The impact of soil temperature increase on organic matter and faunal properties in a frozen calcareous scree in the French Alps

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ABSTRACT

We examine the effect of natural differences in soil temperature at two locations distant by approximately 500 m in the frozen scree of La Plagne en Chartreuse (Savoy, France). We determined humus properties, soil organisms and biologically mediated soil-forming processes in screes from a low part dominated by an open pine forest (OF, 1100 m asl) and in a top part covered by a dense pine forest (DF, 1200 m asl). Our results show a soil temperature increase of about 3.8 °C in the DF plot during June to October, but similar humus morphology at both plots. Soil pH was lower, and C/N ratio higher in the DF plot. Soil faunal composition differed between DF and OF plots for some taxa. While the abundance of the Oribatid mites was higher, abundance of Collembola was significantly lower in the DF plot. As earthworm activity was scarce at the site, Oribatid mites and Collembola presumably play an important role in the humus microstructure which was confirmed by the analysis of the humus micro-aggregation. To date, changes in the pedofaunal communities did not alter the humus form which may be explained by the complexity of biotic soil interactions and the high functional redundancy of the soil fauna.

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1. Introduction

According to the fourth assessment report of the Intergovernmental Panel on Climate Change, the Earth's climate has warmed by about 0.74 °C over the past century (http://www.ipcc.ch). Climate scenarios for the 21st century predict further warming, with a best estimate temperature rise of 4.0 °C (likely range is 2.4 °C to 6.4 °C) for the high scenario A1F1 (IPCC, 2007). It has been suggested that these trends will be particularly pronounced at high latitudes altering snow cover, permafrost stability, growing season length, and productivity in arctic and boreal environments. Recent warming has already caused expansion of shrubs in vascular plant communities in many cold regions of the world (e.g. Theurillat and Guisan, 2001; Tape et al., 2006). In the European Alps, evidence of climatic change in the 20th century was observed through glacier retreat, decrease in snow-cover extent and earlier snowmelt (Beniston, 2006). Moreover, under the influence of climate warming (Post et al., 1982) cold biomes with high soil organic matter accumulation are of primary importance as possible sources of carbon emissions.

Microclimatological studies have identified small alpine enclaves of screes with permafrost in many European mountains. Despite their distribution at much lower altitudes, they present distinctive features that would allow them to be classified into the alpine zone. The cold microclimatic conditions of these sites provide exceptional microhabitats with very thick raw humus (Gude et al., 2003) colonized by many cold living plants (Bertinelli et al., 1993) and periglacial relict species of non-vascular plants (Asta et al., 2001), beetles (Molenda, 1996), spiders (Ruzicka and Zacharda, 1994), and mites (Zacharda et al., 2005). These small-scale habitats, which are older than the surrounding biological matrix, act as refuge by supporting communities unable to survive elsewhere in the landscape. Such paleorefugia are expected to be particularly vulnerable to changes in their environmental conditions (e.g. global warming, but see Nekola, 1999 and Noss, 2001), and may therefore provide a sensitive indicator of climate change processes.

The presence of low-elevation permafrost sites is explained by a complex system of air circulation also called Balch ventilation (Thompson, 1962). Scree slopes formed of broken rocks have an intensive air circulation; with warm air outflow in the upper scree sections during winter, and cold air outflow in the lower sections during summer (Harris and Pedersen, 1998; Kneisel et al., 2000). This air-conditioning system creates a small-scaled spatial heterogeneity with temperatures (throughout the year) near freezing point at the lower part of the scree, which could form perennial ground ice. Furthermore, these severe thermal conditions are a major limitation of invertebrate distribution, which strongly influence the decomposition processes under such environmental constraints (Petersen and

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Luxton, 1982; Sjursen et al., 2005a). The distribution, abundance, and life cycles of soil decomposing animals, are all affected by soil temperature directly (e.g. through desiccation) and indirectly, through modifications in food resources and microhabitat (Setälä et al., 1995; Sulkava and Huhta, 2003; Huhta and Hanninen, 2001; Pflug and Wolters, 2001). These enclaves with alpine features therefore provide an appropriate environment in which to test the relationships between soil arthropods, plants and soil temperature.

In the present study, differences in soil temperature at the top and at the bottom of an alpine frozen scree is used to investigate changes in global warming on biological soil processes. The scree is used as a field laboratory to study long-term effects of soil temperature increase under natural conditions. Other variables such as precipitations, slope, exposure and bedrock are highly homogenous due to the short distance between the top and the bottom of the study area. Through field observations we examine the influence of variable soil

temperature (like those predicted by IPCC global warming scenarios) on humus properties, soil organisms and biologically mediated soil-forming processes. Our work addresses in particular two questions: 1) How do variations in temperature influence humus forms and soil arthropod distribution involved in organic matter decomposition? 2) Can pedofaunal changes alter humus form?

