dominance of spruces on sandstone and beeches on granite. Soils ranged from cambisols to Entic podzols (WRB, 2006) (mean granulometry: SL and SA: 70% coarse sand, 17% fine sand, 2% coarse silt, 5% fine silt and 6% clay; GL and GA: 47% coarse sand, 8% fine sand, 5% coarse silt, 17% fine silt and 22% clay). The humus form was a moder.

Due to the presence of priority habitats (e.g. *Sphagnum* acid bogs) and species (*Tetrao urogallus*) listed in the European Habitats Directive (92/43/EEC) in the European Birds Directive (2009/147/EC) respectively, and because low amounts of lime have been proved to be efficient to counteract acidification and to avoid forest decline in the long term in the Vosges Mountains (Bonneau and Nys, 1997), 2.5 t ha^{-1} were applied at each sites. The two catchments were limed by helicopter in October and November 2003 with fine powder ($CaMg[CO_3]_2$, granulometry < 0.08 mm). The lime was composed by 70%, 17%, 10% and 3% of $CaCO_3$, $MgCO_3$, $CaSO_4$ and KCl, respectively.

2.2. Sampling of soil macroinvertebrates

The four catchments were sampled twice, once in October 2007 and once in June 2008. Macroinvertebrate samples were extracted from three 30 m transects within each site. Transects were set perpendicularly to the slope and were 50 m distant from each other. Each transect has 7 sampling points spaced 5 m apart. At each sampling point, a metallic frame (25 cm × 25 cm) was inserted into the soil. The litter was then collected into the frame and one soil block of 25 cm × 25 cm to 15 cm depth (volume of 9375 cm^3) was dug out under the collected litter. In laboratory, litter samples were placed over 10 days in a Berlese–Tullgren apparatus with a 15 W lamp suspended over each sample to collect macroinvertebrates. Individuals from each soil block were hand-sorted within five days following sampling. All individuals were conserved in 70% ethyl alcohol until identification. Most specimens were identified to species level except for larvae and juveniles which were classed by Family or Order.

2.3. Soil chemical parameters

For each sampling date and catchment, 15 of 21 soil blocks previously sampled to extract the fauna were used for chemical analyses. Soil blocks were air dried and 2 mm sieved before taking a subsample for chemical analyses. Measures of pH_{H2O} in distilled water (1:5 soil:water) were performed. The Cobaltihexamine Chloride Method (NF X 31-130) was used for Cation Exchange Capacity (CEC). CEC was measured by absorbance at 472 nm. Exchangeable cations were quantified by flame atomic absorption spectroscopy (FAAS; Ca, Mg), flame atomic emission
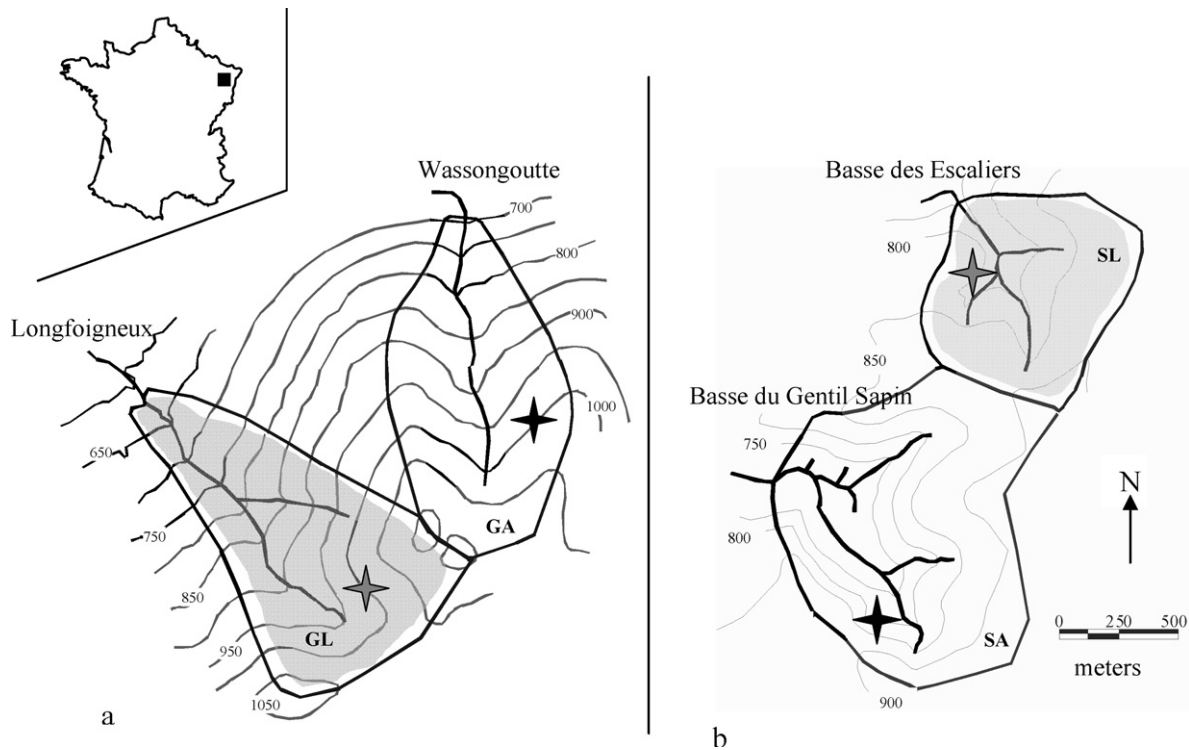
Fig. 1. Location of the limed (grey: GL and SL) and control catchments (white: GA and SA) (Vosges, North-eastern, France) on granite (a) and sandstone (b). Crosses represent the study sites on each catchment: grey ones correspond to limed sites and black ones to control sites.

