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Abstract

This study investigated the responses of soil animal communities, soil functioning and humus forms to forest dynamics and solar radiation. We examined changes in invertebrate communities and soil features in two subalpine spruce forests (Eastern Italian Alps, Trento) growing on a calcareous bedrock, with different sun exposures (north and south), each forming a chronosequence of three developmental phases: clearing, regeneration stand (25-year-old trees) and mature stand (170-year-old trees). Our results indicate that the two forest sites differed in solar energy input, soil chemical properties and the relationships between forest dynamics and animal communities. In the north-facing site, soil fauna communities were very similar in the three forest developmental phases. Conversely, in the south-facing site, the composition of invertebrate communities and the diversity of zoological groups varied greatly among developmental phases. The highest abundance of total invertebrates, and mites in particular, occurred in the south-facing mature stands while the south-facing regeneration stand was characterized by higher densities of Collembola, Chilopoda, Symphyla, Protura and Aranea. The structure of communities in clearings was the same as in regeneration stands but with lower invertebrate abundance. Humus forms and soil features changed with developmental phases in both the south- and north-facing sites, although variations were more pronounced in the southern exposure. Mature stands were characterized by high levels of soil organic carbon and nitrogen, C/N values and low pH, the clearings and regeneration stands being characterized by a greater release of mineral nitrogen. The diversity of zoological groups (Shannon-Wiener index) was linearly correlated to soil pH, Humus Index, the amount of organic carbon and the species richness of herbaceous plants. Our results about the composition and the diversity of invertebrate communities are consistent with the observations of other authors studying south-exposed forests growing on different bedrock

types, indicating that such relationships are widespread. The higher densities of invertebrates in the south-facing site may be attributed to higher solar radiation, and the positive correlation observed between total soil fauna abundance and solar energy supports the ‘more individuals’ hypothesis that assumes a positive relationship between the number of individuals and energy availability. Possible ways by which forest dynamics control soil invertebrate communities are discussed.

Key words

Invertebrate communities, Humus forms, Forest dynamics, Solar energy, Spruce cycle phase**.**

1. Introduction

The richness and abundance of soil fauna, as well as the composition of invertebrate communities, may be regulated by regional factors such as climatic conditions, bedrock, altitude, forest type and succession, (Toutain, 1987; Bernier, 1996; Grossi and Brun, 1997; Materna, 2004), and by local factors such as natural disturbance dynamics, predation, canopy cover, light exposure, humus form, nutrient availability, soil pH and water regime (Ponge, 1993; Paquin and Coderre, 1997; Feener and Schupp, 1998; Bird et al., 2000; Loranger et al., 2001; Kuznetsova, 2002; Magura et al., 2003; Scheu et al., 2003; Cassagne et al., 2003; Salmon et al., 2005).

Vegetational changes, especially those associated with forest dynamics are assumed to greatly affect the abundance and diversity of soil invertebrates since they are correlated to most environmental and soil parameters (Miller, 1981; Bernier and Ponge, 1994; Salmon et al., 2006). Humus forms, and the related soil features (soil pH, moisture and nutrient

77 availability) must particularly be taken into account to understand the relationships between
78 soil animal communities and plant succession, because it constitutes a living substrate for
79 both plants and soil invertebrates, (Peltier et al., 2001; Ponge, 2003). Mull and moder are two
80 out of the three main humus forms (in order of highest to lowest levels of biodiversity)
81 (Ponge, 2003). Mulls (comprising eumull, oligomull, amphimull and dysmull) are generally
82 associated with early developmental stages (regeneration) of forest stands, while moders
83 (eumoder and dysmoder) occur in phases of intense growth of trees up to maturity (Bernier
84 and Ponge, 1994; Salmon et al., 2006).

85 Several studies have investigated the changes in abundance and diversity of invertebrate
86 species, as well as changes in the species composition of communities with forest dynamics
87 (Hågvar, 1982; Baguette and Gérard, 1993; Bernier and Ponge, 1994; Migge et al., 1998;
88 Zaitsev et al., 2002; Chauvat et al., 2003; Grgič and Kos, 2005). However, each of these
89 studies focused only on one animal taxon, so that only Acari, Collembola, Carabid beetles,
90 Lumbricidae and Chilopoda were studied separately in tree stands of various ages, several
91 other soil-dwelling invertebrates including Aranea, Diptera larvae, Symphyla, Protura and
92 Enchytraeidae being excluded. However, different zoological taxa probably contribute
93 differently to soil functions (Verhoef and Brussaard, 1990; Setälä et al., 1991; Vedder et al.,
94 1996) and should be considered jointly. Moreover, investigating the diversity of a wide range
95 of zoological groups in each successional phase, would be a better approach than studying
96 species diversity of just one taxon, to estimate functional diversity, since some studies
97 suggested that ecosystem process rates are more closely correlated with functional
98 composition than with species richness (Vedder et al., 1996; Schwartz et al., 2000; Cortet et
99 al., 2003).

100 A study has already evidenced the changes in soil animal communities associated with
101 spruce (*Picea abies*) dynamics in a forest growing in a south-facing slope on acidic bedrock

(Salmon et al., 2006); however, it is not known whether the observed relationships can be generalised for different geological and climatic conditions.

On a regional scale, little is known about the response of soil animal communities to solar radiation, or to interactions between solar radiation and forest dynamics, although light is known to impact the behaviour and the local distribution of soil invertebrates (Ponge, 1993; Salmon and Ponge, 1998). The 'more individuals' hypothesis (Wright, 1983; Srivastava and Lawton, 1998; Gaston, 2000; Kaspari et al., 2003) assumes that there is a direct relationship between energy availability, the overall resource availability in a particular area and, consequently, the total number of individuals that can be maintained. A comparison of soil animal communities in forests with either a southern or northern exposure, combined with solar radiation measurements would allow this hypothesis to be tested in forest floor ecosystem. Exposure and solar radiation could also interact with forest dynamics to affect changes in soil animal communities. In fact, we may assume that changes in the composition of invertebrate communities may partly result from the decrease in solar radiation (and consequently temperature, Imbeck and Ott, 1987) through the canopy in mature stands.

We examined the changes in the composition of soil animal communities with sun exposure and forest dynamics, and corresponding changes in humus forms, soil nutrients, and soil functioning. The aims of this study were to (1) verify whether the relationships previously observed between animal community composition and abundance and forest dynamics may be extrapolated to other environmental (geologic and climatic) conditions and, (2) study the effect of solar radiation and its interaction with spruce dynamics on soil animal communities and soil functioning.

