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ORIGINAL PAPER

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# Vertical distribution of an ectomycorrhizal community in upper soil horizons of a young Norway spruce (*Picea abies* [L.] Karst.) stand of the Bavarian Limestone Alps

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**Abstract** The vertical niche differentiation of genera of ectomycorrhiza (ECM) was assessed in a 17-year-old Norway spruce (*Picea abies* [L.] Karst.) plantation on a mountainous dolomitic site (1,050 m above sea level) of the Bavarian Limestone Alps. We determined ECM anatomotypes, recorded the abundance of corresponding ECM root tips and classified them into groups of ECM exploration types, which refer to the organisation and the extent of their extramatrical mycelia. The abundance of ECM was highest in the organic soil layers, compared to the mineral soil horizon. The ordination of the ECM communities and of the exploration types revealed segregation related to soil horizon properties. While *Cenococcum geophilum* preferred the organic soil layers, *Lactarius* spp., *Tomentella* spp. and *Craterellus tubaeformis* were generally most abundant in the mineral soil horizons. *Cenococcum geophilum* was the predominant species, possibly based on enhanced competitiveness under the prevailing site conditions. The short-distance exploration types (e.g. *C. geophilum*) preferentially colonised the organic soil layer, whereas the contact types (e.g. most of the *Tomentella* spp., *C. tubaeformis*) together with medium-distance types (e.g. *Amphinema byssoides*) were primarily associated with the underlying A-horizons. Therefore, the soil horizons had an important effect on the distribution of ECM and on their community structure. The spatial niche differentiation of ECM genera and exploration types is discussed in regard to specific physicochemical properties of soil horizon and the assumed ecophysiological strategies of ECM.

**Keywords** *Picea abies* · Ectomycorrhizae · Exploration types · Limestone · Alps · Anatomotypes · Morphotypes

## Introduction

The mountainous vegetation belt of the Bavarian Limestone Alps is naturally covered by mixed Norway spruce (*Picea abies* [L.] Karst.), European beech (*Fagus sylvatica* L.) and Silver fir (*Abies alba* Mill.) forests, growing on moderately dry (*Aposerido-Fagetum caricetosum albae*) to moderately mesic sites (*Aposerido-Fagetum caricetosum ferrugineae*) (Ewald 1997). These virgin forests, rich in structure, are characterised by large amounts of dead and decayed wood on the forest floor and by organic residues that accumulate on the soil surface. Intensive silvicultural practices, in particular, clear-cutting for salt mines since the 15th century until the early 20th century, have led to a substantial loss of the organic matter due to mineralisation processes and erosion by snow gliding on these steep mountain slopes (Zierhut 2003; Bochter et al. 1981; Meister 1969). Accordingly, the forest harvesting practice resulted in a great shift of the humus forms, from thick mor (alpine raw humus) and thick moder in the virgin forests to thin mull humus forms on current woodless sites and in wide canopy openings with only sparse residual overstory trees (Meister 1969). Reforestation efforts on these sites have often been unsuccessful because the planted spruce shows low growth rates, especially when combined with insufficient nutrition, in particular, nitrogen, phosphorus and potassium (Baier 2004; Haupolter 1999).

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Organic matter plays an important role in nutrient cycling in ecosystems, mainly due to the decomposition capabilities of the ectomycorrhizae (ECM) (Read and Perez-Moreno 2003; Smith and Read 1997; Gadgil and Gadgil 1971). Several field studies have reported declines in ECM diversity after forest harvesting. The impacts of forest clear-cutting on ECM communities are related to loss of inoculation potential, decrease in inputs of carbon from host plants, distance to mature trees or a combination of these factors (Cline et al. 2005; Jones et al. 2003). Dickie et al. (2002) and Tedersoo et al. (2003) found markedly different fungal communities among litter, F-layer, H-layer and the B-horizon, indicating the importance of the specific edaphic environment for the ECM community structure. The extramatrical mycelia radiating into the soil act as a transport system and increase the exploited soil volume (Read et al. 2004; Smith and Read 1997; Brownlee et al. 1983; Duddridge et al. 1980).