spectroscopy (Na, K), furnace AAS (Al) and pH measurement (H). Base Cations concentration was calculated: $BC = Ca + Mg + Na + K$ (mEq $100\,g^{-1}$). Base saturation (BS) was calculated as the quotient between BC and CEC. The content of organic carbon and nitrogen were determinate by dry combustion at $1800\,^{\circ}C$. For each chemical parameter, Kruskal–Wallis and Mann–Whitney tests were performed to evaluate the difference between the four catchments ($p < 0.05$), using R software (R Development Core Team, 2008).

2.4. Macroinvertebrate data analyses

2.4.1. Preparation of data

After verification of the homoscedasticity of the variance (Bartlett test; $p > 0.05$) and the normality of the distribution (Shapiro–Wilk test; $p > 0.05$), two-ways ANOVAs were performed to test for the effects of habitat (soil vs. litter) and collecting dates (October vs. June) on macro-invertebrates abundance (after log ($x + 1$) transformation), species richness and Shannon-index for each catchment, separately. A collecting date effect was denoted in the faunal data collected in litter samples from granitic catchment ($p = 0.03$). For catchments lying on sandstone, a habitat effect was measured ($p < 0.001$).

Because we did not aim to evaluate the different reaction of specialist fauna of soil or litter, nor to take into account the level of seasonal variation on fauna response after lime addition, the faunal data (number of taxa and individuals) obtained from corresponding plots of the two collecting dates, soil and litter were pooled to compute the observed bulk taxa abundance for each catchment ($n = 21$ per catchment).

2.4.2. Communities dissimilarities
2.4.2.1. Principal coordinate analysis (PCoA).
A principal coordinate analysis (PCoA) was performed on the pooled fauna data set (site-species abundance, $n = 21$) to examine to which extent

the communities differed according to the sites. We used the Bray–Curtis index (Legendre and Legendre, 1998). These computations were done using R software (R Development Core Team, 2008) and the ade4 (Dray et al., 2007) and labdsv packages (Roberts, 2010). A bootstrap procedure based on 1000 randomizations was done to evaluate the significance of PCoA axes.

2.4.2.2. Multi-response permutation procedure (MRPP).
The significance of community dissimilarities was tested by means of the multi-response permutation procedure (MRPP) (Quinn and Keough, 2002; Rossi et al., 2010). In this context, the Bray–Curtis distances were calculated to test the dissimilarities between the four sites and between two sites from each bedrock type separately. MRPPs were computed using the vegan package of R software (Oksanen et al., 2010).

2.4.3. Total abundance, mean density and taxa richness

In 5 sampling plots (on 84) a high ant density (from 47 to 968 ants/625 cm²) was collected. We removed the data of this colonial taxa in order to smooth out ants aggregation effects upon our estimates of fauna density.

Generalized Linear Models (GLM) with approximate Poisson error (Pinheiro and Bates, 2000) was used to test effects of liming and type of bedrock on mean density.

We computed the average mean taxa richness per sample and the overall richness, i.e. the cumulated richness over all samples (S_{obs}) from a given catchment. A bootstrap procedure was carried out to determine the bias-corrected taxa richness and thus obtain the estimated taxa richness (S_{corr}) (details in Rossi et al., 2010). The variance homoscedasticity of the mean taxa richness per catchment (Bartlett test; $p > 0.05$) and the normality of the distribution of data per catchment (Shapiro–Wilk test; $p > 0.05$) were checked. A two-ways Anova was then used to test the effects of liming and type of bedrock on mean taxa richness per catchment.

Table 1
Mean (±SD) soil properties of the four sites.

	Sandstone		Granite	
	SA (control)	SL (limed)	GA (control)	GL (limed)
pH $_{H2O}$	3.90 ± 0.15^a	4.27 ± 0.34^b	3.93 ± 0.34^a	4.11 ± 0.22^b
C/N	18.15 ± 4.78^a	18.90 ± 3.54^a	18.43 ± 3.54^a	17.67 ± 2.08^a
Exchangeable Ca[a]	0.36 ± 0.31^a	2.12 ± 2.45^b	0.96 ± 2.45^b	1.02 ± 0.63^b
Exchangeable Mg[a]	0.13 ± 0.06^a	$0.65 \pm 0.05^{b,c}$	0.36 ± 0.05^b	0.49 ± 0.07^c
Exchangeable Al[a]	1.67 ± 1.4^a	0.99 ± 0.68^a	4.56 ± 0.68^b	5.61 ± 1.59^c
CEC[a]	4.82 ± 2.01^a	5.70 ± 3.31^a	9.95 ± 3.31^b	10.55 ± 1.91^b
Base saturation (%)	13.06 ± 5.44^a	41.43 ± 24.72^b	16.26 ± 24.72^c	$17.53 \pm 9.58^{a,c}$

Different letters indicate significant differences at $p < 0.05$ (Kruskal–Wallis and Mann–Whitney U-tests).

[a] mEq $100\,g^{-1}$

The observed taxa richness and Shannon-index were compared by means of randomization tests (1000 randomizations).