2. Materials and methods

127 *2.1. Study sites and sampling design*

128 Two natural spruce forests [Picea abies (L.) Karst.] were selected in the Eastern Italian Alps
129 (Province of Trento) at 1680 m above sea level, one on the south-facing slope of the Non
130 Valley and one on the north-facing slope of the Fassa Valley. The climate is continental with
131 a mean annual rainfall and temperature of 863 mm and 5.3 °C in the Non Valley and 1049
132 mm and 4.3° C in the Fassa Valley, respectively. At each site, we considered three
133 developmental phases of spruce: clearing, regeneration and mature trees.

134 The spruce stands were managed with soft silvicultural practices (selective cutting or
135 small clear-cut area) so as to further the forest's natural regeneration.

136 The mean age of spruce in regeneration stands was 27 years (max 41, min 11) and 23 years
137 (max 36, min 17) in the south and north-facing sites, respectively. In mature stands, spruce
138 were 165-year-old (max 221, min 100) and 180-year-old (max 204, min 144) in the south and
139 north-facing sites, respectively. Stands were situated on either Cambisol or Regosol (FAO,
140 1998) formed on sedimentary dolomitic rocks. The density of mature spruce was 600 and 500
141 trees/ha while regeneration density was 8000 and 15500 trees/ha, in the south- and north-
142 facing sites, respectively. The dominant plant species and the cover of the herbaceous layer
143 (cover greater than 35%) are given below.

144 <u>South-facing site (Non Valley):</u>

145 -clearing: cover greater than 90%; *Carex montana, Calamagrostis varia, Brachypodium pin.*
146 *rupestre and Melica nutans.*

147 - regeneration phase: two areas differing by the composition and cover of the herbaceous
148 layer, (1) cover greater than 90% (six samples); *Carex montana, Viola biflora and*
149 *Brachypodium pin. rupestre,* (2) mean cover of 35% (two samples); *Vaccinium vitis-idaea*
150 *and Vaccinium myrtillus.*

- mature phase: two areas, (1) cover varying from 0 to 35% (six samples); *Vaccinium vitis-idaea and Vaccinium myrtillus,* (2) cover greater than 90% (two samples); *Carex montana, Calamagrostis varia, Brachypodium pin. rupestre* and *Melica nutans.*

North-facing site (Fassa Valley):

- clearing: two areas, (1) cover of 75%; *Sesleria albicans, Deschampsia flexuosa, Carex alba, Melampyrum sylvaticum, Oxalis acetosella and Viola biflora,* (2) cover of 15% (for one sample); *Oxalis acetosella and Viola biflora.*

-regeneration phase: two areas, (1) cover of 15% (five samples); *Oxalis acetosella and Viola biflora,* (2). cover of 75% (three samples); *Adenostyles alpina, Carex montana, Viola biflora, Chaerophyllum hirsutum, Sesleria albicans and Deschampsia flexuosa.*

- mature phase: two areas, (1) cover of 20% (four samples); *Hieracium muroru, Clematis alpina,Luzula nivea* and *Rubus saxatilis,* (2) cover of 75% (four samples); *Melampyrum sylvaticum, Sesleria albicans* and *Carex alba.*

Eight sampling points, distant from three to nine meters from each other, were randomly selected in each developmental phase for each exposure. The main south-facing sampling plot covers an area of 1800 m^2 with a mean slope of 15%. As we could collect only four samples in the mature stand, we chose four sampling points of 'mature trees' in a small area (200 m^2) situated 50 m from the main plot to complete the sampling regime. The north-facing sampling plot covers a surface of 1000 m^2 with a mean slope of 16%.

Two soil cores were taken at each sampling point. A total of 48 soil cores were sampled using polystyrene boxes (4.2 l x 8.4 L x 11.3 cm depth) and used for soil analysis and arthropod extraction; forty-eight other soil cores with the same dimensions were collected in plastic bags and used to extract enchytraeids (see below).

2.2. Collection and identification of soil invertebrates

Enchytraeids were extracted two days after soil sampling by the modified wet-funnel method of O'Connor (1957). After 6, 12 and 24 hours, enchytraeids were collected in Petri dishes and immediately counted under a magnifying glass. Arthropods were extracted from the soil cores stored in plastic boxes after a set of respiration measurements and leachate analysis was completed (see below), i.e. 25 days after sampling. During this period soil cores were rehydrated by the addition of 40 ml of deionised water once a week. Animals were extracted by the dry funnel method (Edwards and Fletcher, 1971) and fixed in 90% ethyl alcohol. Each sample was placed in a flat glass cup, the bottom of which was divided into 200 compartments, and observed under a binocular magnifying glass (40X). Whole macrofauna was counted and identified while microarthropods were counted in 50 randomly-selected compartments out of 200 (Salmon et al, 2006). Animals were identified at the level of group, order, super-family or family (Dindal, 1990; Dunger and Fiedler, 1997).

2.3. Environmental factors

We measured ten environmental factors believed to be relevant in controlling the distribution of soil fauna. Total annual solar radiation received at the soil surface was indirectly measured with the hemispherical canopy photography technique (Neumann et al., 1989): an image is captured at an angle of 180° on the perpendicular plane and 360° on the parallel plane to a fisheye lens mounted on a digital camera. A 10x10m grid was placed in each sampling plot and a hemispherical canopy photograph was taken at each grid intersection. Direct radiation ($MJ.m^{-2}.d^{-1}$) was calculated using the software Gap Light Analyzer version 2.0 (Frazer et al., 1999). This software also estimates canopy structural parameters using site characteristics such as latitude, slope, sun exposure and altitude. Results were interpolated with ordinary kriging, generating a radiation map of each entire plot, including the sampling points of the soil fauna.

201 At each sampling point, humus forms (Table 1) were identified using the morphological
202 criteria defined by Brêthes et al. (1995) and Baize et al. (1995), and a Humus Index was
203 attributed to each form (Ponge et al., 2002). Soil nutrients were analysed in leachates released
204 from soil cores contained in the plastic boxes, after adding deionized water to collect 40ml
205 leachates. Percolating water was collected for 12 hours after the irrigation through a tube
206 attached to the underside of the box. Ammonium-N and nitrate-N contents in leachates were
207 measured colorimetrically by continuous flow analysis (Krom, 1980). The concentration of
208 soluble organic carbon in leachates was calculated with an infrared C analyzer after burning
209 40 µl subsamples at + 950 ºC (INRA Laboratory of Soil Analysis, Arras, France). To assess
210 soil functioning at each sampling point, carbon mineralised as CO_2 (CO_2-C) released by soil
211 cores was measured. CO_2 release was determined with an infra-red gas analyser (Polytron IR
212 CO_2 DIMARSOL, Dräger®) after incubation of soil cores in air-tight containers for 4h at
213 15ºC.