The classification of ECM fungi into exploration types, which refer to the amount, organisation and extent of the extramatrical mycelia, is a new attempt to characterise the ecological relevance of ectomycorrhizal communities (Agerer 2001). Therefore, a spatial niche differentiation of ECM species and of ECM exploration types could be related to specific physico-chemical properties of soil horizon and to differential resource utilisation (Kuyper and Landeweert 2002). However, there are only a few investigations on ECM community composition and niche differentiation of ECM mycelium and its spatiotemporal structure in the forest soil (Landeweert et al. 2005; Izzo et al. 2005; Agerer and Göttlein 2003; Tedersoo et al. 2003; Agerer et al. 2002; Dickie et al. 2002).

The aims of our study were to assess (1) the vertical niche differentiation of ECM in the top soil horizons of a young Norway spruce plantation in a semi-natural forest stand on a dolomitic site of the Bavarian Limestone Alps, and (2) the separation of the ECM exploration types, which is assumed to be indicative of differential resource utilisation by ECM.

## Materials and methods

### Study site description

The study took place in a semi-natural forest of the Bavarian Limestone Alps (southern Germany, 47°48′00″N, 12°22′30″O) at 1,050 m above sea level. The site was selected based on unaltered moder humus forms and the presence of residual canopy trees. The forest was classified as an *Aposerido-Fagetum caricetosum albae* vegetation type (Ewald 1997) on a slope with a southern aspect, and the mature overstory was dominated by spruce and fir. The variously aged, 160- to 220-year-old stand with canopy openings was artificially regenerated with regularly planted (distance 1.5 m×1.5 m) Norway spruce (containerised plants, seeds originating from similar stands) in 1989. Soils derived from "Raibler dolomite" were eutric leptosols, rendzic leptosols and cromic cambisols, and had almost alkaline reactions in mineral horizons with pH–($H_2O$) ranging from 7.0 to 8.0 and slightly acidic reactions (pH 5.5 to 6.5) in the humus layers (Buol et al. 1997; Bayerisches Geologisches Landesamt 1967, 1981). The mean annual temperature and precipitation are 4.8°C and 1,900 mm, respectively (interpolated according to Enders 1979 and Fliri 1975), but dry periods during summer are frequent (Liu et al. 1994).

### Sampling and identification of ECM

Samples were taken from 24 randomly chosen spruce trees planted in 1989 within the representative plot area of 2,000 $m^2$. To avoid a possible influence of the seasonality of ECM (Sittig 1999), samples were taken at four times during the 2002 growing season (26 June, 3 August, 26 August, 9 October), each time from six different trees. Because the majority of the roots of individual naturally regenerated spruces on mountain slopes are located on the up-slope side (Lüscher 1990), we assumed the same for the planted trees on the plot. To obtain ECM samples representative for the major rooting zone, five soil cores (3.8 cm diameter, 20 cm depth) were taken on a half circle along the radius of the crown diameter on the uphill side of each tree. Samples were taken from the organic layer down to the mineral soil. The organic horizons F and H and the mineral A-horizon of each of the 120 soil cores (24 trees and 5 replicates per tree) were separated in the lab and replicates of horizons per tree were pooled. Four trees in the plot were growing on thick mor (alpine raw humus without an A-horizon) and therefore only the 68 remaining soil horizon samples (24 F, 24 H and 20 A) were stored in plastic bags at 5°C in the dark until processing. Cleaning was performed by soaking the samples in tap water (24 h, 5°C), followed by screening of roots of silver fir and ground vegetation based on distinct morphological features. Living root tips and ECM morphotypes of each subsample were isolated, categorised and separated based on their outer appearance (morphology), and their total abundance was determined with the aid of a dissecting microscope (Leica, Wild M5) (Agerer 1987,1991, 2002). A subsample of each ECM morphotype was fixed in a formaldehyde–ethanol–acetic acid solution as a voucher (comp. Appendix). For differentiation of the morphotypes into anatomotypes, mantle, hyphae and rhizomorph preparations were used to identify the ECM to genus or, if possible, to species level, using a light microscope (Leica, Dialux 22) (see also Agerer 1991). Subsequently, ECM were classified into exploration types (Agerer 2001, 2002). To evaluate the specific distribution of exploration types within soil horizons, genera with more than one species have been grouped by their genus, and others by species. Total finest root length (diameter <1.0 mm) was measured using the software package WinRhizo (version 4b, Regent Instruments, Canada). The total abundance (total number of living ECM per 100 $cm^3$ soil volume), the relative abundance (number of living ECM per meter of the finest root length) and the relative genus/species abundance in a specific soil horizon (proportion of ECM expressed as the percent of each genus/species per total number of living mycorrhizal root tips in the specific soil horizon) were recorded.