Shared taxa from different sites were computed and taxa rarity was measured by means of absolute and relative frequencies of singletons, i.e. taxa with at most 1 individual per sample, and the number of unique taxa, i.e. taxa that occurred in only one sample. The frequencies of doubletons, i.e. taxa with at most 2 individuals per sample and duplicate taxa, i.e. taxa that occurred in only two samples were also reported.

These computations were done using the R package rich (Rossi, 2011a).

2.4.4. Relationship between community characteristics and soil parameters

We performed a direct ordination method, canonical correspondence analysis (CCA), to evaluate the part of the variation in species assemblages that can be explained by chemical soil parameters. Only taxa occurring at least in two samples were included as dependant variables, so the final first matrix consisted of 60 lines (sampling points corresponding at 15 samples per catchment) and 54 columns (taxa retained with unique taxa removed). The matrix of environmental variables contained 60 lines (sampling points: 15 samples per catchment) and 5 columns (chemical parameters retained: exchangeable Al and exchangeable Ca concentrations, CEC, C:N ratio, pH$_{H2O}$). In addition, the four catchments were put as additional variables. The significance of the CCA was assessed with Monte–Carlo permutation test (1000 permutations) and the significance of the axes was evaluated by mean of ANOVA test. We used the R Software and the vegan and ade4 package (Dray et al., 2007).

3. Results

3.1. Chemical parameters

The main characteristics of soil collected from the studied sites are shown in Table 1. Four years after liming, the C:N ratio was not significantly different between each catchment, whereas the limed sites SL and GL exhibited a significantly higher pH$_{H2O}$ ($p < 0.05$). Mean soil pH in SL and GL were 0.4 and 0.2 pH units higher than those observed in the control sites SA and GA, respectively. Similarly, mean exchangeable Mg was significantly more elevated in SL and GL than in the control sites SA and GA ($p < 0.05$).

However, liming induced more marked effects in the soil lying on sandstone (SL) than on granite, since exchangeable Ca and BS were significantly higher compared with the control SA ($p < 0.001$). The limed soil underlain by granite showed slightly higher but not significant CEC, base saturation and exchangeable Ca ($p > 0.05$).

Finally, the CEC and exchangeable Al were significantly higher on soil lying on granite than on sandstone ($p < 0.001$).

3.2. Communities comparison

3.2.1. Community dissimilarities

The PCoA ordination clearly discriminated the macrofauna communities of the four sites (Fig. 2). The first factorial plane of the PCoA explained 24% of the total inertia and significantly differed from those stemming from $N = 1000$ randomizations (Monte–Carlo, $p = 0.001$). The first axis (15% of the total inertia) strongly separated communities from sites lying on sandstone (SL, SA) from those lying on granite (GL, GA) while the second axis (9% of the total inertia) discriminated limed sites (GL, SL) and control sites (GA, SA).

MRPP (1000 randomizations) applied to the four sites showed that community dissimilarity was highly significant ($p = 0.001$). Similarly, MRPP performed on data from acid and limed catchments, for each type of bedrock separately, revealed significant community dissimilarities ($p = 0.002$ between granite sites and $p = 0.001$ between sandstone ones).

3.2.2. Taxa richness and density

In litter and soil blocks sampled at the both collecting dates, a total of 2386 macroinvertebrates were identified; 101 taxa (species or family and order for larvae and juveniles) were found. Sixty-one taxa (60.4% of the total taxa richness) were sampled at sandstone sites and 82 (81.2%) at sites underlain by granite (Table 2).

Significant lower mean densities were observed in limed sites than in control (mean density = 392 ind m^{-2} at GA; 256 at GL; $F = 11.65$, $p < 0.01$ and 152 at SA and 104 at SL; $F = 6.83$, $p < 0.05$; Table 2). Nevertheless, the mean taxa richness was not significantly different between limed and control sites lying on a same bedrock ($F = 4.24$, $p = 0.05$ at granite site and $F = 0.12$, $p > 0.05$). Moreover, for a given type of rock, the total taxa richness and Shannon-index did not differ when limed sites were compared with their respective control sites (taxa richness: 62 at GL and 60 at GA; $p = 0.60$; 42 at SL and 46 at SA; $p = 0.18$; $p = 0.37$ for Shannon-index for both substrate, $N = 1000$ randomizations; Table 2). Corresponding bias-corrected values estimated from bootstrap were higher but not significantly different between treated and control soils (randomization test, $p > 0.05$). GL harboured more singleton and unique taxa and less doubleton and duplicate taxa than GA (Table 2). Conversely, SL exhibited less singleton and unique taxa and more doubleton and duplicate taxa than SA.

Percent of shared taxa in site pairs ranged from 35% to 48.8% (Table 3). Forty taxa (48.8% of granite taxa) were found to occur at both GL and GA, while 27 taxa (44.3% of sandstone taxa) were shared by SL and SA. Thirty-four taxa were common to the limed sites SL and GL (48.6% of taxa found on limed site pair), while 28 taxa were shared by the control sites SA and GA (37.8% of taxa found on control site pair; Table 3).