2. Material and methods

2.1. The study site

The study site of La Plagne (45°27′ N, 5°55′ E) is situated in the Northern French Alps within the Réserve des Hauts de Chartreuse (Fig. 1). It is located on a limestone scree composed of crushed rocks from the Urgonian period (circa 130–125 million of years ago) with a sporadic permafrost caused by Balch ventilation. The scree has a slope of about 40°
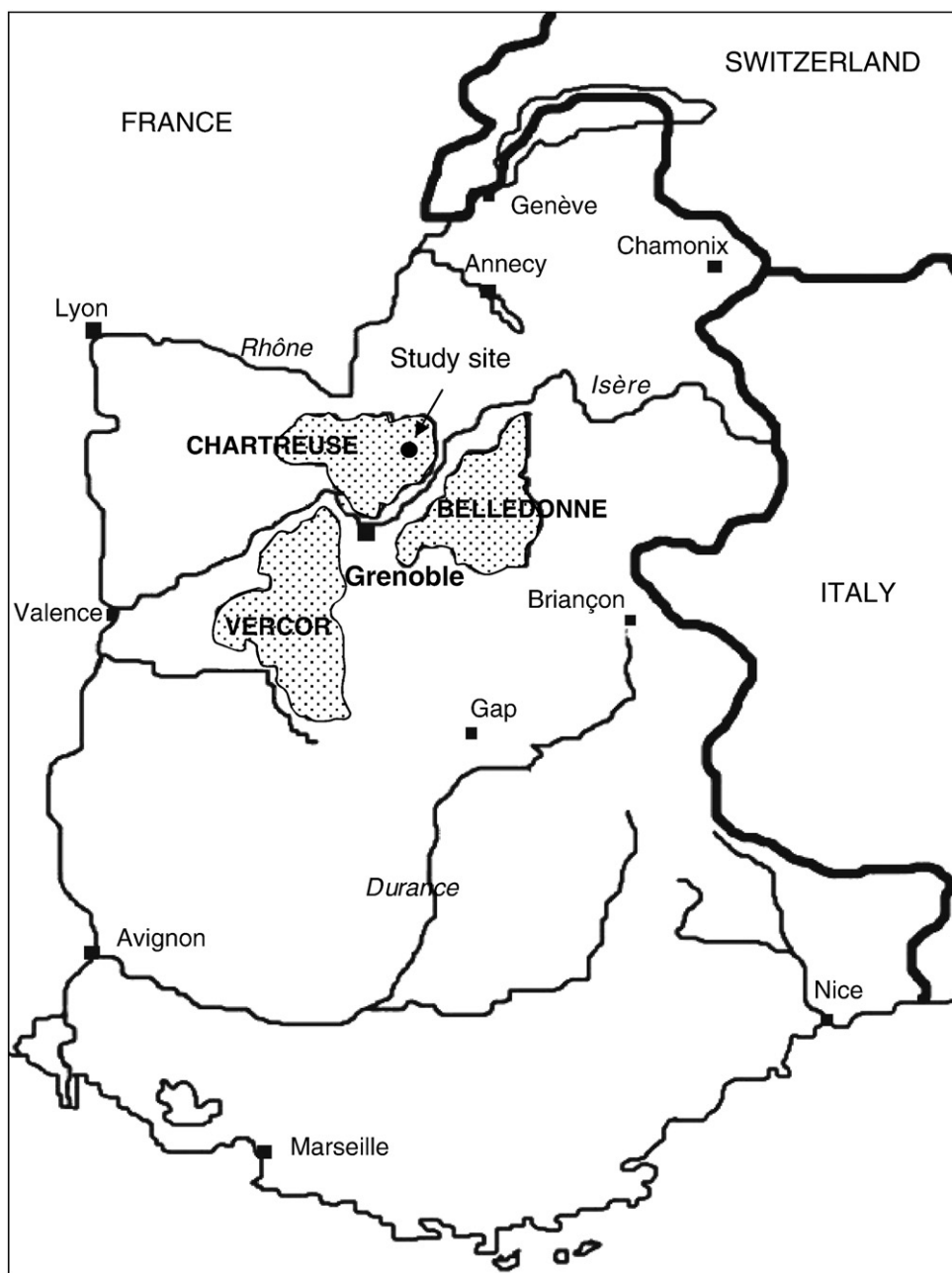

Fig. 1. Geographical location of the study site of La Plagne in the Northern French Alps.

and is exposed to the North-Northwest. The climate of the region is characterized by a mean annual temperature of 7 °C, abundant precipitations of 2000 mm/year and a long period of snow cover lasting from November to April. The site can be described as a cold alpine enclave in a montane ecosystem dominated by Mountain pine (*Pinus uncinata* Mill. ex Mirb.) forest and surrounded by climacic vegetation comprising of spruce and beech–fir forests. The soil can be considered a histosol, according to the USDA Soil Taxonomy (USDA, 1999), with a thick raw humus. The ground flora is a typical association of plants characteristic of raw humus (*Rhododendron ferrugineum* L., *Vaccinium vitis-idaea* L., *V. myrtillus* L.) with an important cover of mosses (*Hylocomium splendens* (Hedw.) B.,S.&G., *Rhytidiadelphus squarrosus* (Hedw.) Warnst., *Pleurozium schreberi* (Brid.) Mitt., *Dicranum scoparium* Hedw., *Polytricum formosum* Hedw.) and lichens (*Cladonia rangiferina* (L.) Web., *C. gracilis* (L.) Willd., *Cetraria islandica* (L.) Ach.) accompanied by alpine calciphilic species (*Dryas octopetala* L., *Saxifraga oppositifolia* L., *Carex sempervirens* Villars or *Arctostaphylos uva-ursi (*L.) Spreng.).

