



# Population responses of oribatids and enchytraeids to ectomycorrhizal and saprotrophic fungi in plant–soil microcosms

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## ABSTRACT

The oribatid mites *Oppeia nova*, *Tectocephus velatus* and *Nothrus silvestris* and the enchytraeid worm *Cognettia sphagnetorum* are four common animal species in boreal forest soils. According to the literature, they respond differently to clear-cutting of forest stands. *O. nova* responds with population decreases, *T. velatus* and *N. silvestris* with small changes and *C. sphagnetorum* with population increases. We hypothesised that the presence/absence of ectomycorrhizal (EM) fungi is a major factor in explaining these reactions. The population responses of these soil animals to inoculation of five species of EM fungi growing in symbiosis with their host tree (*Pinus sylvestris* L.) and one saprotrophic fungus, *Hypholoma capnoides*, growing on wood were tested in pot microcosms with artificial soil (peat and vermiculite) for 70–84 days. Additionally, plants without inoculation of EM fungi, plants growing in forest soil (FS) and plant-free peat and vermiculite (PV) were included. *O. nova* increased significantly in abundance in the treatments with the EM fungi *Suillus variegatus* and *Paxillus involutus*, but not in the other treatments. *T. velatus* increased significantly in abundance in FS, but declined in most of the other treatments, and *N. silvestris* showed a similar, albeit not significant, response. *C. sphagnetorum* did not increase in abundance in any of the treatments with EM fungi but increased its abundance four times in both FS and PV. The results show that the fungivore *O. nova* preferentially feeds on certain EM fungi, especially *S. variegatus*, whereas the EM fungus *Piloderma fallax* and the saprotrophic *H. capnoides* are not preferred. In contrast, *C. sphagnetorum* is restricted in its population growth by the EM fungi studied, and this dominant microbi-detritivore is clearly favoured by the absence of EM fungi.

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## 1. Introduction

Feeding habits of soil fauna have been under debate for decades. Depending on the animal group and methods used, different degrees of feeding specialisation have been detected (Gates, 1961; Hartenstein, 1962; O'Connor, 1967; Ponge, 2000). According to Ponge (1991), oribatid mites have the most specialised feeding among the soil fauna and earthworms is the least specialised group. Many soil living animals have been observed to ingest fungal hyphae, which constitute a large proportion of the microbial biomass in forest soils. At least 30% of the microbial biomass and 80% of the fungal biomass in boreal forest soils consists of extraradical hyphae of ectomycorrhizal (EM) fungi (Wallander et al., 2001, 2003; Högborg and Högborg, 2002). Oribatid mites, which can reach abundances of 430 000 individuals m<sup>-2</sup> in Scots pine forest soil (Persson et al., 1980), are commonly referred to as being fungivorous and potential

consumers of mycorrhizal fungi (Fitter and Sanders, 1992). The abundance of oribatids tended to increase in the presence of EM fungi in a study by Setälä (2000), and according to Schneider et al. (2005), three oribatid mite species preferred to feed on the ericoid mycorrhizal fungus *Rhizoscyphus ericae* when offered ten different fungal species grown on agar.

Enchytraeid worms are very common in coniferous forest soils, and can reach abundances of up to 140 000 ind. m<sup>-2</sup> in stands of Norway spruce (Persson, 2002) and 170 000 ind. m<sup>-2</sup> in clear-cuts of Scots pine (Lundkvist, 1983). The dominant species *Cognettia sphagnetorum* is considered to feed upon fungi, bacteria and detritus (Didden, 1993). Some studies show that enchytraeids feed on fungi rather than on bacteria in feeding preference tests (O'Connor, 1967; Dash and Cragg, 1972), and mycorrhizal hyphae have been found in faecal pellets from enchytraeids in pine litter (Ponge, 1991).