### Soil chemistry

Total element contents (C, N, P, Ca, Mg, K, Na, Fe, Mn, Cu and Zn) and pH-values ($H_2O$ and 1 m KCl) were analysed for each of the 68 horizon samples. C and N were analysed after complete oxidative burning with the LECO CHN-1000 analyser, other elements were measured after $HNO_3$ digestion on an inductively coupled plasma imaging electron spectrometer, Optima 3000 (Perkin Elmer) (BMELF 1990).

### Statistical analyses

For univariate analyses of soil horizon effects on abundance of ECM, ANOVA [Statistical Package of Social Sciences (SPSS) 11.5, SPSS) with a Tukey post hoc test was applied (Lozan and Kausch 2004). Relations between environmental variables and genus/species abundance of ECM fungi, and the effects of soil horizon on overall community structure, were analysed by means of multivariate ordination techniques (Jongman et al. 1995) using the PC-Ord4 software package for Windows (McCune et al. 2002). The original sample size of 68 was reduced to a 63-sample-size data set (22 F, 23 H, 18 A) after outlier analysis using the chemical properties of the horizons. A detrended correspondence analysis (DCA, Hill and Gauch 1980) on the relative abundance was used to show the separation of ECM taxa and the influence of edaphic variables. Soil chemical properties that were subjected to statistical analyses were pH (1 m KCl); total Ca, Mg, K, Mn, P and N; C:N ratio and total humus content. The separation of ECM exploration types, as indicative of a differential resource utilisation, was evaluated by principal component analysis (PCA).

## Results

### ECM community structure

Figure 1 shows, in descending order, the total abundance of the 15 identified ECM genera. With a proportion of 25%, *Cenococcum geophilum* Fr. was the dominant species regarding the total amount of ECM. *Cenococcum geophilum*, *Tomentella*, *Lactarius* and *Sebacina* (Urban et al. 2003) altogether represented 60% of all ECM within the plot. The genera *Dermocybe*, *Cortinarius* and both *Craterellus tubaeformis* (Bull.) Quél. and *Amphinema byssoides* (Pers.) J.Erikss. also had a high total abundance. In contrast, other genera, e.g. *Ramaria*, *Hebeloma*, *Tuber*, *Chroogomphus* and *Hydnellum*, were less numerous, as well as the group of individual indeterminates (indet types) within the site.

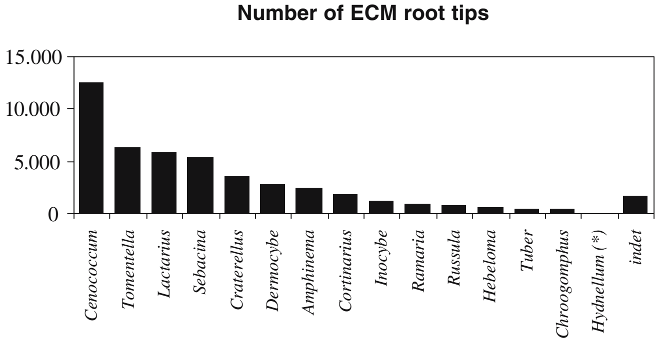


**Fig. 1** Abundance of ECM genera expressed as the total number of ECM root tips within the research site, i.e. from all 24 trees (* actual number of Hydnellum=38 ECM root tips; *indet* individual indeterminates)

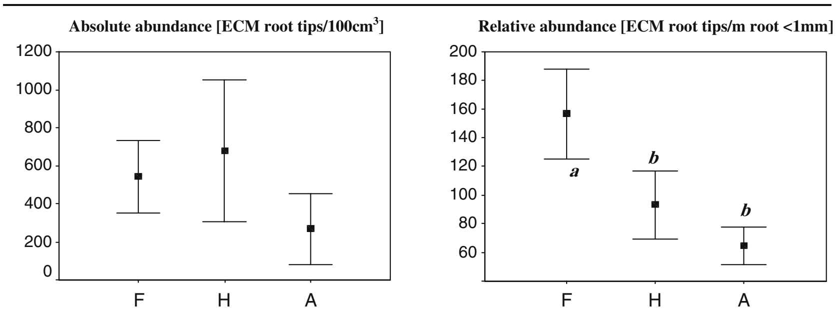
### Vertical distribution of mycorrhizae and exploration types