2.2. Experimental design

Two experimental plots of approximately 150 m² were set up at the top and at the bottom of the alpine part of the scree. The lower plot was situated at 1100 m asl in an open forest (OF), while at the higher plot (1200 m asl) a dense forest (DF) is present. The OF plot is characterized by dwarf *Pinus uncinata* with a maximal height of adult trees being 2–5 m. Crushed rocks are numerous and partly covered by alpine heliophilous species such as *Carex sempervirens* (15% of cover) and *Dryas octopetala* (30% of cover). Forest mosses (especially *Hylocomium splendens*) form an important layer between shrubs of *Arctostaphylos uva-ursi*, *Salix retusa*, *Vaccinium myrtillus* and the dominant *Rhododendron ferrugineum* and *Vaccinium vitis idaea* (both 20% of cover). The DF plot is characterized by a dense cover of Mountain pine trees reaching a height of 10 to 20 m. Mosses form a quasi continuous layer and *Rhododendron ferrugineum* and *Vaccinium vitis idaea* are the principal shrubs with a cover of 25%. *Dryas octopetala* is dominant (20% of cover) where the tree cover is scarce.

Within these two plots, three subplots (circa 3×6 m) dominated by different vegetation (*Dryas octopetala*, *Vaccinium vitis-idea*, *Rhododendron ferrugineum)* were selected. In order to keep the pristine aspect of the scree labelled "Natura 2000", three random sample points were used in each subplot, at which humus forms were described along soil profiles (also used for monitoring of soil temperature). Soil and faunal samples were also collected. Sample points were distant from each other by at least 2 m, resulting in a total of 18 sample points (2 altitudes×3 vegetation types×3 sample points).

2.3. Sampling of humus forms and chemical analysis

In July 2005 we described in situ the humus forms of each sample by identifying the L, F and H horizons through macro-morphological analysis of their structure, composition and other relevant properties using the Canadian classification (Green et al., 1993). Humus samples of a constant volume (250 cm³) were taken below 10 cm depth, brought back to the laboratory where they were sieved (mesh size 2 mm) before being sent for soil analysis at INRA Arras. Soil pH was measured in H_2O, respecting a soil:solution ratio equal to 1:2.5. The cation exchange capacity (CEC) was determined by the Metson method (Metson, 1956). Exchangeable cations (Ca, Mg, K, Na) were measured by atomic absorption spectroscopy after ammonium acetate extraction (Thomas and Marshall, 1999). Organic carbon (ISO 10694, 1999), total nitrogen (ISO 13878, 1999) and total $CaCO_3$ (ISO 10693, 1999) was analysed. Soil temperature was manually monitored once a month from June to November 2005 along the soil profiles at 0, 5, 10, 15, 20, and 25 cm depth using a 10 cm long probe (Hi765PWL, HANNA Instruments, Tanneries, France).

2.4. Soil fauna investigation

At the same time as humus was sampled, one humus core (5.5 cm diameter and 10.5 cm deep) was taken next to each soil profile for faunal extraction in Berlese–Tullgren funnels (Schaller, 1968). From 21st June–5th September 2005, one pitfall trap (6 cm diameter and 8 cm deep) was placed in the vicinity of each soil profile and was emptied once every two weeks. Soil animals were classified into faunal taxa. In August 2005 a survey on earthworm abundance, similar to Callaham's and Hendrix's (1997) surveys, was performed on twelve 0.5×0.5 m-squares randomly chosen in the two plots. Squares were approximately 5 m apart from each other and the soil from each pit was separated into four fractions (litter, 0–5 cm, 5–15 cm, and 15–25 cm) and hand-sorted for earthworms. Adult earthworms were identified to species, juveniles to genus.

2.5. Study of biological aggregation by image analysis

One humus block (Kubiena boxes of 8×5×3 cm) was taken in all subplots dominated by *Dryas* at a depth of 10 cm at the transition between the F and H humus layers. Under *Vaccinium* and *Rhododendron* stands, humus blocks were taken at a depth of 10 cm in the F layer and at 20 cm in the H layer. The 30 samples (6 subplots under *Dryas*, 6 subplots×2 depths for *Vaccinium* and for *Rhododendron*) were stored at 5 °C until sent to the soil laboratory of Savoy University where thin sections of 25 μm were performed. Thin sections were prepared from undisturbed blocks used in the standard procedure of drying samples by acetone exchange before resin impregnation (see FitzPatrick, 1980; Kooistra, 1991; Grieve et al., 2005).

Some difficulties have been encountered during the process of inclusion of the humus blocks and nearly half of the thin sections were unusable. We considered only 10 thin sections to respect a homogenization of the data between the two plots which allowed one description in each subplot. Image acquisition was carried out with a Sony Camera DXC-930P and aggregate structures (size and shape of particles) quantified by National Instruments Vision Assistant 8.0 software. For each thin section, 12 windows of 10×10 mm (grid of 3 horizontal and 4 vertical windows) with a spatial resolution of 18 μm/pixel were surveyed and digitized in a square grid of 768×576 pixels, with a spectral resolution of 256 grey levels. A morphological classification of the aggregation was established from the two measured parameters on each aggregate: its size, estimated from the diameter of its section in the binary image, and its form, estimated from the shape index (Pawluk, 1987; Bruneau et al., 2004). Special attention was given to faecal pellets of macrofaunal origin (>250 μm; thereon macroaggregates) and faecal pellets considered to be associated with meso- and micro-fauna (<250 μm; thereon microaggregates) on the basis of their rounded shape with a shape index ranging from 0.67 to 0.95 according to Pawluk (1987). These two classes have been further subdivided into 8 size classes, relating to soil