Finally, only 42 taxa (41.5% of the total richness) were common to both types of bedrock.
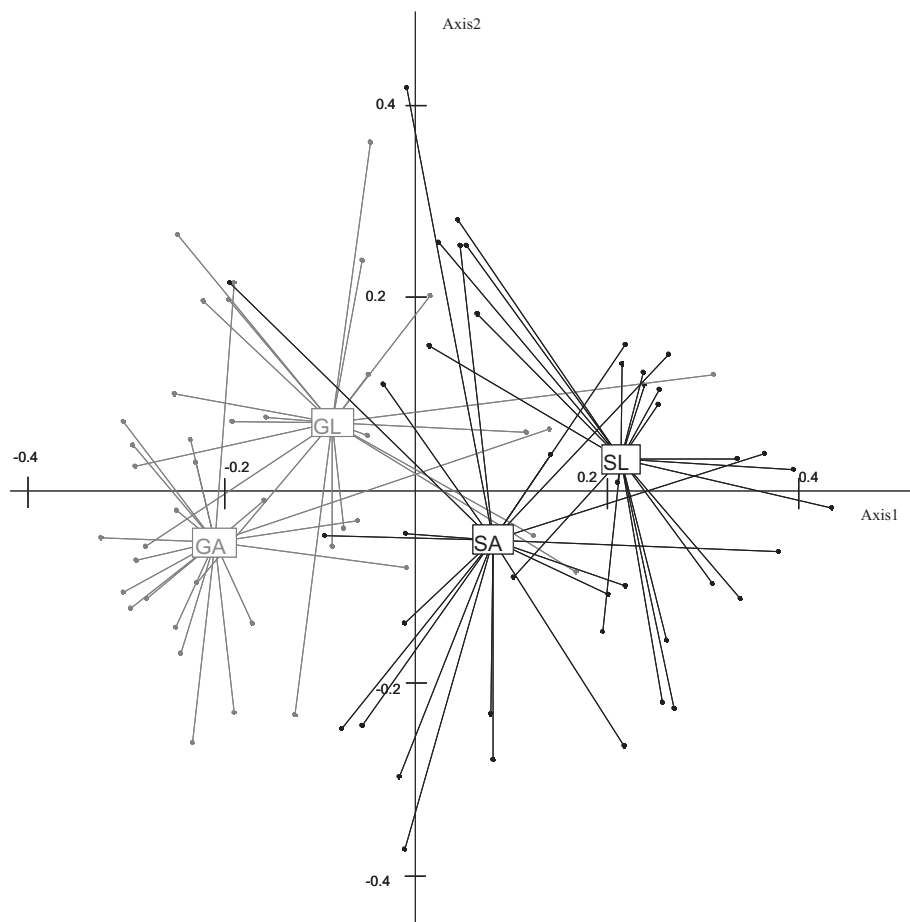
Fig. 2. Projection in the first factorial plane of the Principal coordinate analysis (PCoA) performed on soil macroinvertebrates communities of the four catchments (GA: control granite; GL: limed granite; SA: control sandstone; SL: limed sandstone. Labels are placed at the centre of gravity of each site and are linked to each sample of the corresponding site ($n=21$).

Table 2
Soil macroinvertebrate diversity in sites ($n=21$).

Sites	Acronym	Total abundance	Mean density (/m²)	Mean taxa richness	S_{obs}	S_{corr}	Shannon-index	Singleton	Unique	Doubleton	Duplicate
Granite											
Control	GA	1032	392 (144) a	15 (4) a	60 (3.4)	68.3	2.98	18 (22.0%)	19 (23.2%)	11 (13.4%)	11 (13.4%)
Limed	GL	675	256 (104) b	13 (3) a	62 (3.5)	72.9	2.94	26 (31.7%)	27 (32.9%)	8 (9.8%)	7 (8.5%)
Sandstone											
Control	SA	401	152 (64) c	8 (2) b	46 (2.7)	54.3	2.94	15 (24.6%)	20 (32.8%)	9 (14.8%)	7 (11.5%)
Limed	SL	278	104 (40) d	7 (3) b	42 (2.8)	47.9	2.95	10 (16.4%)	12 (19.7%)	11 (18.0%)	10 (16.4%)

A same letter denotes two values not significantly different ($p < 0.05$; GLM. for density and taxa richness. separately). S_{obs}: observed taxa richness on site; S_{corr}: bias-corrected taxa richness on site. Singleton: taxa with at most one individual; Unique: taxa encountered in only one sample. Doubleton: taxa with at most two individuals; Duplicate: taxa encountered in only two samples. Percentages for singletons, uniques, doubletons and duplicates are indicated in parentheses. Standard errors for mean density and S_{obs} are indicated in parentheses.

Table 3
Observed taxa richness and shared taxa of soil macrofauna in four study sites ($n=21$).

$S = 101$	GL	GA	SL	SA
GL	62 (61.4%)	40 (82)	34 (70)	28 (80)
GA	48.8%	60 (59.4%)	28 (74)	28 (78)
SL	48.6%	37.8%	42 (41.6%)	27 (61)
SA	35%	35.9%	44.3%	46 (45.5%)

S: total taxa richness (all sites pooled) On diagonal, in light grey: observed taxa richness and corresponding ratio to the total richness found for all sites (in parentheses). Above diagonal: absolute number of taxa shared by sites pairs and total number of taxa collected in site pairs (in parentheses). Below diagonal: ratio of the number of shared taxa to the total number of taxa in site pairs.

Table 4
Canonical correspondence analysis: Pearson intra-set correlations ($r \times 100$) of soil parameters ($6 \times$) with the first two axes of CCA ($n = 15$).