The absolute abundance of ECM in distinct soil horizons (Fig. 2, left) shows tendencies (not significant) of mycorrhizal root tips for preferential colonisation of the organic layers F and H. However, there was a significantly higher relative abundance in the F-layer than in H and A, and a higher colonisation of the roots in the H-horizon than in the A-horizon (Fig. 2, right).

The relative abundance of identified ECM genus or species (Fig. 3) per soil horizon showed the dominance of *C. geophilum*, which was distributed over all horizons and occurred twice as frequently in the organic F-layer compared to the mineral A-horizon. In contrast, *C. tubaeformis*, *Lactarius* and *Tomentella* were more abundant in the A-horizon.

The graphic overlay of the DCA (Fig. 4), depicting the different qualities of soil horizons on the community structure of ECM species/genera, resulted from the measured soil characteristics (e.g. pH values, nitrogen content). The coefficient of determination ($r^2$) for the correlations between ordination distances and distances in the original data set was 0.34 for axis 1 and 0.08 for axis 2. Thus, the quality of data reduction and the proportions of variance, explained by the two primary axes, were in the acceptable range for ecological studies. The first axis explains the highest proportion of variance in the data and is easiest to interpret. Humus content, C:N ratio and N content (Pearson's $r$ for axis 1=−0.45, −0.41 and −0.33, respectively) were the most important edaphic characteristics in the ordination. In contrast, Mg ($r$=0.22) was of minor relevance, as the other factors intervened. Pearson's $r$ for axis 1 was high for *Lactarius* (0.77), *Sebacina* (−0.71) and *C. geophilum* (−0.52), followed by *Inocybe* (0.28) and *Tomentella* (0.25). The species/genus–environment biplot showed that *C. geophilum* and *Sebacina* were arranged at the left of the origin of the ordination, correlating with

**Fig. 2** Absolute (*left*) and relative (*right*) abundance of mycorrhizal root tips in soil horizons of all trees studied (*different small letters in italics* indicate significant differences)



increasing humus and nitrogen content and higher C:N values, which are indicative of organic layer qualities. *Lactarius*, *Tomentella* and *C. tubaeformis* were clustered at the right side of the DCA, which is indicative of the dominant influence of increasing pH and K content in the mineral soil horizons derived from limestone. In contrast, the spreading of the genera along axis 2 of the DCA with only a low coefficient of determination shows no meaningful correlation with measured chemical soil properties.

Based on the ECM exploration type classification according to Agerer (2001), contact, short-distance and medium-distance types could be found. The classification of the 33 anatomotypes of the 15 genera into the exploration types, used for the PCA, is shown in Table 1. No long-distance type was recorded. The highly variable genus *Tomentella* formed all three exploration types, with the highest species number in the contact exploration type. *Craterellus tubaeformis* also contributed to the ECM contact type. The main proportion of the short-distance type was represented by *C. geophilum*, followed by *Sebacina*. *Dermocybe* and *A. byssoides* constitute most of the medium-distance ECM types (comp. Fig. 1), with *Lactarius* belonging to the smooth subtype of the medium-distance exploration type.

The PCA (Fig. 5) indicated a separation of the three exploration types, which resulted from differences in the soil properties. The first axis accounted for nearly 47% of the variation, whereas an additional 35% was explained by axis 2 (eigen-value 1.0). Based on an eigen-value of 1.4 for axis 1 and at least 1.0 for axis 2, we interpreted both axes of the PCA. As with the DCA, the overlay with the site variables humus content (*r* for axis 1=−0.42), C:N ratio (*r* for axis 1=−0.35) and N content (*r* for axis 1=−0.32) illustrated the increase of organic layers to the left side of the origin. On the other hand, Ca content (*r* for axis 1=0.36), pH value (*r* for axis 1=0.28) and Mn content (*r* for axis 1=0.26) to the right side are indicative for the mineral A-horizon. Subsequently, the PCA showed that short-distance exploration types favoured a soil environment rich in humus and with high N content, which is characteristic for organic layers. The contact and medium-distance types were associated with the underlying alkaline mineral A-horizons with increasing Ca and Mn due to mineral weathering. The spreading of the contact and the medium-