Table 1
Size classes of biological aggregates with their shape index (4π area/perimeter²) according to Pawluk (1987)

|	Soil fauna organisms	Size	Shape index, (Pawluk, 1987)
Microaggregates (<250 μm)	Acari or Collembola	30–50 μm	0.87±0.06
	Collemba	50–90 μm	0.88±0.04
	Collemba or Enchytreids	90–125μm	0.86±0.05
	Enchytreids	125–250±μm	0.88±0.05
Macroaggregates (>250 μm)	Insecta larvae (Coleoptera,Diptera)	250–300±μm	0,87±0,05
	Diplopoda, Isopoda	300–600±μm	0.91±0.05
	Small Earthworm or Diptera larvae	600–940±μm	0.84±0.06
	Earthworm	>1000±μm	
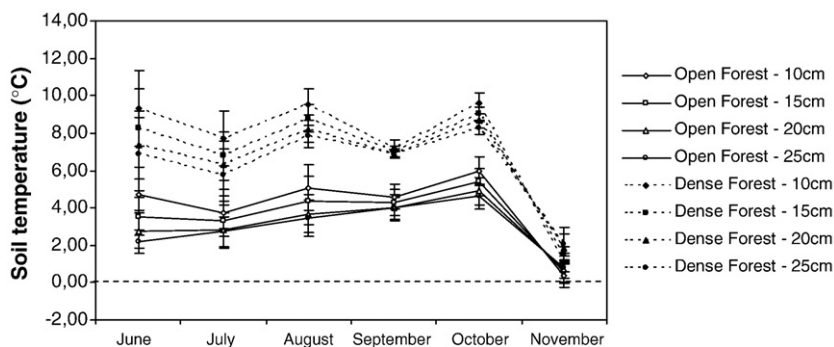
Fig. 2. Soil temperature variations (mean values with standard deviation) into soil profiles during the growing season (June to October) and November 2005 in the Open pine Forest (OF) and Dense pine Forest (DF) plots.

fauna organisms that have been referred to in several studies on humus features (Rusek, 1985; Pawluk, 1987) (Table 1). The results of biological aggregation were expressed as the area of the aggregate relative to the total image area.

2.6. Statistical analysis

Auto-correlation between the soil chemical variables was tested by Pearson correlation test. Differences in soil chemical properties, faunal groups and soil temperature between the two plots were analyzed using ANOVA models. Plot, vegetation in the subplot and its interactions were tested against the variation among random samples. For the analysis of the soil temperature, air temperature was introduced as a covariable and depth of the soil samples and its interaction with plot and vegetation was tested against the variation of the temperature per depth and sample, and time (month) and its interactions with the other factors against the error term. For earthworm analysis, ANOVAs were replaced by the non parametric Mann–Whitney U-test. Relationships between soil aggregation and biological activity were analysed by t-test to compare the plot effect, the humus horizon effect and the size of aggregates (macro- and micro-aggregation). Tukey or Fisher post-hoc test was used to discriminate between significant results within factors. We checked the normality of the data and applied log $(n+1)$ or an arcsin $\sqrt{n}$ transformation when the normality was not respected. All statistical analyses were conducted using Statistica 7.1 software.

3. Results

3.1. Soil temperature variations from −10 to −25 cm

Soil temperature varied significantly between months ($p<0.001$) and plots ($p<0.001$) until November. In November, soil temperatures were similar at the DF and OF plots ($p>0.1$) and reached values near the freezing point in both plots (Fig. 2). Soil temperature was different at all depth except for the OF plots where soil temperature at −20 cm and −25 cm did not differ significantly ($p=0.20$) during the study period. During the growing season from June to October, soil temperature was between 2.7 °C (September) and 4.6 °C (June) higher in the DF-plot.

3.2. Morphological description of humus forms

Despite the differences in temperature from June to October, the soil profiles were similar at both plots (DF and OF). Both plots were composed of three horizons (L, Fm, Hh) which classify them among the Humimor humus according to the Canadian classification. The litter (L), which is composed of a mixture of pine needles and birch