	Axis1	Axis2
C.N	23.4	3.9
pH$_{H2O}$	88.7	2.6
Ca	83.5	−17.9
Al	−8.1	−89.3
CEC	8.1	−99.1

3.3. Relationship between community structure and soil properties

In order to investigate which chemical soil properties could significantly influence the structure of macroinvertebrate communities, a CCA was performed (Fig. 3). After eliminating unique taxa, the data set comprised 54 taxa. The first factorial plane of the CCA explained 59.7% of the total variance ($F = 2.52$; $p < 0.01$, Monte Carlo test, 1000 permutations). The first ordination axis (32.3% of the total variance) represented an increasing gradient of pH (Pearson, $r = 0.88$; Table 4) and an increasing gradient of Ca ($r = 0.84$). This first axis separated acidified control sites (SA and GA) from the limed sites with higher mean pH (SL and GL).

The coordinates of the taxa (Table 5) showed that abundance of two Coleoptera species (*Cephennium thoracicum*, *Othius punctulatus*) and three Aranaea (*Monocephalus castaneipes*, *Coleotes* sp., *Cryphoeca silvicola*) were higher in control sites with lower soil pH value (coordinates from −0.96 to −0.52 on axis 1). Conversely, four Coleoptera (*Polydrusus impar*, *Xantholinus tricolor*, Curculionidae larvae sp., *Strophosoma melanogrammum*) two Chilopoda (*Geophilus* sp., *G. insculptus*, a Diplopoda (*Melogona gallica*) and the Clitellata *Lumbricus castaneus* were found with a higher abundance in soils with higher pH and Ca concentration (limed sites) (coordinates from 0.48 to 3.19 on axis 1).
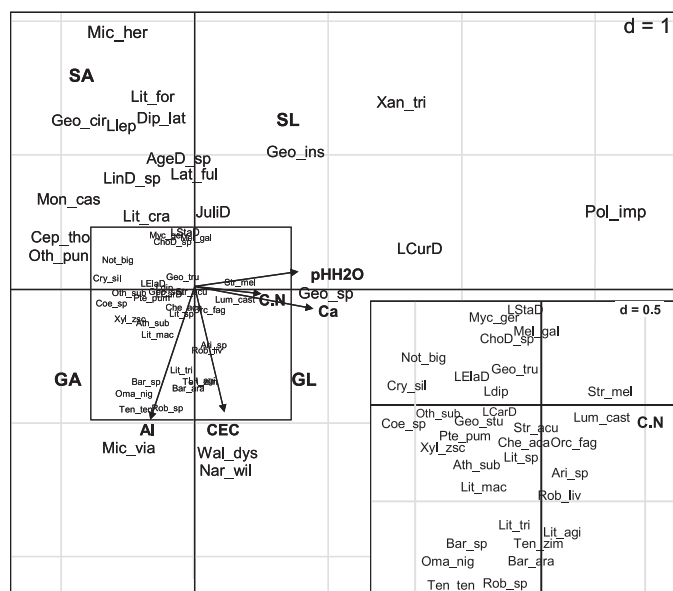

Fig. 3. CCA ordination biplot of macrofaunal assemblages ($54 \times$ taxa) and chemical soil parameters ($5 \times$). Abbreviations of taxa names are given in Table 5. Arrows indicate vectors and abbreviations of soil parameters are: Al: exchangeable aluminium concentration; CEC: Cation Exchange Capacity; C,N: C:N ratio; Ca: exchangeable calcium concentration; pH$_{H2O}$. Taxa labels are placed at the centre of gravity of each taxa. Labels of each site (SA, SL, GA, GL) are placed at the centre of gravity of each site and are linked to each sample of the corresponding site ($n = 15$). The square in the lower right corner corresponds to a zoom on the centre of graph (see Table 5 for precision on coordinates).

The second axis (27.4% of the total variance) was mainly driven by the CEC (Pearson, $r = −0.99$; Table 4) and in a lower extent by exchangeable Al ($r = −89.3$). This axis separated the two sites lying on granite (GL and GA) with higher CEC and Al from the two sites lying on sandstone (SL and SA). Macroinvertebrate assemblages at sites underlain by sandstone were characterized by Aranaea species *Monocephalus castaneipes*, *Diplocephalus latifrons*, *Micrargus herbigradus*, Agelenidae sp and in a lower extent *Linyphiidae* sp. and *Cryphoeca silvicola*, with a higher abundance on SA. Similarly, the Coleoptera *Geostiba circellaris Xantholinus tricolor* and *Lathrobium fulvipenne*, the Lepidoptera larvae, the Chilopoda *Geophilus insculptus*, *Lithobius forficatus*, *L. crassipes* and the Diplopoda *Julidae* sp. were found in higher density in sites lying on sandstone. On the contrary, sites underlain by granite showed higher abundance of taxa such the Coleoptera *Nargus wilkini*, *Omalium nigriceps*, *Athous subfuscus* and *Pterostichus pumilio*, the Aranaea *Walkenaera dysderoides*, *Microneta viaria*, *Robertus* sp., *Tenuiphantes tenebricola* and *T. zimmermanni*, Chilopoda *Lithobius tricuspis*, *L. agilis*, *L.macilentus* and in a lower extent Diplopoda *Xylophageuma zschokkei*, Gastropoda Arion sp. and Dermaptera *Chelidura acanthopygia*.

