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Changes in humus forms, soil invertebrate communities and soil functioning with forest dynamics

Sandrine Salmon

Muséum National d'Histoire Naturelle, UMR CNRS 7179, Département Adaptation du Vivant, 4 Avenue du Petit-Château, 91800, Brunoy, France

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A B S T R A C T

Three field studies have been performed, in order to assess changes in the composition of soil animal communities, soil physical and chemical features and mineralization processes with Norway spruce (*Picea abies*, L.) phases of the forest cycle. These field studies were conducted in three sites that differed in the acidity level of their bedrock (acidic, sub-acidic, and basic). The influence of exposure, through modifying microclimatic conditions, was also taken in consideration by comparing north and south exposures at each site. The data issued from each of these studies have already been published separately, and the aim of the present paper is to confront the three series of data in order to assess: 1) The general trend of changes in soil invertebrate communities, humus forms and mineralization processes with the age of spruce; 2) The impact of the type of bedrock and exposure on these changes.

The results indicate that deep modifications occurred in animal communities, humus forms and soil functioning among clearing, regeneration and mature tree stands. The changes consist in an increase of Humus Index and the density of mites, especially oribatids, with a decrease in mineralization rate and animal diversity, from clearing to mature stands.

Regeneration stands occupy an intermediate level as regards soil features but cumulates highest densities of most groups, highest levels of zoological diversity and mineralization activity. This higher level of richness and functional activity in regeneration stands could be explained by a more heterogeneous habitat in this phase of the forest cycle. Our results thus support the hypothesis that forest dynamics drives soil functioning and diversity, at least during the phase of intense growth of trees.

The evolution of humus forms and animal communities along the developmental phases of forest stands were considerably more pronounced in south-facing sites than in north-facing sites. Unexpectedly, no increase in animal diversity was observed from the more to the less acidic bedrock. Suggestions for forest management are proposed.

1. Introduction

Soils store the bulk of carbon of ecosystems in the form of organic matter (Wall, 1999), and soil biota, which condition the cycling of carbon and nitrogen, participate to the control of nutrient availability for primary production (de Vries et al., 2013). The humus form, that is at the interface between plants, animals, and microbes is the seat of most biological activities occurring in forest ecosystems (Ponge, 2003). Humus forms are the result of most animal and microbial activity in the soil (Rusek, 1975; Kubiëna, 1955) and, in turn they condition the development of terrestrial plants, animal and microbial communities (Ponge et al., 1997; Hooper et al., 2000). Soil fertility depends on soil organic matter content, mineralization rate, incorporation of organic matter to mineral particles, which are related to the humus form. Mull, characterized by the rapid disappearance of leaf litter through the activity of burrowing animals and white-rot fungi, and by the mixing of humified organic matter with mineral particles within macro-aggregates, is associated to the most fertile soils and supports an abundant and diversified herb layer (Ponge, 2003). In moder humus, organic matter accumulates in the form of three holorganic horizons, without cementation of organic matter by mineral particles (Ponge, 2003).

The humus form also depends on bedrock and climate (Toutain, 1987), but, in constant conditions (of climate and substrate) it may change only with the vegetation cover. Bernier and Ponge (1994) studied the change of humus forms in a spruce forest in French Alps by a micromorphological method. They observed that the humus form changed cyclically in a spruce chronosequence. However this finding was based on the observation of a small surface without true replication (one sampling per growth phase), and it seems that in some cases this cycling change does not occur, as in a planted spruce forest in Germany

E-mail address: sandrine.salmon@mnhn.fr.

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(Zaitsev et al., 2002). Further studies are thus necessary to know whether this change is a general phenomenon and to assess in which conditions, especially geologic and microclimatic, it occurs.

As regards soil fauna, several studies have assessed changes in density and diversity of invertebrate species, as well as changes in species composition of communities along forest cycle phases (Hågvar, 1982; Bernier and Ponge, 1994; Migge et al., 1998; Zaitsev et al., 2002; Chauvat et al., 2003; Grgic and Kos, 2005). However, each of these studies focused on the species diversity of only one taxon, so that seven taxa were studied separately in tree stands of various ages: Acari, Collembola, carabid beetles, Lumbricida and Chilopoda, Araneida, Diplopoda excluding some other soil-dwelling invertebrates, especially, Diptera larvae and Enchytraeidae. As different zoological taxa contribute differently to soil functions, depending on their trophic guild, size and life history traits (Verhoef and Brussaard, 1990; Setälä et al., 1991; Vedder et al., 1996) all taxa of soil invertebrates should be studied jointly.