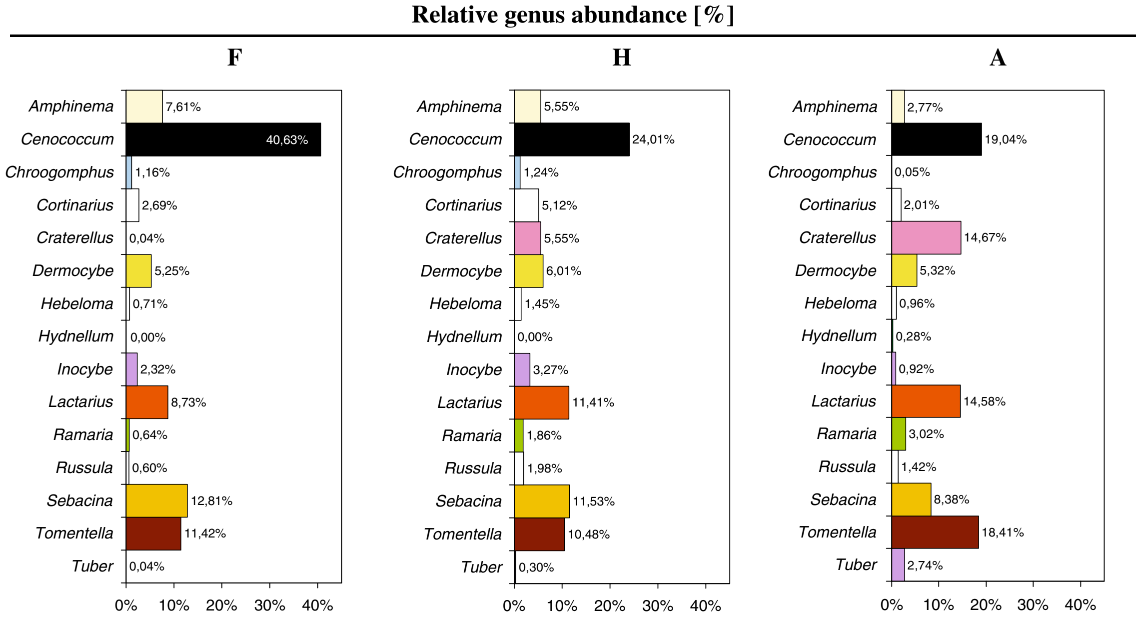


**Fig. 3** Relative genus abundance in the F-, H- and A-horizons [number of ECM of each genus/species per total number of living mycorrhizal root tips in the specific soil horizon (%)]