Table 2
Relative abundance of the soil faunal groups per plot for pitfall traps

	Pitfall traps		Two-way ANOVA					
	Open Forest	Dense Forest	Plot Effect		Vegetation effect		Interactions	
	Plot	Plot	$F(1,84)$	P	$F(2,84)$	P	$F(2,84)$	P
Mollusca								
Gasteropoda	0.04	0.21		ns		ns		ns
Nematoda	0.00	0.00		ns		ns		ns
Oligocheta								
Enchytraeidae	0.00	0.00		ns		ns		ns
Arthropoda crustacean								
Isopoda	0.08	0.90		ns		ns		ns
Arthropoda myriapoda								
Diplopoda	0.15	0.36	4.0	0.049		ns	4.5	0.014
Chilopoda	0.00	0.04		ns		ns		ns
Symphyla	0.00	0.00		ns		ns		ns
Arthropoda chelicerata								
Opiliones	0.08	0.11		ns		ns		ns
Aranea	0.92	1.46	4.04	0.047		ns		ns
Acari Gamasida	1.12	1.38		ns		ns		ns
Acari Oribatida	16.78	43.07	35.63	<0.001	2.81	0.066		ns
Acari Prostigmata	0.54	0.54		ns		ns		ns
Arthropoda hexapoda								
Collembola	11.06	13.19		ns		ns		ns
Diplura	0.00	0.02		ns		ns		ns
Protura	0.00	0.00		ns		ns		ns
Coleoptera	0.15	0.66	7.47	0.008	3.67	0.029		ns
Coleoptera larvae	0.00	0.21		ns		ns		ns
Dermaptera	0.02	0.02		ns		ns		ns
Dictyoptera	0.13	0.02		ns		ns		ns
Diptera	0.47	1.53	3.15	0.079		ns		ns
Diptera larvae	0.13	0.28		ns		ns		ns
Heteroptera	0.00	0.02		ns		ns		ns
Homoptera	0.21	0.24		ns	4.4	0.015		ns
Hymenoptera (formicidae)	1.38	1.87		ns		ns		ns
Other Hymenoptera	0.21	0.26		ns		ns		ns
Hymenoptera larvae	0.02	0.00		ns		ns		ns
Total relative abundance	33.5	66.4						
Total abundance	1558	3087						

Significant results from two-way ANOVAs of plot, vegetation and their interactions ($P \times V$) are shown. ns; $p>0.1$.

Table 3
Relative abundance of the soil faunal groups per plot for soil core samples

	soil core		Two-way ANOVA *	
	Open Forest	Dense Forest	Plot Effect	
	Plot	Plot	F(1,12)	P
Mollusca				
Gasteropoda	0.00	0.00		ns
Nematoda	0.03	0.06		ns
Oligocheta				
Enchytraeidae	0.03	0.06		ns
Arthropoda crustacean				
Isopoda	0.00	0.03		ns
Arthropoda myriapoda				
Diplopoda	0.00	0.00		ns
Chilopoda	0.00	0.00		ns
Symphyla	0.03	0.09		ns
Arthropoda chelicerata				
Opiliones	0.00	0.00		ns
Aranea	0.15	0.12		ns
Acari Gamasida	4.28	6.57		ns
Acari Oribatida	22.14	36.48	4.68	0.051
Acari Prostigmata	0.74	2.41		ns
Arthropoda hexapoda				
Collembola	15.44	10.03	5.06	0.044
Diplura	0.06	0.00		ns
Protura	0.00	0.03		ns
Coleoptera	0.03	0.06		ns
Coleoptera larvae	0.00	0.09		ns
Dermaptera	0.00	0.00		ns
Dictyoptera	0.00	0.00		ns
Diptera	0.03	0.29	21.24	<0.001
Diptera larvae	0.15	0.18		ns
Heteroptera	0.03	0.00		ns
Homoptera	0.33	0.03		ns
Hymenoptera (formicidae)	0.00	0.00		ns
Other Hymenoptera	0.00	0.00		ns
Hymenoptera larvae	0.00	0.00		ns
Total relative abundance	43.5	56.4		
Total abundance	1461	1900		

*Neither vegetation effect nor interactions were significant.

leaves, is accompanied by *Dryas*, *Vaccinium* or *Rhododendron* leaves. Below, we observed a Fm horizon of compact matted structure. This Fm horizon was characterized by plant fragments of the litter intermixed by skeletons of the mosses *Hylocomium splendens* and *Rhytidiadelphus squarrosus* with abundant fine roots of the living vegetation. Living roots were abundant in the underlying Hh horizon characterised by its dark-brown colour and its massive structure with a greasy character. The Hh horizon consisted of dominant micro- and meso-aggregated fine organic matter ranging from 7 to 33 cm in thickness (Appendix A). The humus profile ranging from 20 cm under *Dryas* to 40 cm under *Vaccinium* and *Rhododendron* was directly developed on the calcareous parent rock.

3.3. Chemical description of humus forms

C/N ratio was highly correlated with N, C and Organic Matter content (Pearson correlation, $r > 0.92$, $p < 0.001$). Soil pH was highly correlated to CEC, Ca^{2+} and base saturation (Pearson correlation, $r > 0.84$, $p < 0.001$; mean values of chemical variables are presented in Appendix B). We therefore only described results of C/N ratio and pH as they explained most of the variation observed.

The C/N ratio was significantly higher in the DF plot ($p < 0.01$), but not affected by the vegetation nor their interaction. Both, plot ($p < 0.001$) and vegetation ($p < 0.001$) significantly influenced the pH but also their interaction ($p < 0.05$). The mean pH was significantly

higher on *Dryas* and *Rhododendron* subplots of the OF plot. Plot, vegetation and their interaction were not significantly different for the $CaCO_3$, Mg^{2+}, K^+ and Na^+.

3.4. Community structure of soil fauna

Twenty soil faunal groups were identified from the 90 samples taken from pitfall traps and from the 18 soil cores. Plot location influenced the number of soil animals but not taxonomic richness. Significantly more (about 50%) individuals were captured by pitfall traps in the warmer DF plot ($p < 0.001$), and about 25% more individuals ($p = 0.403$) for soil cores. For both methods, Oribatid mites and Collembola dominated the soil fauna and represented about 60% and 25% respectively of the total diversity.

