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Integrating chemical, biological and soil fauna variables during beech leaf litter decay: A partial least squares approach for a comprehensive view of the decomposition process

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ABSTRACT

Litter decomposition is an ecosystem process that is regulated by a multitude of factors and by their complex interactions. Current decomposition paradigms do not always offer a coherent view of the process because it can be hardly understood without a thorough analysis of interacting factors. Thus, there is a need to further understand the mechanics of litter decay with a comprehensive approach, especially in temperate forest ecosystems where decomposition plays a crucial role in regulating them as source or sink of CO_2. Therefore, the aim of this work was to identify the interactions between chemical, biological and soil fauna variables in order to discern driving variables and the changes in their interactions during long-time (1300 days) beech leaf litter decomposition. In order to investigate patterns of variation and co-variation within and between datasets, we used Two-block Partial Least Squares, helping us to interpret the decomposition process with a systemic approach. Our key findings showed that the decomposition process of beech litter in two Mediterranean forests was driven by litter quality at the beginning and in the later stages of decomposition, while edaphic and climatic factors were implied in the central steps, with a dramatic change of scenario around 2.5 years. Simultaneous and interacting changes in chemical variables, extracellular enzyme activities, and soil fauna were shown, with a significant role of lignocellulosic components and enzymes involved in their degradation, Mn residual weight, and abundance of Collembola.

1. Introduction

Litter decomposition is an ecosystem functioning process that is regulated by a multitude of factors and by their complex interactions. Several researches carried out on decomposition dynamics suggested main controls either on the effect given by climate and litter quality (Kasurinen et al., 2007), or the nature and abundance of decomposer organisms and/or pedofauna (Fujii and Takeda, 2017; García-Palacios et al., 2013).

Litter quality affects both the decomposition rate and the limit value of decomposition (i.e. the limit for the accumulated mass loss when the decomposition may ultimately approach the rate zero and thus leave a recalcitrant or stabilized residue), the amount of humus produced and its chemical features (Berg, 2014). Great importance has been given to N and/or Mn (Berg et al., 2015; Innangi et al., 2015b) and the ratio of easily decomposable vs. recalcitrant compounds (Berg, 2014; Cotrufo et al., 2015). Thus, the C:N ratio, as well as the cellulose:lignin and cellulose:lignin:N ratios, are useful indices that would predict the decomposition rate (García-Palacios et al., 2016; Trap et al., 2013). Nevertheless, during decomposition, new organic matter originates by structural and chemical changes of original dead organic matter as well as by-products of soil biota, and these secondary molecules may be resistant to decomposition (Danise et al., 2018).

Climate affects the decomposition rates and the limit value of decomposition as well (Berg et al., 2010; Kasurinen et al., 2007). The effects can be either direct, e.g. by leaching of soluble compounds (Dise et al., 2009; Innangi et al., 2017a), or indirect by controlling species composition and activity of microbial and fauna communities (Aubert et al., 2010).

Litter decomposition rates appear also related to the complexity of the soil microbial and fauna communities (Rouifed et al., 2010). Microbial communities are the main agents of the process through the secretion of extracellular enzymes (Burns et al., 2013), with a dominant role of fungi (Schneider et al., 2012). The diversity of the communities

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and their succession during decomposition ensures the degradation of organic matter and mineralization processes (Voříšková and Baldrian, 2013). Thus, extracellular enzyme dynamics, which are involved in the degradation of the major structural constituents of plant material, may provide information on specific metabolic and functional aspects of microbial communities (Sinsabaugh et al., 1991) as well as assess changes of microbial soil communities in response to environmental or chemistry variations (Fioretto et al., 2018). Soil fauna participates in the fragmentation of plant detritus and stimulate the activity of bacterial and fungal colonies (Hättenschwiler et al., 2005). In forest ecosystems soil and litter arthropod communities play a major role in the decomposition of fresh organic matter and in the formation of the humus profile (Rouifed et al., 2010). In particular, Oribatid mites and Collembola are important members of the detrital system in temperate forests (Menta et al., 2014).

Thus, there is a need to further understand the mechanics of the decomposition process with a comprehensive approach (García-Palacios et al., 2016), especially in temperate forest ecosystems when decomposition plays a crucial role in regulating forests as source or sink of CO_2 (Meier and Leuschner, 2010; Pan et al., 2011). This is particularly true under climate change scenarios, especially in Mediterranean ecosystems that are highly susceptible to shifts in temperature and precipitation (Innangi et al., 2015a). Accordingly, beech forests have been extensively studied, given their substantial C stock and vulnerability (Chiesi et al., 2010; Curcio et al., 2017; Innangi et al., 2015a).