4. Discussion

Four years after the liming operation with a low dose of 2.5 t ha^{-1} of strongly acidified catchment, a higher pH and exchangeable Mg concentration still occurred in limed soils as compared to controls. Review on liming effects on forest soil parameters showed that changes depend on initial organic and mineral soil properties (Kreutzer, 1995; Godbold, 2003; Schaaf and Hüttl, 2006). In the Vosges Mountains, CEC and exchangeable Al were significantly higher on soil lying on granite than sandstone. The differences in soil chemical parameters between bedrock types could mainly be explained by the highest clay content in granitic soils (22% in granitic soils, and 6% in soils lying on sandstone). Soils with higher clay and organic matter have higher cation exchange capacity (Bonneau and Souchier, 1994). After lime addition, the concentration of exchangeable Al increased by comparison with control on soil lying on granite. Added lime displaces H$^+$ from the exchange sites. In addition, Ca^{2+} and Mg^{2+} cations can be uptaked by plants, leached by released nitrogen or by lateral water drainage and Al cations may be released by decaying organic matter (Ulrich, 1983; Boudot et al., 1994; Hruska and Kram, 1994). Moreover, the chemical weathering of granite released higher aluminium concentration than sandstone. Consequently, when the soil solution contained high aluminium cation and small base cation concentrations as in granitic soils, the Al^{3+} cations may be preferentially held and displace others from exchange sites (Waring and Running, 2007).

Furthermore, Moncoulon et al., 2007 reported a pH from 4.1 and a ratio Al/BC from 1.2 from 1900 to 1950 in the first 10 cm of a vosgian podzosol under beech lying on sandstone. Their results showed an increase of the Al/BC ratio (up to 3.8) and decrease of pH (3.9) over the period 1950–1980 as a result of acid deposition increase. After 1980, the soil pH increased (up to 4) and Al/BC decreased (up to 2.1) while acid deposition decreased. In our study the control soil on sandstone had a pH of 3.9 and Al/BC = 2.6. These values corresponded to results observed by Moncoulon et al. (2007) in 2003. Four years after liming addition, the pH increase to 4.3 and Al/BC decreased up to 0.4. One of the main goal of liming was to increase soil pH and mineral nutrient contents. Thus on sandstone these goals appeared achieved, while Al/BC ratio was smaller than before acidification. We may hypothesize that higher base cation concentration were available for organisms than before acidification. Soil pH of the granite control was 3.9 and Al/BC = 2.7 which

Table 5

Macroinvertebrate taxa (54×) recorded in the four catchments with code numbers used in CCA and coordinates along first two axes of CCA (n = 15).

