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Linking forest dynamics to richness and assemblage of soil zoological groups and to soil mineralization processes

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ABSTRACT

We conducted a study in a spruce forest, grown on a sub-acidic bedrock, in the Italian Alps in order to assess whether (1) forest dynamics influences animal communities, and in particular whether the richness of zoological groups peaks during the regeneration phase, (2) the diversity of zoological groups is correlated to C mineralization, considered as a measurement of soil functioning, (3) aspect influences the above relationships. We compared soil animal communities, soil physico-chemical features and nutrient mineralization in three developmental phases of spruce, with increasing tree cover (clearing, regeneration and mature trees) and two sun exposures (North, South). Animal communities changed with spruce dynamics. Mature spruce stands were characterized by higher densities of Acari, while regeneration stands and clearings were mainly characterized by higher densities of Collembola and most groups of macrofauna. As hypothesized, the richness of zoological groups was highest in regeneration stands, especially in the south facing site, probably because of the simultaneous occurrence of a dense herbaceous cover and spruce litter, leading to higher local soil heterogeneity. However, zoological group diversity (Shannon index), which was lowest in mature stands, was better explained by the herbaceous cover, i.e., by the quality of food resources, in both south and north facing sites. Variations of soil characteristics with the developmental phase of trees, reflecting a higher litter input and slower litter decomposition rate beneath mature trees, are in line with the distribution of zoological groups. As expected, the diversity of zoological groups was positively correlated to C mineralization. Changes in animal communities with phases of the forest cycle were much more pronounced in the south compared to the north facing site. In light of previously published results, we discuss how the diversity and composition of soil animal communities are plant driven.

1. Introduction

Identifying patterns and determinants of biological richness is a major theme of community ecology and has a fundamental importance to ecosystem management and preservation of biological diversity (Schwartz et al., 2000). A related scientifically and politically important question concerns the ecological consequences of biological diversity; that is, is there a relationship between biological diversity and ecosystem functioning? Traditionally, there are three factors that are believed to determine diversity in terrestrial and aquatic communities: resource supply, environmental heterogeneity (or habitat variety) and disturbance (Rosenzweig, 1995; Gaston, 2000; Bardgett, 2002; Bardgett et al., 2005; Dufour et al., 2006). The heterogeneous nature of the soil environment offers diversified resources and habitats, leading to the coexistence of a high number of species (Jordana et al., 2000; Bardgett et al., 2005) provided that quantity and quality of resources be favorable (Wardle, 2005). Recently, Bardgett et al. (2005) argued that the pattern of soil biodiversity is primarily related to the heterogeneous nature of the soil environment at different spatial and temporal scales. We may assume that soil heterogeneity could vary with phases of the forest cycle (e.g., clearing, regeneration and mature trees) in lightly managed forest ecosystems, since humus forms change with the age of trees (Bernier and Ponge, 1994; Salmon et al., 2006). This environmental heterogeneity would be maximum in the intermediate successional phase, which is the more diversified phase as a result of highest plant diversity (Connell, 1978). A diverse plant community may not only result in a heterogeneous habitat but also provide a diverse resource supply for soil invertebrates. If we consider the

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three main phases of natural dynamics of spruce forests (clearing, regeneration and mature trees), we may assume that the regeneration phase will constitute an intermediate level in which the richness of zoological groups should be at its highest level, due to the simultaneous presence of herb layer and spruce litter that increases local soil heterogeneity and diversifies resource supply.

Several studies assessed changes in abundance and diversity of invertebrate species, as well as changes in species composition of communities with phases of the forest cycle (Hågvar, 1982; Baguette and Gérard, 1993; Bernier and Ponge, 1994; Migge et al., 1998; Zaitsev et al., 2002; Chauvat et al., 2003; Trofymow et al., 2003; Grgič and Kos, 2005). However, each of these studies focused on the species diversity of only one or a few animal taxa, so that only five taxa were studied separately in tree stands of various age: Acari, Collembola, Carabidae, Lumbricidae and Chilopoda. Several important soil-dwelling invertebrates such as Araneida, Diptera, Diplopoda, Symphyla and Enchytraeidae were not studied. Paquin and Coderre (1997) studied multiple taxa to the exception of Collembola and Acari, which account for a large part of forest arthropod communities. We may assume that functional differences between species, resulting from ecological requirements, life history-traits and size of organisms, are greater when species belong to different zoological groups, than when they belong to the same group, and that variations in assemblage and diversity of zoological groups may impact more greatly soil functioning, e.g., mineralization rates than variations at the species level of one group. Moreover, many microcosm experiments suggested that the functional composition of soil invertebrate communities is more closely related with process rates than species richness (Vedder et al., 1996; Schwartz et al., 2000; Loreau et al., 2001; Cortet et al., 2003). Although many field and experimental studies indicated that a large number of species is required to sustain ecosystem functioning, at least aboveground (Naeem et al., 1996; Tilman et al., 1996; Loreau et al., 2001), several researchers emphasized that the relationship between species richness and function may be variable, negative or non-existent (Schwartz et al., 2000; Wardle et al., 1997). In particular, Setälä et al. (2005) stated that some animal species in soil communities are functionally redundant because of the plasticity of their trophic regime, which could explain why soil functioning is not systematically correlated to animal species richness. Consequently, considering the species diversity of just one or a few number of taxa is not the better approach to the study of functional diversity. The diversity of all zoological groups may be a better and simpler mean to correlate invertebrate diversity to soil processes such as mineralization rates.