For pitfall traps, relative abundance of Oribatid mites (+17%), Diplopoda (+0.5%), Aranea (+0.5%) and Coleoptera (+0.5%) was significantly and of Diptera (+1%) marginally higher in the warmer DF plot (Table 2). Relative abundance of Coleoptea and Homoptera were significantly influenced by the vegetation while Oribatida were only marginally influenced. Soil fauna extracted from soil cores was not affected by vegetation type (Table 3). In soil core samples from the warmer DF plots, abundance of Collembola significantly decreased by about 5%, while Diptera increased about 10-fold. Relative Oribatida abundance was about 13% higher, but only marginally significant.

A total of 6 specimens representing 3 genera of earthworms in OF plot, and 21 specimens representing 4 genera and 6 species in DF plot were extracted from the 24 sampling points (Table 4). Diversity of earthworm was very low on OF plots (average 2 ind./m^2) and significantly higher on DF plots (7 ind./m^2; *U*-test, $p < 0.05$), which suggests that earthworms play a limited role in building up the humus structure.

3.5. Relationships between aggregation and biological activity

At a micromorphological scale, faunal droppings were observed in the F and H horizons. Microaggregates dominated the F horizon, in which the round excrements of oribatid mites were recognizable, especially those included in skeletons of needles or leaves, together with small irregular faecal pellets of Collembola (Appendix C). Mixtures of micro- and macro-aggregates belonging to several faunal groups such as Diplopoda or Isopoda were clearly observed in the H

Table 4
Relative abundance and relative biomass of earthworms in the plots studied

		Relative abundance		Relative biomasse	
	Functional group	Open Forest	Dense Forest	Open Forest	Dense Forest
Dendrobaena octaedra (Sevigny. 1826	epigeic	0.00	4.17	0.00	1.51
Dendrobaena sp.	epigeic	0.00	4.17	0.00	0.92
Dendrodrilus rubidus (Savigny, 1826)	epigeic	4.17	0.00	1.33	0.00
Lumbricus friendi Cognetti, 1904	epianecic	4.17	4.17	14.38	9.83
Lumbricus meliboeus Rosa, 1884	epianecic	0.00	4.17	0.00	11.90
Lumbricus sp.	epianecic	8.33	29.17	6.47	23.30
Nicodrilus caliqinosus caliqinosus (Savigny, 1826)	endogeic	0.00	8.33	0.00	7.52
Nicodrilus caliqinosus tuberculatus (Eisen, 1875)	endogeic	0.00	4.17	0.00	5.06
Nicodrilus sp.	endogeic	0.00	4.17	0.00	2.27
Octodrilus juvyi Zicsi, 2005	epigeic	0.00	16.67	0.00	14.84
Octodrilus sp.	epigeic	4.17	0.00	0.67	0.00
	Total	20.8	79.2	22.8	77.2

U-test ($n = 12$) shows significant difference between the two plot for abundance ($p = 0.022$) and for biomass ($p = 0.024$).
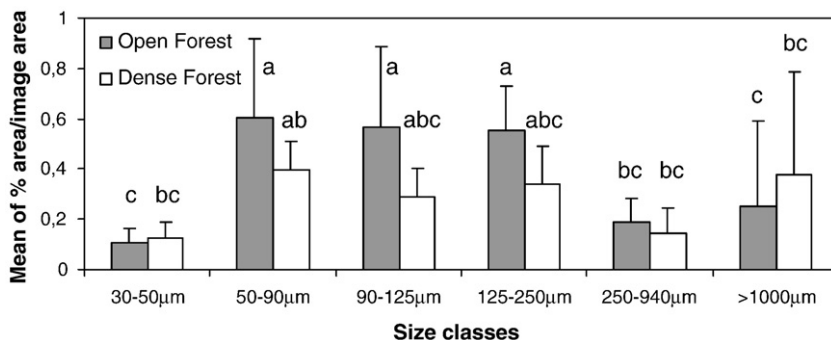
Fig. 3. Mean area and standard error ($n=6$) occupied by each size classes of biological aggregates from 10 thin section of La Plagne scree in the Open forest (OF plot) and the Dense forest (DF plot). Letters indicate significant differences between size classes after one-way ANOVA ($p<0.01$) with Fisher (LSD) test. Means with the same letters are not significantly different.

horizon. A part of the macroaggregates (>1 mm) could be assigned to earthworm activity whereas others, with a more angular shape, were assigned to physical processes.

Using round particle shape as an index of biological aggregation in the image analysis, we compared the evolution of soil fauna aggregates in the humus profile. Our results showed that neither plot nor Fm and Hh horizons had an effect on the distribution of biological aggregates in the site. Differences were observed when aggregates were classified into macroaggregates and microaggregates. The mean area occupied by microaggregates was significantly higher than the area occupied by macroaggregates with a proportion of 2/3 and 1/3 respectively (t-test, $p<0.01$). When separating the aggregates into size class, three classes (50–90μm, 90–125 μm and 125–250 μm) were significantly higher for the OF plot than the others (ANOVA; $p<0.001$; Fig. 3). These biological microaggregates are mostly related to faecal pellets of Collembola (cf. Table 1). Enchytraeids also contribute to these aggregations but it could not be confirmed in our study as no specimens were collected by the extraction method (O'Connor, 1955).