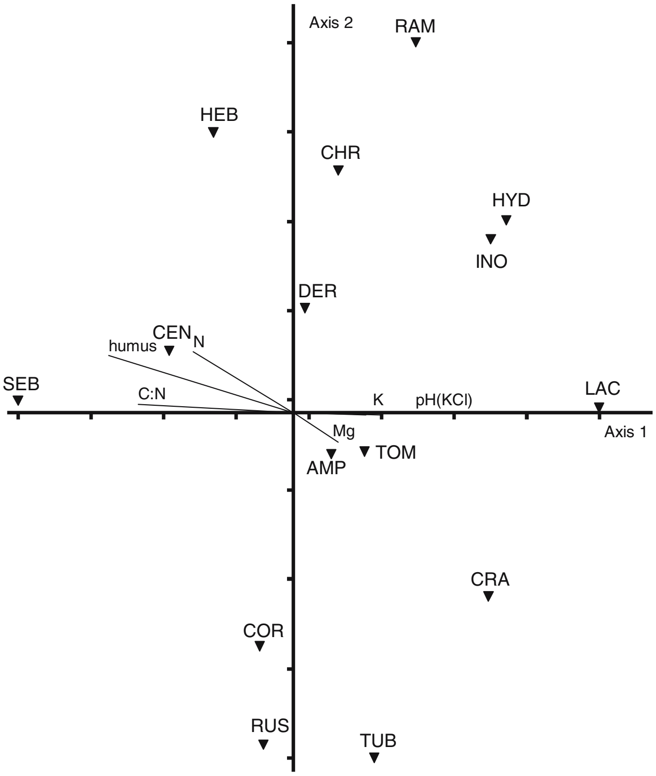


**Fig. 4** DCA ordination biplot of ECM communities and environmental factors (63 data sets, 15 genera and 9 variables)

distance types along axis 2 may be related to increasing P content ($r$ for axis 2=0.26) for the medium-distance types and increasing Ca content ($r$ for axis 2=−0.26) for the contact types.

## Discussion

As expected for the community structure and the abundance in soil horizons, only a few taxa represented the majority of all ECM within the site, and the ECM preferred the organic layers (Figs. 1 and 2). According to the vertical niche differentiation in soil horizons (Fig. 3), the ordination of the ECM communities and of the exploration types by DCA and PCA revealed segregation in dependency on differences in soil properties (Figs. 4 and 5).

The ECM abundance curve (Fig. 1), dominated by *C. geophilum*, *Tomentella*, *Lactarius* and *Sebacina*, and accompanied by a descending number of ECM of other taxa, showed a high similarity to those of other studies (e.g. Jonsson et al. 2000). It is typical for mycorrhizal community structures that a few dominant species contrast with a high number of rare ECM (Erland and Taylor 2002; Taylor 2002; Peter et al. 2001). Moreover, it has been shown in many studies comparing above- and below-ground ECM communities that ECM fungi not producing conspicuous sporocarps (e.g. *C. geophilum*, *Tomentella*) were predominant (Tedersoo et al. 2003; Horton and Bruns 2001; Peter et al. 2001; Fransson et al. 2000; Jonsson et al. 2000). The predominance of *C. geophilum* within the studied site is in accordance with the results of Göbl and Thurner (1996), who also recorded a very high percentage (63%) of *C. geophilum* ECM in alpine regions. *Cenococcum geophilum* appears to be very competitive under adverse alpine climates, due to active growth at low soil temperatures, drought tolerance, pioneering capabilities, persistence of sclerotia in the soil and, in addition, associations in alpine ecosystems with herbaceous plants as hosts, such as *Polygonum viviparum* (Cairney and Chambers 1999; Read 1995; Read and Haselwandter 1981; Vogt et al. 1981).

Most of the nutrients in the F and H humus layers are organically bound, and therefore, these upper soil horizons are considered as the most important sites of mineralisation processes and nitrogen mobilisation (Smith and Read 1997; Tamm 1991; Abuzinadah and Read 1989). The preference of mycorrhizal root tips for the organic layers is reflected by the highest absolute abundance in F- and H-layers compared to A-horizons and the significantly

**Table 1** Collected ECM genera and the corresponding anatomotypes, classified into their exploration types

| Contact | Short-distance | Medium-distance |
|---|---|---|
| *Chroogomphus helveticus* (CHR-01, -02) | *Cenococcum geophilum* (CEN-01) | Fringe subtype |
| *Chroogomphus* sp. (CHR-00) | *Hebeloma* sp. (HEB-01) | *Amphinema byssoides* (AMP-01) |
| *Craterellus tubaeformis* (CRA-01) | *Inocybe* sp. (INO-01) | *Cortinarius* sp. (COR-00) |
| *Russula* sp. (RUS-00) | *Inocybe* sp. (INO-02) | *Dermocybe* sp. (DER-00) |
| *Russula* cf. *densifolia* (RUS-01) | *Sebacina* sp. (SEB-01) | Mat subtype |
| *Russula* cf. *sanguinea* (RUS-02) | *Tomentella* sp. (TOM-05) | *Hydnellum* sp. (HYD-00) |
| *Russula* cf. *vinosa* (RUS-03) | *Tuber* sp. (TUB-00) | *Ramaria* sp. (RAM-00) |
| *Tomentella* sp. (TOM-00) | *Tuber* cf. *borchii* (TUB-01) | Smooth subtype |
| *Tomentella* cf. *pilosa* (TOM-01) | *Tuber* cf. *melanosporum* (TUB-02) | *Lactarius* sp (LAC-00) |
| *Tomentella* sp. (TOM-02) | | *Lactarius* sp. (LAC-02) |
| *Tomentella* sp. (TOM-03) | | *Lactarius deterrimus* (LAC-01) |
| *Tomentella* sp. (TOM-04) | | *Tomentella* sp. (TOM-06) |
| *Tomentella* sp. (TOM-07) | | |
| *Tomentella* sp. (TOM-08) | | |
| *Tomentella* sp. (TOM-09) | | |

