



Changes in litter chemistry associated with global change-driven forest succession resulted in time-decoupled responses of soil carbon and nitrogen cycles



María José Fernández-Alonso^{a,*}, Jorge Curiel Yuste^{b,c}, Barbara Kitzler^d, Carlos Ortiz^a, Agustín Rubio^a

^a Departamento de Sistemas y Recursos Naturales, Universidad Politécnica de Madrid, Ciudad Universitaria s/n, 28040 Madrid, Spain

^b BC3 - Basque Centre for Climate Change, Scientific Campus of the University of the Basque Country, 48940 Leioa, Spain

^c IKERBASQUE - Basque Foundation for Science, María Díaz de Haro 3, 6 solairua, 48013 Bilbao, Bizkaia, Spain

^d Department of Forest Ecology and Soils, Austrian Research Centre for Forests, Seckendorff-Gudent-Weg 8, 1131 Vienna, Austria

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ABSTRACT

Global change-driven forest succession may modify key soil processes with potentially important impacts over carbon (C) and nutrient cycling. We studied how changes in litter throughout the replacement of *Pinus sylvestris* by *Quercus pyrenaica* influence the structure and functioning of soil microbial communities and the capacity of soils to sequester C and retain nitrogen (N). We designed a microcosm experiment to simulate the chronological sequence from pine to oak forest conversion in Central Spain, using mixtures of senescent litter (oak leaves, pine needles and an equal mixture of needles:leaves) and soils (from pure oak, mixed and pure pine stands). We investigated changing patterns of soil C and N contents, microbial community structure (PLFA) and greenhouse gas fluxes (CO₂, CH₄, N₂O) across the chronosequence. The succession from pine to oak forest was associated with substantial changes in microbial community structure and functioning. Soil-C sink capacity was reduced, although soil-N availability was enhanced. We further show how effects of secondary succession on the C cycle were mismatched with N dynamics in response to two chronologically decoupled facts. First, there was an acceleration in soil organic matter (SOM) turnover after microbial –especially bacterial– growth ceased to be so intensely inhibited by needle litter (ecotone soils), resulting in lower fungal to bacterial ratios; and second, N mineralization was stimulated once pine-derived SOM was no longer present in soils (pure oak forest soils), resulting in further acceleration of SOM turnover, suppression of CH₄ consumption and an increase in gram-negative bacteria. Our findings suggest that different sensitivities of key mechanisms (SOM decomposition, N mineralization, CH₄ consumption) to factors associated with succession (e.g. recalcitrance of pine SOM and allelopathic effects over bacteria) could have significant impacts on soil microbial ecology, C and nutrient cycling.

1. Introduction

We are currently facing successional changes in forests responsible for essential shifts in the functional diversity of terrestrial ecosystems on a large scale (Ruiz-Benito et al., 2017). This is partly a consequence of the altitudinal migration of dominant tree species driven by the ongoing global change (Allen et al., 2010; Camarero and Gutiérrez, 2004; Sanz-Elorza et al., 2003). On the Iberian Peninsula, a gradual replacement of Scots pine (*Pinus sylvestris* L.) by several species from the genus *Quercus* sp. (Carnicer et al., 2014; Díaz-Pinés et al., 2014; Galiano

et al., 2010) may occur as a result of both the predicted changes in temperature and precipitation and changes in land use and forestry (Álvarez et al., 2014; Hereş et al., 2012; Martínez-Vilalta and Piñol, 2002). This succession from temperate needle-leaved forests to temperate broad-leaved forest lead to an abrupt change in ecosystem functional traits (Ruiz-Benito et al., 2017) that will be linked to further changes in soil functioning. However, few studies have addressed how this ecological succession modulates the time and the direction of changes in soil greenhouse gas (GHG) fluxes, carbon (C) sequestration and nitrogen (N) cycling.

* Corresponding author. Present address: ETSI Montes, Forestal y del Medio Natural, Ciudad Universitaria, Madrid 28040, Spain.

E-mail addresses: mj.fernandez@upm.es (M.J. Fernández-Alonso), jorge.curiel@bc3research.org (J. Curiel Yuste), barbara.kitzler@bfw.gv.at (B. Kitzler), carlos.ortiz.onate@upm.es (C. Ortiz), agustin.rubio@upm.es (A. Rubio).

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A change from needle-leaved forest to broad-leaved forest alter important quantitative and qualitative traits of plant litter inputs to the soil (e.g. litterfall rates, C:N ratios and lignin content), and thus affect soil organic matter (SOM) decomposition dynamics (Delgado-Baquerizo et al., 2015; Knapp et al., 2011) and biogenic production of GHGs –methane (CH₄), nitrous oxide (N₂O) and carbon dioxide (CO₂) (Heimann and Reichstein, 2008). Hence, shifts in the plant cover may affect factors directly controlling SOM decomposition, responsible for at least half the CO₂ emitted from soils (Bond-Lamberty et al., 2004). Changes of the input of fresh litter to the soil may also directly affect various mechanisms (e.g. nutrient limitation, co-metabolism) responsible for stimulating SOM decomposition –the so called “priming effect” (Blagodatskaya and Kuzyakov, 2008; Creamer et al., 2015). According to the inherent quality of the broad-leaved litter we may predict an acceleration of the turnover rate of the bulk SOM, but our understanding of other potential triggers and the timing of this response throughout the successional process is still limited. Another aspect that usually regulates SOM decomposition rate is the nutrient level (Berg, 2000). Conifers generally slow down the recycle of nutrients whereas deciduous trees require faster nutrient cycling to generate new foliage each year (Curiel Yuste et al., 2005). Thus, the encroachment of deciduous late successional trees may also have important consequences for coupled forest C and N cycling that currently are difficult to predict (Nave et al., 2011).