4. Discussions

The experiment at the La Plagne scree offers a unique opportunity to assess the long-term effect of a temperature rise similar to the predictions of the IPCC climate scenario A1F1 (IPCC, 2007) on the humus form and the soil fauna. In contrast to most other field studies where the effects of global warming are simulated over a limited number of years (Ineson et al., 1998; Sinclair, 2002; Lindberg and Persson, 2004; Sjursen et al., 2005b), climatic conditions have been similar at La Plagne scree for many centuries. A higher soil temperature (of about 3.8 °C) in the DF plots, led to a remarkable change in the soil faunal composition over time, favouring in particular Oribatid mites. However, this altered soil faunal community did not induce a change in the humus structure.

Soil temperature can affect humus form at various levels. The humus form is the result of functional relationships between primary producers and decomposers of the food web, which is affected by changes in environmental conditions. Given the sensitivity of humus forms to temperature, we hypothesize a hierarchical control as described by Aerts (2006) for litter decomposition, with both direct and indirect temperature effects on productivity and soil fauna.

Temperature, particularly in cold biomes, is a limiting factor for biological activities and organic matter decomposition (Berg, 2000; Prescott et al., 2000; Berg and Laskowski, 2005; Kirschbaum, 2006). Based on our observations, we suggest that persistence of temperatures (averaging 4 °C from June to October and presumably near the freezing point the rest of the year in the OF plot) is the major cause of incomplete decomposition thus limiting soil fauna activity, which leads to humimor formation.

Secondly, soil temperature indirectly affects plant growth which ceases below species specific thresholds. In the OF plot, low soil temperature may constraint the growth of Mountain pine by inhibiting root or shoot meristem activity as observed on dwarf red spruces in a similar ecosystem (Körner and Hoch, 2006). However, mean temperature above 7 °C (as in the DF plot) favours plant growth and may increase the input of recalcitrant leaf litter of acidophilic plants. This may explain the increase in soil acidity and the higher C/N ratio in the DF plot. Our results may be seen as the long-term response to soil warming on the boreo-alpine vegetation of the scree and confirms results of short-term experiments which showed shifts in plant growth with increasing soil temperature (Chapin et al., 1995; Jarvis and Linder, 2000; Brooker and Van Der Wal, 2003). We consider that the effect of temperature on humus form operates indirectly on the organic matter decomposition rates through the change in plant community structure.

Moreover, temperature may induce changes in the species composition and structure of decomposer and detritivore communities in the long-term. At our site, the soil faunal group (Oribatid mites and Collembola) that reacted to higher temperature is small in size and has low dispersal power. Nevertheless, changes in those two dominant communities have to date not induced a change in the humus structure. This may be explained by the extraordinary complexity of biotic interactions between components of soil food webs (Berg et al., 2001; Bardgett, 2002; Moore et al., 2004).

In the scarcity of earthworms, Collembola and Acari are significant contributors to decomposition processes, presumably in addition to Enchytraeids and Nematodes, as shown in arctic and alpine regions (Sjursen et al., 2005a). These decomposer organisms are commonly favoured in humus with important organic matter accumulation. However, no Enchytraeids have been found in our study. On the other hand, the humus thin sections which indicate a high Collembola and Enchytraeid activity, underline the importance of the micro- and meso-fauna. Moreover, results of the soil cores and pitfall traps indicate an important contribution by Acari which is not reflected by the analysis of the humus thin sections. The systematic analysis used to separate plant debris from biological aggregates on the basis of the shape index does not take into account faecal pellets of Acari produced in the skeleton of leaves (cf. App 3) because irregular and elongated shapes of plant debris are excluded. This creates a bias relating to Acari activity in the size class 30–50 μm, for which the mean area occupied may be underestimated. The Collembola abundance in the pitfalls was also similar for both plots whereas the number of Collembola specimens significantly decreased in the soil cores. This may be explained by the different information on invertebrate community given by these two methods. Pitfall traps tended to catch the large surface-active species while soil core samples give a quantitative estimate of soil dwelling species more susceptible to react to soil temperature variations which is strongly reflected by the Collembola (Dollery et al., 2006). Our results are therefore similar to those found

by several other authors in soil warming experiments of boreal and arctic ecosystems where warming led to decreases in Collembola and increases in Oribatida (Lindberg et al., 2002; Haimi et al., 2005; Sjursen et al., 2005b; Dollery et al., 2006; McGeoch et al., 2006).

5. Conclusion

Our work is among the first that details the ecological components of the alpine ecosystems developed on frozen screes and confirms the importance of spatial and temporal scales in measuring an ecosystem response to environmental change.