Class	Order	Family	Genus species	Code (Fig. 3)	Axis 1	Axis 2
Annelida	Clitellata	Lumbricidae	*Lumbricus castaneus* (Savigny 1826)	Lum_cast	0.48	−0.12
Arachnida	Araneae	Agelenidae	Agelenidae sp.	AgeD_sp	−0.06	0.98
		Agelenidae	*Monocephalus castaneipes* (Simon 1884)	Mon_cas	−0.88	0.67
		Amaurobiidae	Coelotes sp. Blackwall 1841	Coe_sp	−0.53	−0.15
		Hahniidae	*Cryphoeca silvicola* (C.L. Koch 1834)	Cry_sil	−0.51	0.04
		Linyphiidae	*Diplocephalus latifrons* (O.P.-Cambridge 1863)	Dip_lat	−0.20	1.28
		Linyphiidae	*Micrargus herbigradus* (Blackwall 1854)	Mic_her	−0.54	1.92
		Linyphiidae	*Microneta viaria* (Blackwall 1841)	Mic_via	−0.44	−1.19
		Linyphiidae	*Tenuiphantes tenebricola* (Wider 1834)	Ten_ten	−0.29	−0.93
		Linyphiidae	*Tenuiphantes zimmermanni* (Bertkau 1890)	Ten_zim	0.21	−0.73
		Linyphiidae	*Walckenaeria dysderoides* (Wider 1834)	Wal_dys	0.31	−1.23
		Linyphiidae	Linyphiidae sp.	LinD_sp	−0.42	0.83
		Theridiidae	*Robertus lividus* (Blackwall 1836)	Rob_liv	0.23	−0.50
		Theridiidae	Robertus sp. (O. P.-Cambridge 1879)	Rob_sp	−0.05	−0.92
Insecta	Coleoptera	Carabidae	Carabidae larvae	LCarD	−0.06	−0.06
		Carabidae	*Notiophilus biguttatus* (Fabricius. 1779)	Not_big	−0.43	0.19
		Carabidae	*Pterostichus* (*Haptoderus*) *pumilio* (Dejean 1828)	Pte_pum	−0.15	−0.11
		Curculionidae	*Barypeithes* (*Exomias*)*araneiformis* (Schrank 1781)	Bar_ara	0.10	−0.78
		Curculionidae	Barypeithes sp.	Bar_sp	−0.22	−0.73
		Curculionidae	*Orchestes* (*Salius*) *fagi* (Linnaeus 1758)	Orc_fag	0.26	−0.19
		Curculionidae	*Polydrusus* (*Metallites*) *impar* (Gozis 1882)	Pol_imp	3.19	0.58
		Curculionidae	*Strophosoma melanogrammum* (Forster 1771)	Str_mel	0.49	0.02
		Curculionidae	Curculionidae larvae	LCurD	1.73	0.31
		Elateridae	*Athous* (*Haplathous*) *subfuscus* (O.F. Müller 1764)	Ath_sub	−0.15	−0.29
		Elateridae	Elateridae larvae	LElaD	−0.18	0.02
		Leiodidae	*Nargus* (*Demochrus*) *wilkini* (Spence 1815)	Nar_wil	0.28	−1.28
		Scydmaenidae	*Cephennium thoracicum* (Müller and Kunze 1822)	Cep_tho	−0.96	0.39
		Staphylinidae	*Geostiba circellaris* (Gravenhorst 1806)	Geo_cir	−0.82	1.26
		Staphylinidae	*Lathrobium fulvipenne* (Gravenhorst 1806)	Lat_ful	0.05	0.89
		Staphylinidae	*Othius punctulatus* (Goeze 1777)	Oth_pun	−0.86	0.30
		Staphylinidae	*Omalium nigriceps* (Kiesenwetter 1850)	Oma_nig	−0.29	−0.82
		Staphylinidae	*Othius subuliformis* (Stephens 1833)	Oth_sub	−0.32	−0.06
		Staphylinidae	*Xantholinus* (*Purrolinus*) *tricolor* (Fabricius 1787)	Xan_tri	1.59	1.39
		Staphylinidae	Staphylinidae larvae	LStaD	0.05	0.41
	Dermaptera	Forficulidae	*Chelidura acanthopygia* (Gene 1832)	Che_aca	0.08	−0.17
	Diptera		Diptera larvae	Ldip	−0.12	−0.03
	Lepidoptera		Lepidoptera larvae	Llep	−0.50	1.21
Chilopoda	Geophilomorpha	Geophiilidae	*Geophilus insculptus* (Attems 1895)	Geo_ins	0.81	1.02
		Geophiilidae	*Geophilus studeri* (Rothenbühler 1899)	Geo_stu	−0.05	−0.05
		Geophilidae	Geophilus sp	Geo_sp	1.03	−0.03
		Geophilidae	*Geophilus truncorum* (Bergsoe & Meinert 1866)	Geo_tru	0.06	0.06
		Linotaeniidae	*Strigamia acuminata* (Leach 1815)	Str_acu	0.14	−0.06
	Lithobiomorpha	Lithobiidae	Lithobius sp	Lit_sp	0.04	−0.22
		Lithobiidae	*Lithobius* (*Lithobius*) *agilis* (C.L. Koch 1847)	Lit_agi	0.19	−0.71
		Lithobiidae	*Lithobius* (*Monotarsobius*) *crassipes* (L. Koch 1862)	Lit_cra	−0.31	0.54
		Lithobiidae	*Lithobius* (*Lithobius*) *macilentus* (L. Koch 1862)	Lit_mac	−0.12	−0.38
		Lithobiidae	*Lithobius* (*Lithobius*) *forficatus* (Linnaeus 1758)	Lit_for	−0.27	1.34
		Lithobiidae	*Lithobius* (*Lithobius*) *tricuspis* (Meinert 1872)	Lit_tri	0.03	−0.64
Diplopoda	Chordeumatida	Chordeumatidae	*Melogona gallica* (Latzel 1884)	Mel_gal	0.17	0.35
		Chordeumatidae	*Mycogona germanica* (Verhoeff 1892)	Myc_ger	−0.04	0.37
		Chordeumatidae	Chordeumatidae sp	ChoD_sp	0.01	0.32
	Julida	Julidae	Julidae sp	JuliD	0.19	0.59
	Chordeumatida	Haaseidae	*Xylophageuma zschokkei* (Bigler 1912)	Xyl_zsc	−0.33	−0.26
Gastropoda	Pulmonata	Arionidae	Arion sp.	Ari_sp	0.28	−0.45

corresponded to measurements of Moncoulon et al. (2007). After liming, as expected the pH increased (4.1) but Al/BC increased to 3.1. Thus on granite, the goal of lime addition may not fully achieve. Unfortunately we did not have any faunal data before acidification from studied sites. Consequently we could not assess whether the fauna communities which occured on sites after liming operation correspond to initial communities which were present before acidification.

The mean densities of soil and litter-dwelling macroinvertebrates in limed forest soils were lower as compared to control. Secondly, no difference in taxa richness and Shannon-index has been observed between limed and control site. However, 52.2% (42 taxa on the total number of taxa recorded) was different between limed and control sites lying on granite and 55.7% was different on sandstone (34 taxa). Thereby, liming may induce important changes in community structure as illustrated by MRPP and PCoA analysis. The CCA showed that some taxa were found preferentially on limed soil with higher soil pH and Ca concentration: Gastropoda and Curculonidae, Lepidoptera and Diptera larvae, the majority of Curculionidae adult species, especially *Polydrusus impar*, and most species of Geophilidae. Similarly, the density of epigeic earthworm *Lumbricus castaneus* was higher in limed soil. Positive effect of liming on earthworm population density and particularly on the epigeic earthworm populations has been previously shown by different studies (Robinson et al., 1992; Edwards and Bohlen, 1996; Davidson et al., 2004; Potthoff et al., 2008). Other taxa have a higher density on control site than on limed ones: the majority of Araneae families, most of the Lithobiidae species, and Staphylinidae species. Finally, some taxa did not differed according to liming such as Staphylinidae larvae or the *Chelidura acanthopygia* species.