214 Organic carbon and total nitrogen contents in soil were estimated from 50 mg of dried
215 soil from each soil core after arthropod extraction. The soil samples were grounded to 100 µm
216 and homogenised before measurements with a CHN atomic analyser (Perkin Elmer CHNS/O
217 Analyzer 2400 Series II.). Soil pH-H_2O was determined using soil mixed with deionised
218 water (soil:water 1:5 v/v) for 5 min; pH was measured 4 h after mixing (Anonymous, 1999).

219

220 *2.4. Statistical analyses*

221 Data were first analyzed by Correspondence Analysis (CA) using StaboxPro 5 software
222 (Grimmersoft®) in order to compare invertebrate communities in the different stands and
223 exposures. CA allows representing active variables, namely abundance of taxa, and samples
224 simultaneously by projecting points on a plane formed by the two first factorial axes. Physical
225 and chemical soil parameters (pH, soil organic carbon, soil nitrogen, C/N ratio, humus index),

226 leachate nutrients (mineral nitrogen, nitrates, ammonium, soluble organic carbon), direct solar
227 radiation, animal community characteristics (predator abundance, total abundance, taxonomic
228 richness), sun exposure (north or south) and the developmental phase of trees (clearing,
229 regeneration or mature trees) acted as passive variables to explain the distribution of active
230 variables, without affecting and constraining their ordination. Predator taxa include
231 centipedes, cantharids, staphylinids, gamasid mites and spiders (Scheu and Falca, 2000). All
232 variables were standardized prior to analysis, and each variable was associated with a
233 conjugate, varying in an opposite sense in such a way that each animal group is represented
234 by two points, one indicating higher densities for this group, the other lower densities (see
235 Salmon et al., 2006 for data transformations). Rank correlations between variables and
236 factorial axes were calculated using Spearman's method.

237 Correlations between total animal abundance and direct solar radiation, and between the
238 diversity of zoological groups (Shannon-Wiener index) and the cover and species richness of
239 herbaceous plants, were calculated for both north- and south-facing sites pooled together,
240 using simple linear regressions (Sokal and Rohlf, 1995; XLSTAT 2006.5® software). A
241 multiple linear regression was performed between Shannon-Wiener index and soil pH,
242 Humus Index, and soil carbon and nitrogen content (relationships revealed by CA).

243 As data set and transformed data set did not meet homosedasticity requirements, we
244 could not perform two-way ANOVA to test differences in the total abundance, zoological
245 richness (number of zoological groups, i.e. names in bold type in Table 1), zoological
246 diversity (Shannon-Wiener index based on zoological groups), solar radiation and soil
247 characteristics in each growth phase of trees. Differences were thus tested by the Kruskal-
248 Wallis test, together in north-facing and south-facing sites. When the difference was
249 significant, the six means were compared two by two and the significance level of this
250 multiple comparison was corrected according to Bonferoni (Dunn, 1964; XLSTAT 2006.5®

software). Coordinates of axis 1 and 2, (that express the community composition) in each developmental phase and each exposure were compared by a Kruskal-Wallis test and a Mann-Whitney test respectively. At last, a one-way ANOVA with two replicates, (the south and north-facing sites being considered as two replicates) was performed in order to assess whether the variations in total abundance, zoological richness and diversity, respectively, between the developmental phases of spruce occur in the same way in different sites.

3. Results

The results of the first CA showed that one sampling point in the mature stand of the south-facing site (MS7) was an outlier; therefore, we performed CA without MS7 (Figs. 1 and 2). Axis 1 of the CA (representing 20% of the total variance in zoological taxa) depicts a gradient of increasing abundance of most zoological taxa (Fig. 1). The projection of developmental phase, exposure, and zoological variables on this axis indicates that the abundance of most taxa and total fauna, as well as zoological richness increased from the north- to the south-facing site and from clearings and mature stands to the south-facing regeneration stand (Fig. 1). Increased animal abundance in the south-facing site was mainly due to the high numbers of mites (especially Oribatida, 56% of total abundance) in mature and regeneration stands, and Collembola (especially Entomobryomorpha and Poduromorpha; 23% of total abundance) in the clearing and regeneration stand (Table 1). A similar pattern was observed for other groups such as Coleoptera and mite larvae, uropods, gamasids, and predators, which were more abundant in the south- than in the north-facing site, whereas the number of Symphyla, Chilopoda, Coleoptera (including Staphylinidae), Protura, Aranea and Actinedida was more increased in the south-facing regeneration than in the south-facing clearing and the three north-facing developmental phases of spruce (Fig. 1, Table 1).

Axis 2 of CA displays a clear separation between the structure of invertebrate communities in clearing and regeneration stands and that in mature stands (Fig. 1). The abundance and occurrence of several taxa (Chilopoda, Symphyla, Aranea, Protura, Coleoptera, and to a lesser extent, Collembola,) was higher in clearing and regeneration phases than in the mature phase (Fig. 1). In fact, for both the north- and south-facing sites, these open forest phases do not display profound differences in animal communities, and form a homogeneous group, characterized by the highest fauna diversity (Shannon -Weaver index) on the negative side of axis 2. Axis 2 also shows a gradient of fauna abundance with higher total animal density in mature stands due to the high density of Acari (especially Oribatida, Gamasida and mite larvae).

Both, axis 1 and 2 of CA show that the composition of communities was more similar to each other in the three north-facing stands than in different stands in the south-facing site (Fig. 1). The pattern of Shannon-Wiener index in the north-facing site paralleled nevertheless that in the south-facing site, with a lower zoological diversity in mature stands (Fig. 1, Table 2). Considering the two sites as replicates, ANOVA indicated that Shannon index was as high in regeneration stands as in clearings, and the lowest in the mature stands ($p= 0.016$); the variations of zoological richness between developmental phases were not significant ($p>0.05$), and total abundance was higher in mature stands than in the two other stands, which did not differ significantly from each other.