Regarding soil biota, global change-driven shifts in plant cover may also disrupt important and stable ecological interactions selected by nature in soils, since soil microbiota are physiologically adapted to the particular conditions occurring within an ecosystem as a result of historical selection processes (Keiser et al., 2011; Strickland et al., 2009). Microbial communities would therefore be more efficient decomposers of the plant-derived organic matter with which these communities have historically co-evolved, described as the “home-field advantage theory” (HFA) (Barba et al., 2015; Veen et al., 2015). However, the enormous functional redundancy of these communities may counteract this HFA, since many taxa are able to perform equivalent functions at the community level (Allison and Martiny, 2008; Curiel Yuste et al., 2014; Wohl et al., 2004). The HFA of soil microbial communities in relation to litter decomposition is not fully understood (Ayres et al., 2009) and could play a critical role in destabilising SOM in current large-scale scenarios of species substitution driven by global-change.

The above-mentioned aspects evidence that to predict how soils will respond to changes in forest functional traits we need to understand how the origin of SOM and the structure of soil microbial community relates to soil functioning. This study aims to disentangle how changes in the chemical composition of the litter input to soils (deciduous leaves vs conifer needles) affect the ecology of soil microbial communities and the key microbial functions controlling soil C and N dynamics. The question of how potential regulating factors hasten decomposition in soils and hence influence GHG fluxes in response to the encroachment of broad-leaved species in coniferous forests is highly significant, since Scots pine forest soils store roughly double the C and N stocks of oak soils in Mediterranean temperate forests (Díaz-Pinés et al., 2011). As environmental variability in the field may mask the effects of litter quality on decay processes (Vesterdal, 1999), we followed a full-factorial microcosm approach by mixing three types of forest soils with three types of senescent litter collected within a Mediterranean ecotone transect between Pyrenean oak (*Quercus pyrenaica* Willd.) and Scots pine forests in the Valsain mountains (Central Spain). These microcosms were used to recreate the chronological sequence of the vegetation change. After a 54-day incubation period, we examined the changes across the chronosequence on microbial community structure, total C (TOC) and N contents (TN) and their more accessible pools (extractable organic carbon (EOC) and total dissolved nitrogen (TDN)), and the production of soil GHGs (CO₂, CH₄ and N₂O).

2. Material and methods

2.1. Study site

The experimental site is located in a representative ecotone area between Pyrenean oak and Scots pine forests in Valsain, on the northern slopes of the Guadarrama range in Central Spain (40° 51' N, 4° 3' W, h30, ETRS89, ~1350 m.a.s.l.). In these mountains, pine forests occupy higher altitudes (1300–1900 m) than oak forests (400–1300 m). The current climate change and the abandonment of the traditional use of Pyrenean oak coppices during the 1970s have contributed to a gradual altitudinal expansion of oak trees into the former pure Scots pine forest (Álvarez et al., 2014). At this location, three different stands were identified along a 1400 m transect, ranging from a pure Pyrenean oak forest to a pure Scots pine forest, with a mixed Scots pine-Pyrenean oak forest in the ecotone between both pure stands. The study area presents a continental Mediterranean mountain climate with high year-round fluctuations in precipitation and temperatures. Summers are warm with three/four months of drought, whereas winters are cold and may have a thin snow cover lasting up to several weeks. For the period 2014–2017, the mean annual precipitation was 621.4 ± 64.8 mm and the maximum and minimum mean annual temperatures were 16.5 ± 0.4 °C and 5.4 ± 0.1 °C respectively (data collected from a weather station run by the State Meteorological Agency situated 9 km away, http://www.aemet.es/es/serviciosclimaticos/vigilancia_clima). Soils are cambisols (Soil Survey Staff, 2014) with a granite bedrock. The textures are silty clay loam in the oak forest, silt loam in the mixed forest and sandy loam in the pine forest. At the study site, the pH (4.0–5.5 in KCl, slightly more acidic in pine stands) and the accumulation of C in topsoil (0–50 cm: 40, 80 and 92 Mg C ha⁻¹ in Pyrenean oak, mixed and Scots pine forest respectively) are strongly influenced by tree species. For more information on the general and silvicultural characteristics of the study site, see Díaz-Pinés et al. (2014).

2.2. Soil and litter sampling

Soil sampling was done before the autumn rainfall period in September 2015 at a gravimetric field moisture content of about 7%. In each forest type, five plots measuring 4 m² were randomly established with a minimum separation distance of 125 m. In each plot, five soil samples were collected from a depth of 0–5 cm using a core sampler (5 cm in diameter) after removing the plant litter layer (undecomposed litter that forms a transient layer in the oak forest but has ~1 cm thickness in pine forest). The 25 soil subsamples collected in each forest were hand mixed and homogenized to obtain three composite forest soil samples that were shipped on ice to the laboratory in Vienna. Samples were sieved through a 4-mm mesh and stored at 4 °C for no longer than a week until used in the incubation experiment.

Litter samples were collected before needle and leaf abscission in the late autumn of the previous litterfall period. Litter sampling was done by hand, picking only senescent needles and leaves from randomly selected representative trees in both pure oak and pine forests. Given that the litter collected had no previous contact with soils, we assumed it had not yet been inoculated by soil microorganisms. The collected litter was mixed to form a single and homogeneous sample per tree species. Bulk needle and leaf litter were oven-dried at 45 °C to constant weight, and then cut into 1-cm length pieces to standardise the samples and aid their decomposition during incubation.

2.3. Experimental setup

Twelve microcosms (4 litter amendments × 3 soil inoculums) were used to assess whether substantial changes occurred in the structure and physiology of soil microbial communities when exposed to a non-

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