Korenko et al. (2008) reported no effect of lime treatment upon spider community in birch stand of the Krušné hory Mountains. Results from a study 5 years after lime treatment into catchment wetlands in Wales, showed that liming had positive effect on Linyphiidae and Tetragnathidae but not on Lycosidae (Buckton and Ormerod, 1996). Moreover, Theenhaus and Schaefer (1995) showed that Diptera and Lithobiidae populations increased due to liming, whereas Deleporte and Tillier (1999) reported a smaller abundance of Chilopoda after lime addition.

Calculation of unique and duplicate taxa, singleton and doubleton showed that the rare taxa (taxa collected as low number individuals) in all studied sites ranged from 8.5% to 32.9%. Similarly, Rossi et al. (2006, 2010) reported high rare species number for soil macrofauna and highlighted the value of additional statistics such as bootstrap corrections. Moreover, 101 macroinvertebrates taxa have been sampled in our study, while Diptera, Lepidoptera and Coleoptera larvae were not identified at a species level. The estimation of species richness was *de facto* underestimated.

The idea that liming can be considered as a disturbance was expressed by different authors (Bengtsson, 2002; McKie et al., 2006). Liming may change soil parameters and cause aluminium toxicity as showed by Larssen et al. (1999) and thus may imply changes into the community structure. Sousa (1984) described a disturbance as a "discrete punctuated killing displacement or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established". A disturbance was defined by several properties: (i) its areal extent (spatial scale), which was the catchment in our study, (ii) its magnitude by its intensity, i.e. the strength of the disturbing, which can be for a liming operation the quantity spread on soil, and (iii) its severity, i.e. the measure of the damage caused by the disturbing force, which can be the changes on chemicals properties of soil; (iv) its frequency (v) its predictability and its turnover rate. These two last points do not concern our study because of a single controlled spreading operation was performed. The consequences of liming disturbance as a direct effect of soil pH four years after spreading a low dose may consist in deep changes in community structure due to the shift of ten species. Moreover, some species benefited from the disturbance such as colonists and regenering survivors like *Lumbricus castaneus* or *Polydrusus impar* favoured by better chemical conditions and resources, while others suffered and decreased like most spider species depending on their specific adaptation responses (Sousa, 1984; Loreau, 1994; Moretti et al., 2006). Nevertheless, four years may be a too short period to allow the (re)colonization of limed sites by species with low dispersal capacity. This highlights the importance to have a high biological diversity (pool of species) and hideaway areas before perturbation and during the community reorganisation phases on a larger scale (Bengtsson et al., 2000; Bengtsson, 2002; Potthoff et al., 2008). Hence, from a management point of view, maintaining of diversity and heterogeneity in soil forest habitats may ensure the pool of species which may be essential for ecosystem stability and ecosystem functioning (Bengtsson et al., 2000). This idea has been already evoked in studies dealing with ground-dwelling fauna assemblages re-colonizing heterogeneous habitats such as open-cast mining reclamation area (Topp et al., 2010; Frouz et al., 2001 and Frouz et al., 2011).

Furthermore, at a higher spatial scale that take into account limed catchment and its control together, we may consider that taxa richness was increased with liming since after liming one community of acidified soils (the same for both catchments) was replaced by two communities, one specific of acidified soils and the other preferring less acidified soils, i.e. limed ones. More knowledge on the spatial distribution of species and on their life history traits such as the capacity of colonization or habitat preference

is required to better understand processes involved in the recolonization of limed areas (Cole et al., 2008; Auclerc et al., 2009).

The *Intermediate disturbance-hypothesis* (IDH) (Connell, 1978) proposed that disturbance can create high heterogeneity and consequently an increase of diversity of resources and habitat in tropical forests. In addition, Sousa (1984) stated that disturbance must renew resources to allow continued recruitment and persistence of species that would otherwise be driven locally extinct. Therefore, the disturbance must occur with some intermediate frequency and intensity in order to allow species accumulation within the patch and prevent it from domination by one or a few of them (McCabe and Gotelli, 2000). In this context, the species assemblage can be maintained in a non-equilibrium state and local coexistence of species is possible. Thus, this may allow a better and durable ecosystem functioning by increasing the diversity of resources and species and avoid the risk of compensatory mortality of individuals after liming operation. We can ask the question if several disturbance as several liming applications may be a better alternative to counteract acidification and to reach ecosystem stability. However, the quantity of lime which must be used in order to avoid irreversible changes of ecosystem remains an open question. Finally, to restore ecosystem another strategy would be to elaborate synthetic indicators to help developing sustainable forest management (Lindenmayer et al., 2000; Doran and Zeiss, 2000; Niemelä, 2000; Rossi and Van Halder, 2010; Rossi, 2011b).

5. Conclusion

Four years after one liming operation with a low dose of $2.5\,t\,ha^{-1}$ of strongly acidified catchment, a smaller density of macroinvertebrates was observed on limed than control soil, whereas the community species richness were not different. Our study showed that liming by change of soil pH may be considered as a disturbance for the soil fauna community according to a species-dependant response. In European forests, liming has been used as a restoration method to counteract the effects of acid rain, in particular for production of wood biomass in nutrient-poor ecosystems. Thus, liming has been showed to mitigate ecosystem acidity. However, in the perspective of sustainable development, the production of wood biomass should not be the only target when operating liming. Due to the role they play in the functioning of ecosystems we advocate that other biological compartments such as macroinvertebrates should be also studied in order to evaluate if this restoration method may allow building resilient communities and ecosystems in a long-term period.

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