The significant difference of the axis 2 coordinates among the three developmental phases in each exposure (Table 2) confirms that taxa assemblages in mature stands differed from those in clearings and regeneration stands. Coordinates of axis 1 were marginally significant ($p = 0.08$) although the a posteriori Bonferroni test (significant at $p = 0.003$) indicated that the structure of communities in the south-facing regeneration differed at least

300 partly from that of the south-facing clearing and the three north-facing developmental phases
301 of spruce (Table 2).
302 Direct solar radiation was positively correlated to axis 1, and as expected, was the
303 highest in the southern exposure (Figs. 1 and 2, Table 1), but no difference was observed
304 among developmental phases of spruce. The linear regression between direct radiation and
305 total animal abundance was marginally significant ($p = 0.059$, $R^2 = 0.077$), and animal
306 abundances were distributed into two clusters according to exposure. Two linear regressions
307 were thus performed separately in each exposure. In the north-facing site, no correlation was
308 observed between solar radiation and the abundance of invertebrates ($R^2 = 0.000$, $p = 0.963$),
309 whereas both variables were significantly correlated in the southern exposure ($R^2 = 0.259$, $p =$
310 0.013).
311 Humus forms in the both north- and south-facing clearings consisted in Eumull and
312 Amphimull. In regeneration stands humus forms were more heterogeneous, varying from
313 Eumull to Dysmull, including Oligomull, in the south-facing site, and from Eumull to
314 Amphimull in the north-facing site. At last, in mature stands Dysmoder and Amphimull were
315 observed in the south-facing stand, while only Amphimull occurred in the north-facing stand.
316 The soil of mature stands were characterized by high Humus Indices and low pH values, high
317 soluble and soil organic carbon and increased C/N ratio, as indicated by the axis 2 of CA (Fig.
318 3, Table 1). These physical and chemical properties reflect the presence of a thick litter layer
319 accompanied by a slow decomposition of organic matter. In contrast, the soil in clearings and
320 regeneration stands was characterized by a low Humus Index, and high pH level. High
321 mineral nitrogen content, especially nitrates, in leachates, was particularly observed in the
322 south-facing regeneration stand (Fig. 2, Table 1). These parameters indicate an increased
323 decomposition in the clearing and regeneration stands, especially in the south-facing site.
324 However, although the higher rate of soil organic matter decomposition was associated to

clearings and regeneration stands (Fig. 2), it was not correlated to axis 2 because its pattern varied among the south- and north- facing sites (Table 2), soil respiration being unexpectedly low in the north-facing regeneration stand.

Most mineral nitrogen in leachates was in the form of nitrates (Table 1). Nitrates and consequently total mineral nitrogen in the south-facing site exceeded those in the north-facing site (Table 1). This was also true for soil organic carbon and nitrogen contents (Table 1) although it is not depicted by CA because these variations does not concern regeneration stands (Fig. 2). Seven soil parameters out of ten varied among the developmental phases in the north-facing (soluble organic carbon, mineral nitrogen and nitrates in leachates, soil organic carbon, C/N ratio, Humus index, CO_2-C/soil organic carbon) (Table 1). These variations paralleled those in the south-facing site except for CO_2-C/soil organic carbon (see above). The relationship between soil pH, soil carbon and nitrogen content, Humus Index and Shannon-Wiener index revealed by CA (Figs. 1 and 2), was confirmed by the multiple linear regression (adjusted $R^2 = 0.372$, $p < 0.0001$), but the best model that explains the values of Shannon-Wiener index was obtained using pH, carbon and Humus Index without nitrogen as explicative variables (adjusted $R^2 = 0.383$, $p < 0.0001$) in both south and north-facing sites. A significant linear regression was observed between Shannon-Wiener index and the species richness of herbaceous plants ($p = 0.038$, $R^2 = 0.072$), but the relationship with herbaceous cover was not significant.

4. Discussion

4.1 Forest dynamics and soil characteristics

In the south-facing site, humus form, physical and chemical parameters and composition of invertebrate communities were correlated with the developmental phase of spruce, confirming

350 the pattern observed in three previous studies that were conducted in spruce stands growing
351 on different types of bedrock (Bernier and Ponge, 1994; Salmon et al., 2006 submitted).
352 Indeed, these studies showed that mull is associated with early developmental stages
353 (regeneration) of forest stands, while moder is more common for phases of intense growth up
354 to maturity. In our study, the increase of Humus Index from clearing to mature stands support
355 this pattern, but the presence of amphimull, an intermediate form between moder and mull,
356 characterized by an accumulation layer of small fecal pellets (OH horizon), in the clearings
357 and mature stands of both the south- and north-facing sites, indicates that these forest stands
358 are still in evolution. The unexpected and exclusive presence of amphimull in the north-facing
359 mature stand instead of moder (dysmoder) was probably also due to the relatively low density
360 of mature trees in this stand.
361 Dysmoder and amphimull found in mature stands at both the north- and south-facing sites
362 were characterized by a lower decomposition rate, indicated by (1) higher organic carbon and
363 total nitrogen content; (2) greater quantities of soluble organic carbon; (3) lower levels of
364 mineral nitrogen, especially nitrates; and (4) lower pH (pH 4.4) than clearing and regeneration
365 stands. The mineralizing activity (respiration) was also the lowest in the south-facing mature
366 stand. These results confirm previous reports in the literature (Berg et al., 1982; Ponge, 2000)
367 indicating a lower biological transformation efficiency of organic matter under mature trees.
368 The decrease in mineralization and decomposition rate with stand age is in line with the
369 decrease in metabolic activity, microbial activity and bacteria number observed by Chauvat et
370 al. (2003) from 5-25 to 45-95 year-old spruce stands, while the fungal biomass increased.
371 Several studies suggest that the accumulation of polyphenols (in spruce needles) and
372 antibiotic organic matter (in fungal hyphae) slow down microbial mineralization in mature
373 stands (Gallet, 1992; Bending, 2003). In this context, the low mineralization activity (ratio
374 CO2-C/soil organic carbon) in the north-facing regeneration is unexpected, even though

values of Humus Index indicate that humus form in the north-facing regeneration is more similar to that in mature stand than that in clearing (as it is the case in the southern exposure).

The hypothesis that spruce dynamics interacts with exposure and more precisely with solar energy through temperature (Imbeck and Ott, 1987) to impact microbial activity (Parmelee, 1995), and consequently regulate decomposition rate according to the area of canopy, was not supported by our results since solar radiation levels were similar in the three developmental phases.