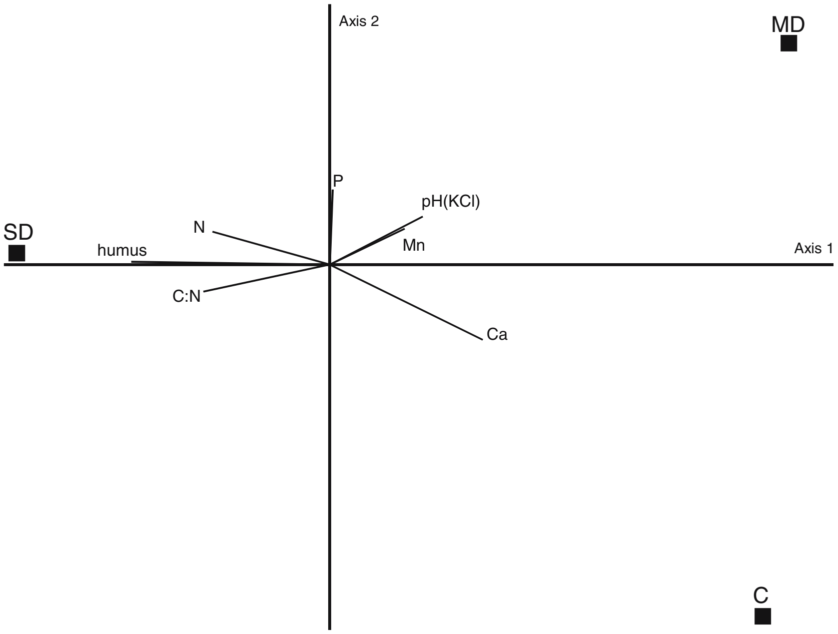


**Fig. 5** PCA of the exploration types and the overlay of site variables (63 data sets, 9 variables; *SD* short-distance type, *MD* medium-distance type, *C* contact type)

increased relative abundance in the F-layer (Fig. 2). On a comparable alkaline dolomitic site, Sandhage-Hofmann (1993) found the highest fine root density of Norway spruce in the organic layer, explained by more efficient nutrient acquisition, specifically for potassium, due to lower ion antagonism with calcium and/or magnesium in acidified organic layers. Hence, our results are consistent with other studies reporting the majority of the ECM fungi in the organic layers (e.g. Read and Perez-Moreno 2003; Dahlberg 2001).

The separation of some ECM genera along gradients of soil properties was shown by DCA ordination (Fig. 4). *Cenococcum geophilum* and *Sebacina* spp. can apparently cope well with high humus contents and large C:N ratios. The fact that *C. geophilum* prefers organic layers and/or A-horizons enriched with organic compounds has also been shown by other studies (Fransson et al. 2000; Ponge 1990; Kottke and Oberwinkler 1988; Vogt et al. 1981). *Cenococcum geophilum* possibly preferentially colonises the F-horizon due to its ability to tolerate changing environmental conditions better than other species, because the F-layer is subject to the highest fluctuations of soil temperature and moisture. Drier conditions, which are frequent on the southern exposure slope, have already been shown to positively influence the abundance of black ECM (e.g. *C. geophilum*) (Kårén et al. 1996; Pigott 1982; Worley and Hacskaylo 1959). Another reason for the preference of organic layers could be a potentially higher ligninolytic capacity of *C. geophilum* in comparison to other ectomycorrhizal fungi (Bending and Read 1997) or its higher dependence on nitrogen nutrition for growth (Eaton and Ayres 2002). In contrast, the genera *Craterellus*, *Lactarius* and *Tomentella* showed the highest frequency in mineral A-horizon (Figs. 3 and 4), characterised by a higher, basic pH. Apparently, the genus *Lactarius* is not very tolerant to water stress (Cairney and Chambers 1999). Therefore, ECM formed by *Lactarius* might profit from a higher and more constant moisture level in mineral A-horizons. It is interesting to note that *Lactarius* respiration activity in a beech stand was altered more by low water potential than that of *C. geophilum*, indicating that *Lactarius* ECM on beech is less tolerant for drought stress than *C. geophilum* (Jany et al. 2003). A member of *Tomentella* sp. was favoured after liming a Norway spruce stand (Brand et al. 1992). Therefore, some species of *Tomentella* prefer possibly high pH-values and base saturation. In conclusion, the ordination of ECM genera with DCA indicated that the different soil horizons had the most pronounced effect on the ECM community structure, probably due to chemical and/or physical properties. Accordingly, Tedersoo et al. (2003) and Dickie et al. (2002) demonstrated the preference of ECM fungi for different substrate qualities, organic layers and mineral soil horizons.