We may assume that changes in richness, diversity or assemblage of soil zoological groups with forest dynamics could impact soil functioning. Only four studies have related function, i.e., the decomposition of organic matter and nutrient cycling, to forest dynamics (Bernier and Ponge, 1994; Bauhus et al., 1998; Salmon et al., 2006, 2008). Bernier and Ponge (1994) observed changes in humus forms, namely the result of interactions between vegetation and animal/microbial activity in the soil (Rusek, 1975; Kubiëna, 1955), along a spruce chrono-sequence. More precise analyses of mineralizing activity were undertaken by Bauhus et al. (1998), who concluded that microbial C and N declined with stand age as a result of a decreasing quality of soil organic matter in mature tree stands. Salmon et al. (2006, 2008) observed higher C/N ratio and C and N contents in mature than in regeneration stands of spruce forests growing on acidic and calcareous bedrocks. These two studies (Salmon et al., 2006, 2008) also showed that the assemblages of soil zoological groups changed with developmental phases of spruce on both acidic and calcareous bedrocks. A comparison with the pattern observed here, on a sub-acidic bedrock, will allow to ascertain whether the observed relationships can be generalized for different geological and climate conditions. As for humus forms, soil function and the composition of invertebrate communities are affected by microclimate conditions (Toutain, 1987; Ponge, 1993). The effects of aspect on the relationships between forest dynamics, mineralization rate and animal diversity have thus to be explored.

In the present study, our objectives were: (1) to determine whether and how the diversity and the composition of soil invertebrate communities are correlated with spruce forest dynamics and, more specifically, to examine the relationships between the richness of zoological groups and the diversity of resources and habitats, assumed to peak in the regeneration phase as a result of the simultaneous presence of spruce litter and dense herb layer; (2) to assess whether the mineralization rate, used as a measurement of soil functioning, and humus forms parallel changes in invertebrate communities, and may be explained by the diversity of zoological groups; (3) to determine how environmental factors, such as aspect, influence the above relationships.

2. Material and methods

2.1. Study sites and sampling

Soil samples were taken at the beginning of October 2003 in a managed, productive spruce forest (95% *Picea abies*, with a low percentage of *Larix decidua* and *Pinus cembra*) in the Southeastern Italian Alps, located near the Lake Paneveggio in the Fiemme Valley (Province of Trento, Italy). Two sites were selected, 2.3 km apart (46°18′54″N, 11°44′19″E and 46°17′45″N, 11°45′08″E, respectively), at an altitude of 1750 m, on a sub-acidic bedrock and facing north and south, respectively. The two sites were located on slopes of the same valley, one directly opposite the other.

The management of these sites was conducted following 'naturalistic' silviculture, which means that wide clearcuts were replaced by small clearings about 200–1000 m^2 area. Natural regeneration of *Picea* occurs in these small areas, sometimes even under mature trees.

The substrate of the north facing site is derived from the moraine of the glacier of Pale di S. Martino Mountains, Permian volcanic rocks, and Verrucano lombardo (a red, coarse-grained, crimbling, fluvial deposit). The mean annual temperature is 3.9 °C, and the mean annual rainfall 782 mm. The substrate of the south facing site is moraine with acid post-Hercynian molasses, covered with mixed moraine. The most common component was volcanic rock, except in half of the clearing and regeneration areas where calcareous marls/calcareous schists also occurred. The mean annual temperature in this site is 4.4 °C, and the annual rainfall 1103 mm.

In each site, sampling was completed in three contiguous areas corresponding to three developmental phases of spruce: regeneration, mature trees and clearing. Characteristics of the six areas are given in Tables 1 and 2. Eight sampling points, (i.e., eight pseudoreplicates) were selected randomly in each area, except in the north facing clearing area where four pseudoreplicates were done. At each sampling point, distant from 3 to 9 m from each other, two soil cores were extracted using a polystyrene crystal rectangular box 4.2 cm × 8 cm × 11.3 cm Lxlxh. Each sample core contained organic and upper mineral layers and was used for: (1) collection of arthropods, respiration measurements, leachate analysis, determination of soil carbon and nitrogen contents and soil pH; (2) extraction of enchytraeids. Samples were transported in their polystyrene crystal box to the laboratory and kept at 4 °C for 24–72 h until respiration measurement and leachate collection,