4.2. Forest dynamics and animal communities

The thick holorganic layers of moder soil are a good habitat for some soil invertebrates, especially mites (Ponge, 1985; Hågvar and Kjøndal, 1981; Hasegawa and Takeda, 1996). This is supported by the high number of mites observed in mature stands. In our study, the distribution of mites, particularly oribatids is in contrast with that recorded in a spruce plantation by Zaitsev et al. (2002), who observed the highest oribatid density in the 25 (compared to 5, 45 and 95) year-old tree stand while Migge et al. (1998) found no differences in oribatids between developmental phases. The discrepancies in mites density between the different studies probably result from variations in the evolution of soil characteristics associated with spruce dynamics, depending on altitude (Bernier, 1996) and forest management, since the thickness of organic layers and soil pH shown here do not parallel those in spruce plantations in Germany (Zaitsev et al., 2002).

The abundance of Collembola was higher in the clearings and regeneration stands (mean pH 6.5) than in the mature stands (pH 4.4), especially in the south-facing site. Many studies have demonstrated that contrary to our observations, Collembola populations do not change with the age of spruce (Chauvat et al., 2003; Scheu et al., 2003), or increase with the age of trees and level of soil acidity (Hågvar, 1982; Loranger et al., 2001). This suggests that

400 the influence of spruce dynamics on the variation of Collembola density probably varies with
401 forest management, and may depend on factors other than soil pH such as tree physiology.
402 The dense root system of spruce, which may induce a decrease in water and nutrient
403 availability (Babel, 1977; Miller, 1981), and the lower species richness and cover of herb
404 layer (especially in the south-facing site), more palatable than the recalcitrant spruce litter
405 (Edwards, 1974; Ponge, 1991; Gallet, 1992), may be responsible for the lower abundance of
406 Collembola (Christiansen, 1964) in mature stands. Variation in the densities of Collembola
407 among developmental phases of spruce depended on their superfamily, which confirms the
408 relationship between the spatial distribution of collembolan species (particularly
409 entomobryids) and tree stand type reported by Huhta and Mikkonen (1982), and the influence
410 of soil pH on the species composition of collembolan communities (Chagnon et al., 2000).
411 Chilopoda and Aranea were more numerous in regeneration stands than under clearing
412 and mature trees, which corroborates previous observations in beech and spruce forests (Grgič
413 and Kos, 2005; Salmon et al., 2006, submitted) and mull versus moder humus forms
414 associated to developmental phases of trees (Athias-Binche, 1982; David et al., 1993). Their
415 distribution may be explained by the presence of litter (habitat) and the greater number of
416 potential prey, especially Collembola, in the regeneration stand (Lawrence and Wise, 2000).
417 The distribution of Symphyla, which occurred at higher density in the clearings and
418 regeneration stands, probably depends on higher pH values (Edwards, 1958).
419 The composition of invertebrate communities in clearings was similar to that of
420 regeneration stands, but both stands differed by the abundance of most taxa, particularly in the
421 south-facing site, which confirms results of other studies (Addison et al., 2003; Grgič and
422 Kos, 2005). The absence of spruce litter and holorganic layers, that are the habitat of a
423 number of arthropods, probably results in such a variation of abundance.

Zoological diversity (Shannon-Wiener index based on taxonomic groups) was higher in regeneration stands and clearings (mull and amphimull) than in mature stands (dysmoder and amphimull) in both the north- and south-facing sites. This pattern results from the increased abundance of Collembola, Protura, Symphyla and Aranea in open habitats (including regeneration) and reflects a higher functional diversity, compared to closed habitats. This result corroborates the observation of Salmon et al. (2006, submitted) and the assumption of Schaefer and Schauermann (1990) that higher zoological diversities are related to mull humus forms in forests. Paquin and Codere (1997) also observed a decline in macroarthorpod diversity with forest succession but the three studied successional phases were composed of varied tree species. This relationship between invertebrate diversity and developmental phases of trees is partly explained by the decrease in the diversity (perhaps through the quality) of herbaceous plant and soil pH, and the increase in soil organic carbon and Humus Index, induced by actively growing and mature tree, as indicated by the correlations between Shannon-Wiener index and the four variables. The accumulation of litter, resulting from the increase of spruce needle input beneath mature stands, is accompanied by a decrease of soil pH that affects the distribution of soil animals (Salmon and Ponge, 1999; Schaeffer and Schauerman, 1990).

The composition of soil fauna communities and their abundance were relatively homogeneous among the three developmental phases of spruce in the north-facing compared to the south-facing site; the pattern of humus forms and chemical parameters in the north-facing site does not parallel that of invertebrate communities since seven parameters indicated higher decomposition rate in the regeneration and clearing than in mature stands. The greater homogeneity among soil animal communities of different developmental phases in the north-facing site confirms that observed on a slightly more acidic bedrock (Salmon et al., submitted). In the same way, changes in animal diversity and composition of communities

with the developmental stage of spruce that we observed here, in a forest growing on a calcareous substrate, paralleled those previously observed in a south-facing slope on acidic and sub-acidic parent-rocks (Salmon et al., 2006, submitted), particularly those results for regeneration stand, which had the highest soil animal diversity and the highest abundance of Collembola and Chilopoda. This variation between southern and northern exposures can't be explained by a higher decrease of solar radiation through the canopy of mature trees (affecting microclimatic conditions; Imbeck and Ott, 1987) in the south-facing site, since solar radiations were not significantly different in the three stands, in the both southern and northern exposures.

4.3. Influence of exposure and solar radiation

Total animal abundance was higher in the south- compared to the north-facing site, especially in regeneration stands. The two sites received different quantities of solar energy, with low inputs at the north-facing site and higher inputs at the south-facing site. The positive correlation between the total abundance of soil fauna and solar energy support the "more individuals" hypothesis (Wright, 1983; Srivastava and Lawton, 1998; Gaston, 2000; Kaspari et al., 2003) which predicts a relationship between energy availability and the total number of live individuals. We may assume that the higher energy input in the south-facing site results in an increase in soil temperature (Imbeck and Ott, 1987), which creates better conditions for the survival and development of microbial communities, and therefore, of soil arthropods (Parmelee, 1995). Squartini (unpublished observations, 2006), carried out a similar study on the same sites, and found a higher bacteria biomass in the south-facing site, which corroborates our assumption.

4.4. Conclusions

Our results show that changes in soil animal diversity and community composition, as well as physical and chemical soil characteristics, and humus forms with the developmental phase of trees may be generalised to all south-facing alpine spruce forests, growing on diverse geological substrates. The common pattern consists of the increase of invertebrate abundance, and a decrease in the zoological diversity and decomposition rate with the age of trees.