Litter decomposition in beech ecosystems has been studied extensively, but there are few studies that address the ecological phenomenon of decomposition with a systemic approach. Therefore, the aim of this work was to identify the interactions between chemical, biological and soil fauna variables in order to discern driving variables and the change in their interactions during long-time (1300 days) leaf litter decomposition. To achieve this goal, we have studied beech leaf litter decomposition in two Mediterranean forests, which were already previously studied under different aspects, from decomposition regimes to carbon stocks and microbial activity (De Marco et al., 2016; Fioretto et al., 2018; Innangi et al., 2015b). Leaf litter was collected and incubated in the same sites, but a transplant experiment was also carried out by incubating the litter coming from each of them on the opposite site. In order to address the need of a comprehensive view of the decomposition phenomenon, we did not focus extensively on single variables, which have been amply studied in soil ecology research, but we have concentrated on Two-block Partial Least Squares (2B-PLS) regression, a data analysis process that allowed us to discriminate and interpret patterns of variation and co-variation between sets of variables throughout the decay process.

2. Material and methods

2.1. Site descriptions

The two beech forest sites have been chosen according to their strong diversity in terms of soil characteristics and climate, yet with the same age (70–80 years at the beginning of the experiment) and management. A thorough description of these forests is given in (De Marco et al., 2016; Fioretto et al., 2018; Innangi et al., 2015b), yet a brief summary of the main forest features is provided.

Pradaccio (44.24 °N, 10.01 °E, 1350 m a.s.l.), is located on the northern Italian Apennines, within the “Guadine-Pradaccio” National Reserve (Emilia-Romagna region). The site has a mean temperature of 6.0 °C with total average rainfall of 2900 mm per year. Parent material is sandstone, giving the soil an extremely acidic reaction (pH = 4.0). The other forest, Laceno (40.47 °N, 15.05 °E, 1150 m a.s.l.), lies in the southern Italian Apennines within the Regional Park of Monti Picentini (Campania region). The forest has an overall average rainfall of 2300 mm per year and a mean annual temperature of 8.7 °C. The parent material is carbonate, and the soil is strongly acidic (pH = 5.5).

2.2. Litter collection and litterbag preparation

Newly shed litter was collected between the second half of September and the end of November 2011 by equally-spaced 6 net traps (80 cm Ø) on a surface of about 1 ha in each site. Litter was collected several times until fall was complete. Given that leaves were the most abundant fraction of total litter, we included only leaf litter in the litterbags.

Before their inclusion in the litterbags, aliquots of litter was dried in an oven at 75 °C until constant weight to evaluate dry weight. For the decomposition experiment, 576 standard terylene litterbags of 20 cm × 10 cm were prepared, with a mesh size of 1 mm × 1.5 mm, allowing interaction with most of the soil fauna except the largest animals (Bokhorst and Wardle, 2013). Each litterbag was filled with approximately 4 g of dried newly shed litter.

For the microarthropods study, instead, 108 modified terylene/plastic litterbags of 25 cm × 16.5 cm and different mesh sizes on the upper and lower surface of the litterbag were prepared. Top side had a mesh size of 2 cm × 2 cm, to allow the entry of most soil fauna, while the bottom one had a mesh size identical to the standard litterbags. Each litterbag was filled with approximately 6 g of dried newly shed litter.

Of the 288 standard litterbags and 54 modified litterbags prepared with litter from the forest site of Laceno, half of them were placed on the surface or organic soil in Laceno forest (LL) and the other half in Pradaccio forest (LP) in 6 randomized microsites in December 2011. Similarly, the litterbags enclosing the litter coming from Pradaccio were located at Pradaccio (PP) and Laceno (PL).

2.3. Litterbag collection and processing

Standard litterbags were sampled in both sites at 200, 535, 680, 935 up to a maximum of 1300 decomposition days, while modified litterbags for soil fauna were collected at 535, 935, and 1300 decomposition days. Each time, 3 litterbags per each leaf material were harvested from the 6 microsites in both forests (overall 18 bags).

After collection, each standard litterbag was opened in laboratory and carefully cleaned with a soft brush in order to remove large fauna and particles of soil. Afterwards, a little amount of the litter (about 0.5 g) from each litterbag was weighted, dried at 75 °C for 48 h and again weighted to evaluate its dry weight and to calculate the residual mass in each litterbag. Subsequently, the residual material of the three litterbags coming from each microsite was pooled to obtain a homogeneous sample for each incubation microsite. An aliquot was dried and ground until passing a 0.5 cm screen, while the rest was stored at −80 °C until enzyme activity measurements. By considering M as the dry mass in g of litter from each bag and t_x as the days of decomposition, residual weight was measured as $[M(t_x)/M(t_0)] \times 100$. Decomposition trends were evaluated according to the single exponential model (Olson, 1963), obtaining the decomposition constant k (days^{-1}) as $-\{\ln [M(t_x)/M(t_0)] \times [1/t_x]\}$.

2.4. Soil fauna extraction and classification

In the laboratory, soil particles and living plant parts were removed from the surface of the litterbags. Animals were extracted by each modified litterbag using a Berlese-Tüllgren funnel at 35 °C for 10 days. The specimens were collected in a preserving solution (3:1 ethanol/glycerol v/v) and identified to class level for Myriapoda and order level for Hexapoda, Chelicerata and Crustacea (Menta et al., 2014) using an optical microscope. The organisms belonging to each taxon were counted in order to estimate their abundance in the litterbag.

2.5. Chemical analyses

Organic matter was measured by loss-on-ignition method by