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Relationships between soil fauna communities and humus forms: Response to forest dynamics and solar radiation

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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 characterised 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 characterised by high levels of soil organic carbon and nitrogen, C/N values and low pH, the clearings and regeneration stands being characterised 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.

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 availability) must particularly be taken into account to understand the relationships between soil animal communities and plant succession, because it constitutes a living substrate for both plants and soil invertebrates (Peltier et al., 2001; Ponge, 2003). Mull and moder are two out of the three

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main humus forms (in order of highest to lowest levels of biodiversity) (Ponge, 2003). Mulls (comprising eumull, oligomull, amphimull and dysmull) are generally associated with early developmental stages (regeneration) of forest stands, while moders (eumoder and dysmoder) occur in phases of intense growth of trees up to maturity (Bernier and Ponge, 1994; Salmon et al., 2006).

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

A study has already evidenced the changes in soil animal communities associated with 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 (geological 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

2.1. Study sites and sampling design

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

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

The mean age of spruce in regeneration stands was 27 years (max. 41, min. 11) and 23 years (max. 36, min. 17) in the south- and north-facing sites, respectively. In mature stands, spruce were 165 years old (max. 221, min. 100) and 180 years old (max 204, min 144) in the south- and north-facing sites, respectively. Stands were situated on either Cambisol or Regosol (FAO, 1998) formed on sedimentary dolomitic rocks. The density of mature spruce was 600 and 500 trees ha^{-1} while regeneration density was 8000 and 15,500 trees ha^{-1}, in the south- and north-facing sites, respectively. The dominant plant species and the cover of the herbaceous layer (cover greater than 35%) are given below.

South-facing site (Non Valley):

- Clearing: cover greater than 90%; *Carex montana*, *Calamagrostis varia*, *Brachypodium pin. rupestre* and *Melica nutans*.
- Regeneration phase: two areas differing by the composition and cover of the herbaceous layer, (1) cover greater than 90% (six samples)— *Carex montana*, *Viola biflora* and *Brachypodium pin. rupestre*, (2) mean cover of 35% (two samples)— *Vaccinium vitis-idaea* 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 3 to 9 m 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 × 8.4 L × 11.3 cm depth) and used for soil analysis and arthropod extraction; 48 other soil cores with the same dimensions were collected in plastic bags and used to extract enchytraeids (see below).