Although our study failed to demonstrate the impact of the interaction between forest dynamics and exposure in the assemblage and diversity of soil invertebrates, (especially in the southern exposure where solar radiation was similar in the three growth phases), it contributed to show the considerable impact of exposure on below-ground systems, affecting both the abundance of soil fauna and the relationships between the composition of communities and forest dynamics. Conversely, the pattern of zoological diversity did not vary with exposure. This means that in both southern and northern exposures, the structure of communities changes with spruce dynamics, with a decrease in the number of dominant zoological groups in mature stands (Shannon-Wiener index), but the taxa that compose invertebrate communities varied only between the growth phases of spruce in the southern exposure, particularly between mature and regeneration stands.

Our results are consistent with the hypothesis that forest dynamics, through tree physiology, drive the soil functioning (including the composition and biodiversity of soil invertebrate communities) during the build-up phase of succession (between regeneration and mature trees) and is ultimately determined by the functional traits of the dominant species present (Wardle, 2002), namely spruce. In fact, changes in invertebrate communities and humus forms with successional stage may be explained by (1) a decrease in the quality of food resource for most invertebrates except Acari, with the decrease of the diversity and abundance of herbaceous plants and their replacement by spruce needles in mature stands, especially in the southern exposure where changes in the composition of invertebrate

communities between the developmental phases were the most pronounced, (2) the increasing input of spruce needles (habitat) expressed by higher Humus Index, C/N ratio, and the greater amount of organic carbon, accompanied by an increase of soil acidity, and (3) an impoverishment of soil nutrients expressed by the decrease in mineral nitrogen.

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691 **Legends**

692

693 Fig. 1. Correspondence analysis. Projection along Axes 1 and 2 of zoological taxa (active
694 variables), and the following passive variables: exposure (EXPS, EXPN), tree stands (mature,
695 regeneration, clearing), sampling areas (CN, RN, MN: clearing, regeneration and mature in
696 the north-facing site, and CS, RS, MS: clearing, regeneration and mature in the south-facing
697 site) and descriptors of soil fauna communities (H', predators, zoological richness,
698 abundance). See codes of zoological taxa in Table 1. Bordered and underlined names are
699 significantly correlated to Axis 1 and 2, respectively.

700

701 Fig. 2. Correspondence analysis. Projection along Axes 1 and 2 of environmental
702 characteristics (passive variables), exposure (south-facing: EXPS, north-facing: EXPN), tree
703 developmental phase (clearing, regeneration, mature), and sampling areas (CN, RN, MN:
704 clearing, regeneration and mature in the north-facing site, and CS, RS, MS: clearing,
705 regeneration and mature in the south-facing site). See codes used for environmental variables
706 in Table 1. Bordered and underlined names are significantly correlated to Axis 1 and 2,
707 respectively.

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710

711 Table 1. Density of zoological groups, predators, and total fauna (mean per m^2), in three
712 developmental phases of spruce: regeneration (R), mature (M) and clearing (C), in north-
713 facing and south-facing sites. Different letters inside the lines “predators” and “total
714 abundance” indicate a significant difference ($p < 0.05$) between the six stands. Codes
715 correspond with those used in the correspondence analysis graphs (Figs. 1 and 2).
716 Entomobryom.= Entomobryomorpha.

		North			South		
Zoological taxa	**Code**	**C**	**R**	**M**	**C**	**R**	**M**
Acari	MITES	66645.4	61047.3	131873.6	81207.5	155612.2	261576.9
Oribatida	ORIBT	43154.8	49036.3	83120.7	56831.1	112705.5	176338.0
Actinedida	ACT	283.4	283.4	0.0	0.0	141.7	0.0
Acaridida	ACAR	141.7	106.3	2019.6	389.7	141.7	491.8
Gamasina	GAM	4464.3	1984.1	3011.6	3365.9	6519.3	7007.6
Uropodina	URO	3862.0	5350.1	2948.8	5527.2	5846.1	5163.5
Acari larvae	L.ACA	14739.2	4074.5	40320.3	14455.8	30257.9	72676.0
Collembola	COLL	33340.4	37131.5	22959.2	42594.2	63740.1	13236.6
Entomobryom.	C.ENT	18388.6	20797.9	15058.1	19061.8	44997.2	5327.4
Poduromorpha	C.POD	7405.0	15270.7	7865.6	24270.1	21293.9	7868.2
Symphypleona	C.SYMP	425.2	921.2	0.0	177.2	0.0	40.9
Neelipleona	C.NEEL	7121.6	566.9	35.4	318.9	992.1	0.0
Aranea	ARAI	70.9	177.2	70.9	70.9	212.6	41.0
Protura	PROT	1665.2	992.1	1098.4	3047.1	5456.3	1147.4
Thysanoptera	THYS	0.0	0.0	0.0	35.9	0.0	204.9
Coleoptera adult	COL	70.9	318.9	106.3	141.7	425.2	122.9
Coleoptera larvae	L.COL	318.9	70.9	354.3	118.9	425.2	1147.4
Homoptera	HOM	248.0	212.6	177.2	354.3	141.7	204.9
Diptera larvae	L.DIP	0.0	850.3	354.3	177.2	389.7	573.7
Chilopoda	CHIL	106.3	0.0	35.4	0.0	318.9	0.0
Diplopoda	DIP	0.0	35.4	0.0	35.4	35.4	0.0
Symphyla	SYMPH	283.4	35.4	70.9	35.4	283.4	0.0
Enchytraeidae	ENC	5881.5	7901.1	3259.6	5172.9	3862.0	5491.3
Predators		5031.2	2586.5	3224.2	3507.7	7263.3	7130.6
Total abundance		109835.6^{c}	108737.2^{c}	160360.0^{abc}	133290.8^{bc}	230902^{a}	283747.2^{ab}

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Table 2. Zoological richness, Shannon-Wiener index and the composition of invertebrate communities expressed as coordinates of axes 1 and 2 of CA, in three developmental phases of spruce: regeneration (R), mature (M) and clearing (C), in north-facing and south-facing sites. Different letters inside a line indicate a significant difference ($p < 0.05$) between the six stands or the two exposures.