In our natural ecosystem, higher soil temperature led to a different soil faunal composition over time. Nevertheless, soil faunal variations do not affect the humus form which remains similar on the entire scree. This suggests the need of further investigations on soil species response to changing climate and the impact on soil nutrient dynamics. Several studies have been focused on polar or alpine ecosystems (Marion et al., 1997; Hodkinson and Wookey, 1999; Sjursen et al., 2005b), whereas fewer studies looked at the temperate fauna.
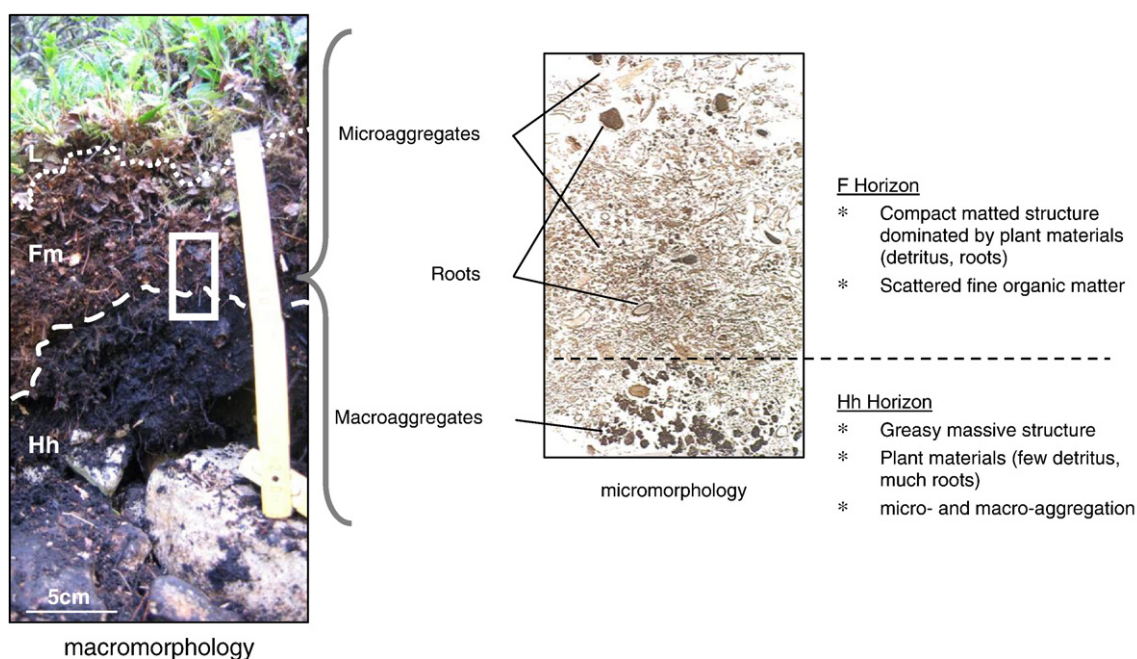
Alpine ecosystems of frozen screes appear to be well adapted for such investigations allowing comparisons to be made with previous works on similar communities in high latitudinal and altitudinal regions.

In conclusion, works on these alpine enclaves could help to predict the effects of changes in soil temperature on the alpine belt and to measure the magnitude of induced process shifts, such as faunal response.

Appendix A. Morphological features of humus forms developed on La Plagne's frozen scree.

F Horizon
* Compact matted structure dominated by plant materials (detritus, roots)
* Scattered fine organic matter

Hh Horizon
* Greasy massive structure
* Plant materials (few detritus, much roots)
* micro- and macro-aggregation

Appendix B.

Mean±standard error, minimum and maximum value for soil chemical parameters significantly different between the Open Forest (OF) plot and the Dense Forest (DF) plot

	OF (n=9)			DF (n=9)			Two-way ANOVA					
	Mean±SE	Min	Max	Mean±SE	Min	Max	Plot		Vegetation		P x V	
							F(1,12)	p	F(2,12)	p	F(2,12)	p
N (g/kg)	15.28±0.18	14.7	16.6	13.42±0.42	11.2	15.5	16.25	0.0016				
C/N	24.11±0.57	22.1	28.1	31.39±1.78	24.0	41.3	14.80	0.0023				
C (g/kg)	368.78±8.93	340.0	424.0	415.44±11.70	364.0	463,0	11.09	0.0059				
Organic matter (g/kg)	637.89±15.59	587.0	734.0	718.44±20.23	630.0	801,0	10.95	0.0062				
pH H2O	6.23±0.22	5.2	7.1	4.87±0.17	4.31	5.85	75.91	0.0000	15.03	0.0005	5.20	0.0236
CEC (cmol+/kg)	107.45±3.26	95.1	121.0	89.34±1.41	84.3	95.5	50.68	0.0000	4.42	0.0364	5.19	0.0237
Ca (cmol+/kg)	92.43±5.93	63.6	113.0	45.48±8.83	0.8	89.3	36.43	0.0000	7.40	0.0080		
Base saturation (%)	90.99±3.49	72.4	103.6	55.84±10.03	1.96	107.2	17.29	0.0013	5.53	0.0198		

Appendix C. Round faecal pellets of Oribatida (a) in a leaf of Dryas and irregular faecal pellets of Collembola (size < 90 µm) (b) observed in the Humimor from La Plagne's scree.
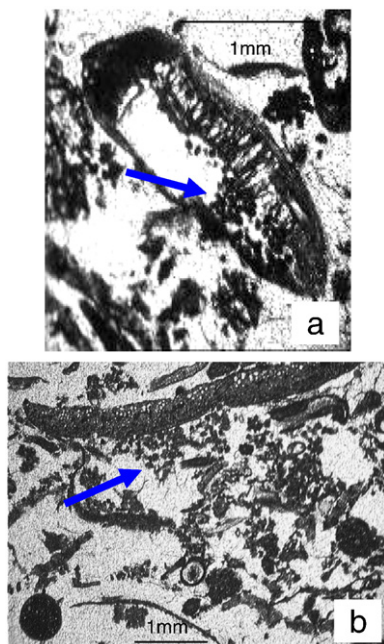
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