The palatability of fungi can be influenced by the substrate on which the mycelia are growing (Leonard, 1984; Fitter and Sanders, 1992; Klironomos et al., 1992; Kaneko et al., 1995; Kaneda and Kaneko, 2004), and by differences in chemical and physical structure of the individual fungal species. Certain EM fungi have

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developed morphological features that are suggested to be defensive structures against grazing (Taylor and Alexander, 2005). Many EM fungi, e.g. *Piloderma fallax*, produce ornamented hyphae that are coated with crystals of calcium oxalate or other crystalline deposits (Brand, 1991a; Taylor and Alexander, 2005), which can make them even more unattractive as food. However, uptake of calcium oxalate might be beneficial for the accumulation of calcium (Coleman, 2008) and for the hardening of the cuticle of the mites. In addition, oribatid mites sometimes seem to prefer melanised fungi (Schneider and Maraun, 2005).

To study feeding preferences and avoidance reactions of soil fauna in relation to individual species of EM and saprotrophic fungi, we chose three common oribatid species in boreal forest soils, *Oppiella nova*, *Tectocephus velatus* and *Nothrus silvestris*, and one enchytraeid worm, *C. sphagnetorum*. The animal species are considered fungivores (*O. nova*, *T. velatus*) or microbi-detritivores (*N. silvestris*, *C. sphagnetorum*) (Schneider et al., 2004; Didden, 1993), but detailed knowledge of their feeding preferences is poor. Remén et al. (2008) found that the total abundance of oribatid mites was significantly lower in plots with girdled trees than in plots with ungirdled trees. Tree-girdling efficiently stops the allocation of carbohydrates from the canopy to tree roots and their associated EM mycelia. The species declining after tree girdling were assumed to respond to the lack of EM fungi, since they probably use these fungi as food. In contrast, enchytraeids increased in abundance after tree girdling (T. Persson, unpublished) and the abundance and biomass of *C. sphagnetorum* tended to be lower in the presence of EM fungi (Setälä, 2000; Liiri et al., 2007). The species also respond very differently to silvicultural practices. For example, *O. nova* responds with marked population decreases after clear-cutting (Malmström et al., 2009), and *T. velatus* and *N. silvestris* respond with small changes. *C. sphagnetorum*, on the other hand, responds with population increases after clear-cutting (Huhta et al., 1967, 1969; Huhta, 1976; Lundkvist, 1983; Siira-Pietikäinen et al., 2001a,b; Malmström et al., 2009), thus in the opposite direction as *O. nova*. Most of these authors concluded that *C. sphagnetorum* probably responds to the increase in resources in the form of felling residues, whereas Siira-Pietikäinen et al. (2001b) concluded that increasing soil moisture and increasing amounts of dead organic matter from dead roots and mycorrhizal fungi (but not slash) were factors responsible for the changes in *C. sphagnetorum* populations.

We hypothesised that the presence of EM fungi is a major factor in explaining these population changes following clear-cutting. Thus, *O. nova* should be favoured by the presence of specific EM fungi, while *C. sphagnetorum* should be suppressed by EM fungi but probably increase in treatments with the saprotrophic fungus. We also assumed that *T. velatus* and *N. silvestris*, which are non-specialist fungivores or microbi-detritivores, would show good survival and reproduction in the presence of high amounts of fungi and high amounts of organic matter rather than to selected species of soil fungi. These hypotheses were tested in pot microcosms with six different fungal species. Five of these species were EM fungi growing in symbiosis with their host tree and one was a saprotrophic fungus growing on wood. The EM species differed in morphology and types of potential defensive structures.