	North			**South**		
	C	**R**	**M**	**C**	**R**	**M**
Shannon index	0.39^{a} (0.06)	0.40^{a} (0.06)	0.22^{b} (0.04)	0.37^{a} (0.04)	0.35^{a} (0.03)	0.16^{b} (0.03)
Zoological richness	5.8 (0.7)	5.4 (0.8)	5.1 (0.9)	5.9 (0.5)	6.9 (0.6)	5.3 (0.8)
Coordinates of axis 1 of CA (p=0.08)	-0.002^{a} (0.011)	-0.005^{a} (0.009)	-0.010^{a} (0.006)	-0.004^{a} (0.005)	0.02^{b} (0.006)	-0.001^{ab} (0.007)
Coordinates of axis 2 of CA	-0.008^{a} (0.003)	-0.009^{a} (0.003)	0.005^{bc} (0.007)	-0.005^{ab} (0.002)	-0.007^{ab} (0.002)	0.028^{c} (0.004)
Coordinates of axis 1 of CA		-0.006 (0.004)^{a}			0.006 (0.005)^{b}	

Table 3. Mean density and standard error of the physical-chemical soil and leachate parameters in stands of three developmental phases of spruce: regeneration (R), mature (M) and clearing (C), in north-facing and south-facing sites. Different letters inside a line indicate a significant difference ($p < 0.05$) between the six stands. Codes correspond with those used in the correspondence analysis graphs (Figs. 1 and 2).

		North			South		
	Code	**C**	**R**	**M**	**C**	**R**	**M**
Soil parameters							
Direct solar radiation (MJ.m-2.d-1)		0.083 ^{b} (0.005)	0.061 ^{b} (0.005)	0.073 ^{b} (0.003)	0.501 ^{a} (0.008)	0.493 ^{a} (0.004)	0.435 ^{a} (0.036)
Organic carbon (g.kg^{-1})	C	100.3 ^{c} (12.7)	146.7 ^{bc} (24.0)	240.0 ^{b} (40.2)	184.8 ^{b} (27.4)	147.0 ^{bc} (15.1)	412.0 ^{a} (20.6)
Total nitrogen (g.kg^{-1})	N	5.8 ^{c} (0.5)	8.4 ^{bc} (1.0)	8.9 ^{bc} (1.4)	10.5 ^{b} (1.7)	8.4 ^{bc} (0.9)	18.6 ^{a} (0.8)
C/N	C/N	16.7 ^{b} (0.5)	17.0 ^{b} (0.7)	21.8 ^{a} (1.0)	17.8 ^{b} (0.9)	17.6 ^{b} (1.3)	22.1 ^{a} (1.1)
pH-H_2O	pH	5.7 ^{c} (0.1)	5.6 ^{bc} (0.3)	5.7 ^{bc} (0.2)	6.4 ^{ab} (0.1)	6.6 ^{a} (0.1)	4.5 ^{d} (0.2)
Humus index		1.8 ^{c} (0.5)	3.8 ^{ab} (0.6)	5.0 ^{a} (0.0)	2.7 ^{bc} (0.6)	2.2 ^{bc} (0.4)	5.8 ^{a} (0.4)
CO_2-C(mg soil core^{-1}. day^{-1})	CO_2-C	49.4 (32.4)	30.8 (15.53)	51.3 (10.7)	54.7 (28.93)	43.5 (29.5)	41.7 (19.2)
CO_2-C/soil organic carbon	CO_2-C/C	0.58 ^{a} (0.54)	0.22 ^{bc} (0.10)	0.34 ^{ab} (0.22)	0.30 ^{ab} (0.13)	0.29 ^{ab} (0.14)	0.11 ^{c} (0.02)
Soil leachates parameters							
Mineral nitrogen (µg. soil core^{-1})	N_{min}	95.69 ^{bc} (27.35)	251.94 ^{ab} (78.35)	63.98 ^{c} (37.60)	816.41 ^{a} (221.25)	820.76 ^{ab} (225.17)	170.90 ^{bc} (91.08)
Nitrate (µg. soil core^{-1})	NO_3^-	92.66 ^{bcd} (28.36)	232.25 ^{abc} (84.80)	52.04 ^{d} (36.10)	800.24 ^{a} (204.72)	820.76 ^{ab} (225.17)	107.48 ^{cd} (74.96)
Ammonium (µg. soil core^{-1})	NH_4^+	3.02 ^{bc} (2.19)	19.70 ^{ab} (13.32)	11.94 ^{ab} (5.86)	16.17 ^{ab} (12.39)	0.00 ^{c}	63.43 ^{a} (47.93)
Soluble organic carbon (mg. soil core^{-1})	C_{sol}	0.84 ^{c} (0.23)	1.39 ^{bc} (0.44)	3.64 ^{a} (0.90)	0.73 ^{c} (0.31)	2.35 ^{ab} (0.21)	4.67 ^{a} (1.31)