Three field studies have been performed in the scope of the Dinamus project, in order to assess changes in the composition of soil animal communities, soil physical and chemical features and mineralization processes along Norway spruce (*Picea abies*, L.) forest cycle phases. These field studies were conducted in three sites characterized by the acidity level of their bedrock: acidic, sub-acidic, and basic. The interaction of exposure with bedrock and spruce dynamics was also taken in consideration by comparing north and south exposures at each site. Data issued from each of these studies have already been published separately, and the aim of the present paper is to confront the three series of data in order to assess:

(1) The general trend of changes in soil invertebrate communities, humus forms and mineralization processes with the age of spruce.
(2) The impact of the type of bedrock on these changes.
(3) The interaction of exposure with forest dynamics in changes of communities through modifying microclimatic conditions.

2. Material and methods

2.1. Description of sites and sampling design

Animal communities and decomposition of organic matter were studied in three spruce forests in the Italian Alps, with the following environmental conditions:

- Acidic bedrock (granite), facing south (near Madonna di Campiglio), in September 2002
- A calcareous bedrock, facing south (in the Non valley) and north (in the Fassa valley), in June 2003
- Sub-acidic bedrock (moraine), facing south and north (near the lake of Pannevegio, in the Fiemme valley) in October 2003.

In each site, soil animal communities were studied in three phases of the spruce forest cycle (Fig. 1): clearing (0–5 years), regeneration (20–24 years) and mature trees (136–180 years), except on the acidic bedrock where the clearing phase has not been studied. Clearing, regeneration and mature stands in south and north-facing sites, respectively, will be abbreviated as follow: CS, RS, MS, CN, RN and MN. Eight sampling points were chosen randomly under each spruce cycle phase (Fig. 2).

Sample sites were located at an altitudinal range of 1750–1770 m a.s.l and regeneration was natural and happened following marginal cutting or by opening the canopy. See Salmon et al. (2006, 2008a,b) for the description of vegetation, geological and climatic features, as well as plot size.

At each sampling point, two soil cores were extracted using a rectangular crystal polystyrene box (Fig. 3): (1) for the collection of arthropods and chemical analysis, (2) for the extraction of enchytraeids. Sample size was 9.5 cm x 5.5 cm (15 cm depth) on the acidic bedrock and 4.2 cm x 8.3 × 11.3 cm (depth) for the other sites.

2.2. Experimental set-up

Immediately following sampling, one set of soil cores (1) was put into a crystal polystyrene box with a wide aperture on the top (covered with a nylon gauze of 35 µm mesh to prevent invertebrates from escaping), and a 5 mm hole at the bottom (to collect leachates, Fig. 3). CO2-C (respirationFig.) and leachate release (produced by irrigating soil cores with deionised water) were performed four and eight days after sampling respectively, on the soil cores contained in polystyrene crystal boxes. These cores were then placed at the top of a Berlese funnel for the extraction of arthropods. Dried soil remaining at the end of the arthropod extraction was analysed for carbon (C) and nitrogen (N) content as for soil pH (see below).

The other set of soil cores (2) was used for the extraction of enchytraeids immediately after soil sampling.

In the case of the acidic bedrock, size of sample units and experimental set-up were lightly different (see Salmon et al., 2006). Values of CO_2-C, CO_2-C/C, mineral N and soluble organic C (see below) displayed here are means of three successive measures per replicate in the course of time.

2.3. Mineralization

The mineralization of carbon in the soil cores was followed by measuring CO_2 release from each soil core after 4H incubation in an air-tight enclosure, with a CO_2 analyzer based on the infra-red method.

Soluble organic C, nitrate and ammonium content were measured in leachates obtained by irrigating soil cores with deionised water to obtain 40 ml of leachate 12H after irrigation.

2.4. Collection and identification of fauna

Soil arthropods were extracted by the dry funnel method (Edwards and Fletcher, 1971). Animals were identified at the group, order, super-family or family level and classed into morphotypes on the basis of their morphological features (Salmon et al., 2006). Enchytraeids were extracted by the modified wet-funnel method of O'Connor (1957), then immediately counted under a magnifying glass.

2.5. Physical and chemical soil characteristics

Each humus form at each sampling point was identified and given a Humus Index (Brêthes et al., 1995; Ponge et al., 2002).

Soil pH-H_2O was measured on soil mixed with deionised water (Anonymous, 1999).

Organic C and total N content were measured in 50 mg of dried, ground and defaunated soil with a CHN atomic analyzer.

Refer to Salmon et al. (2006, 2008a,b) for further details about methods.

2.6. Statistical analysis

Prior to analysis, variables and indices were calculated to characterize animal communities: total density, taxonomic richness (number of main zoological groups), morphotype richness (number of morphotypes). The Shannon index was calculated using zoological (taxonomic) groups.

Data (density of zoological groups) have been previously treated with correspondence analysis (CA). Three CA (one per type of bedrock) have been performed to ordinate zoological groups and samples, with zoological groups as active variables. Environmental variables (cycle phases, exposure, CO_2-C …) and animal community indices (morphotype richness…) were used as passive variables. Results of CA will not