## 2. Materials and methods

### 2.1. Fungal isolates

Six basidiomycetous fungal species were used in the study, of which five were EM species: *Hebeloma velutipes* Bruchet (Isolate code UP184, GenBank Accession No. AF432845), *Paxillus involutus* Batsch (Fr.) (UP578, EF493246), *P. fallax* (Lib.) Stalpers (UP113, DQ179125), *Rhizopogon roseolus* (Corda) Th. Fr. (UP588, EF493255),

and *Suillus variegatus* (Sw.) Kuntze (UP597, EF493256). In the following text and tables, these species are abbreviated as Heb, Pax, Pil, Rhi, and Sui, respectively. In addition, one saprotrophic species, *Hypholoma capnoides* (Fr.) P. Kumm. (AJ236080, MMN 23805) (Hyp) was included. The isolates are kept at the Department of Forest Mycology and Pathology, Swedish University of Agricultural Sciences, Uppsala. The identity of these isolates was confirmed by Internal transcribed spacer (ITS) sequence analysis using standard techniques. DNA was extracted (Gardes et al., 1991) and polymerase chain reactions (PCR) were carried out using the primers ITS1 and ITS4 as described by White et al. (1990). The fungal cultures were maintained in darkness at 25 °C on half-strength modified Melin–Norkrans (MMN) medium (Marx, 1969).

The five EM species differ in morphology. *P. fallax* is a yellow mat-forming species and has rich ornamentation of both extraradical hyphae and mantle with needle-shaped crystals (Brand, 1991b). *H. velutipes* may have verrucose crustations on emanating hyphae and granular content in cells of the mantle (Haug, 2002). *S. variegatus*, *R. roseolus* and *P. involutus* are capable of producing abundant extraradical mycelium and extensive rhizomorph systems (Agerer, 2001). *S. variegatus* forms smooth to woolly mantles, and both hyphae and rhizomorphs may be rough of warts or sometimes crystals (Mleczo and Ronikier, 2007). *R. roseolus* forms a mantle, which loosely outer layer of hyphae are embedded in a gelatinous matrix and densely covered in crystals and soil particles (Raidl and Agerer, 1998). Emanating hyphae are also covered with warts and fine crystals. *P. involutus* forms abundant, somewhat rough but thin-walled emanating hyphae and have club-shaped cystidia on the mantle surface (Mleczo, 1997). All five species produce abundant emanating hyphae that could potentially serve as food for fungivores. *H. capnoides* is found growing on the ground, in mosses or on stumps, roots or debris (Hansen and Knudsen, 1992), and the hyphae are relatively smooth.

### 2.2. Mycorrhizal synthesis

A 1:4 mixture of peat and vermiculite was moistened with modified Melin–Norkrans (MMN) medium (360 mL L<sup>-1</sup> substrate, full-strength mineral nutrients and half-strength C) (Marx, 1969) and autoclaved. The mixture was placed in sterile Petri dishes that were cut with overlapping notches. Two *Pinus sylvestris* (L.) seedlings, germinated for four weeks on water agar, were placed in each Petri dish, with the shoot placed through the notch. Agar plugs from six-week-old EM fungal cultures were placed on the pine roots. The Petri dishes were sealed with Parafilm® and sterile anhydrous lanolin and covered with aluminium foil to protect the roots and mycorrhizas from light. Petri dishes were maintained vertically in a small plastic container in a plant growth facility at 14–16 °C during a 16 h photoperiod at a photon flux density of between 250 and 300 μmol mm<sup>-2</sup> s<sup>-1</sup> and 6–8 °C during the 8 h dark period. Non-mycorrhizal seedlings were treated in a similar way, but without added fungal inoculum.

### 2.3. Experimental system

The main experiment consisted of eight plant and fungal treatments: Scots pine seedlings colonised with one of five different EM fungi (Heb, Pax, Pil, Rhi and Sui), the wood-living fungus *H. capnoides* (Hyp) grown on a 5 × 2 × 0.5 cm piece of pine wood, Scots pine seedlings without inoculated mycorrhizal fungi (non-mycorrhizal control, NM), and Scots pine seedlings without inoculated mycorrhizal fungi in fresh mor humus (forest soil, FS). In all treatments except the FS treatment, pots (270 cm<sup>3</sup>) were filled with a 1:1 mixture of steam-treated peat and vermiculite. The peat–vermiculite mixture had not been autoclaved to avoid destruction of the peat structure. In the FS treatment, the pots (270 cm<sup>3</sup>) were filled with mor humus collected

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