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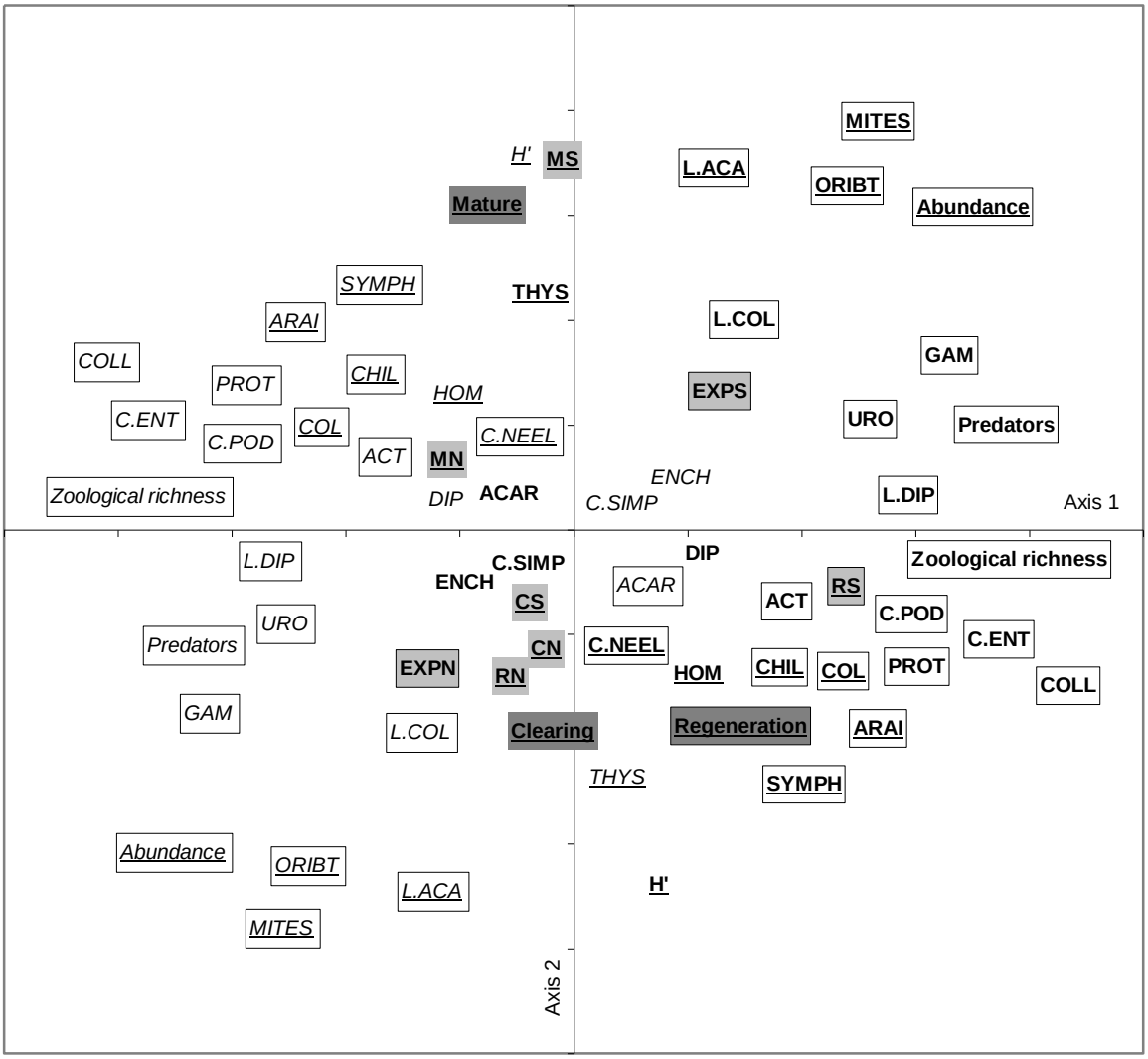
2 Fig. 1


MITES
H'
MS
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ORIBT
Mature
Abundance
SYMPH
THYS
ARAI
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GAM
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HOM
EXPS
C.ENT
URO
Predators
COL
C.POD
C.NEEL
ACT
MN
ENCH
Zoological richness
DIP
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C.SIMP
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Axis 1
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C.ENT
Predators
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EXPN
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GAM
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Clearing
Regeneration
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ORIBT
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1 Fig. 2

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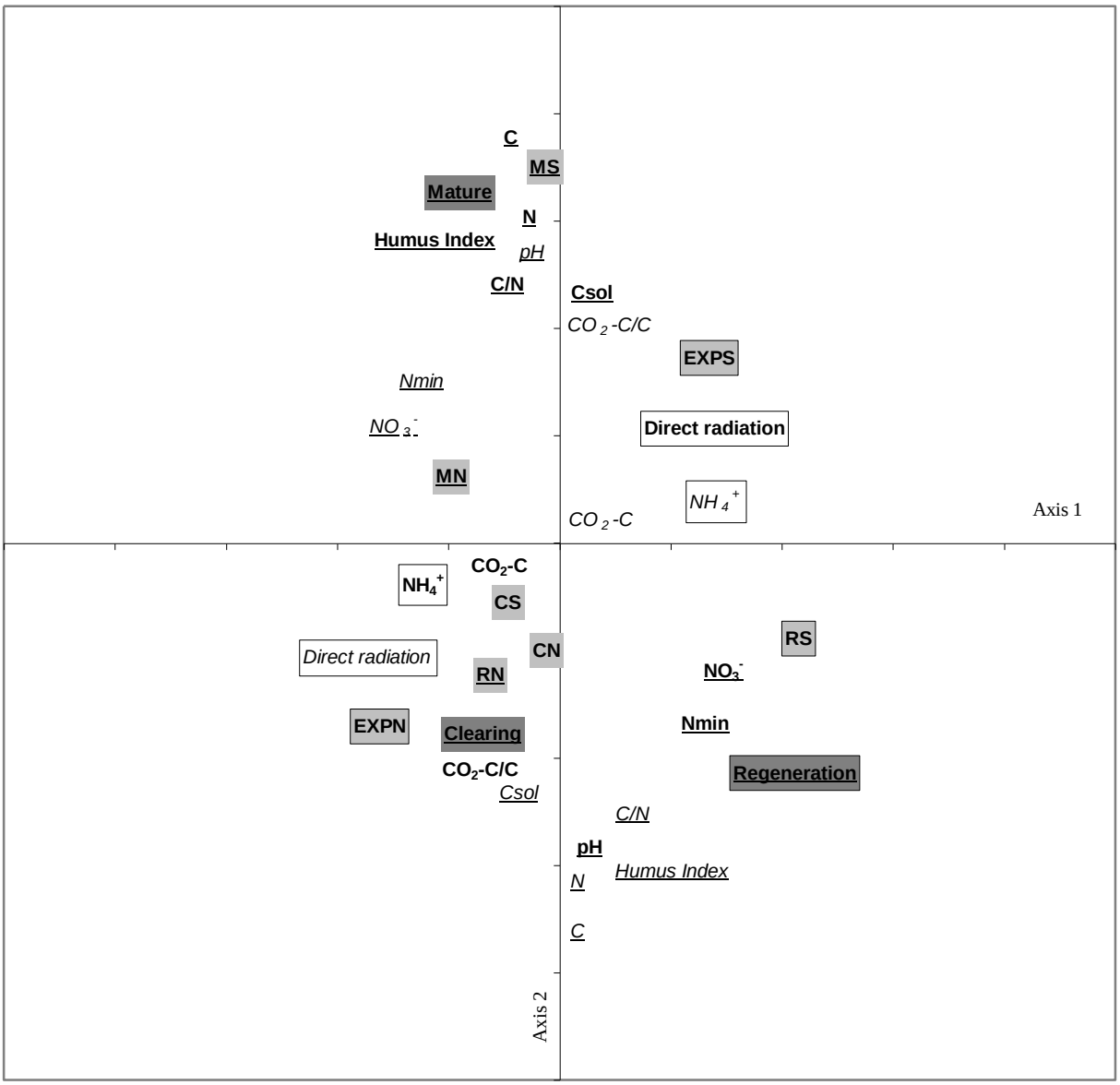

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