The spatial niche differentiation may also be related to differential resource utilisation by ECM (Kuyper and Landeweert 2002). Agerer and Göttlein (2003) have recently shown that differences in small-scale distribution of ECM genera might be correlated with various functions to make different nutrient sources accessible. The ability of ECM fungi to capture and transport nutrients and the extent of depletion, e.g. for nitrogen, phosphorus and potassium, differs between fungal symbionts due to various specific enzymes (Read and Perez-Moreno 2003). In addition, the shape of ECM with, for example, emanating hyphae and/or rhizomorphs, which were used to classify ECM into the exploration types (Agerer 2001), may represent distinct ecophysiological strategies, especially for nutrient exploitation.

The first axis of the PCA (Fig. 5) appeared to be associated with differences between distinct soil horizons. It was notable that contact types (e.g. most of the *Tomentella* species, *C. tubaeformis*) and medium-distance types (e.g. *A. byssoides*) were associated with soil properties indicative for mineral A-horizons. The contact types with a smooth mantle and only a few emanating hyphae (e.g. some *Tomentella* species, *C. tubaeformis*) are typically sandwiched between the surrounding substrates, and therefore, well equipped to explore dense soil horizons with narrow pores (Agerer 2001). This might explain their preference for the mineral soil horizon with a higher bulk density than organic layers. In addition, the A-horizon on calcareous soils is characterised by hardly degradable organic matter, stabilised in calcium–magnesium–humic compounds (Scheffer-Schachtschabel 2002). Contact types might be able to utilise these sources because they are often hydrophilic and are possibly able to degrade lignin to increase access to nitrogen complexed to phenolic substances (Agerer 2001; Agerer et al. 2000). ECM formed by *Lactarius* belong to the smooth subtype of the medium-distance exploration type, almost lacking emanating hyphae and with a few, mostly undifferentiated rhizomorphs that grow frequently in close contact with the substrate. Hence, the same might also be true for the predominantly occurring *L. deterrimus* as the major representative of the medium-distance smooth subtype. *Lactarius* species reveal a potential ligninolytic capacity (Agerer et al. 2000). This might be the reason for their predominant occurrence in A-horizons with stable humic nitrogen compounds (Haselwandter et al. 1990; Trojanowski et al. 1984). Another important source for organic nitrogen in mineral soils and a main fraction in the nitrogen cycle is dissolved organic nitrogen (DON) (Hedin et al. 1995). Katzensteiner (2003) found DON as the dominant N fraction in percolates of mature and regeneration stands on comparable sites in the Northern Limestone Alps (Austria). Therefore, it is possible that contact and medium-distance types utilise DON of the slow percolating humus outflow in the narrow pores of the underlying A-horizon as an additional nitrogen source. The concentration of *Russula* and *Lactarius*, mostly forming contact and medium-distance smooth subtype ECMs (Agerer 2001), in the humic mineral A-horizon has already been mentioned by Brand (1991).

In contrast, the PCA ordination revealed that the short-distance types (e.g. *C. geophilum*, *Sebacina* sp.) preferred the organic layer. Short-distance types are characterised by a dense cover of emanating hyphae (Agerer 2001). Hence, they are very suitable to grow and make multiple contacts with the loose organic material in upper organic layers. The fresh organic residues accumulated in the organic layer are characterised by the highest N contents within soil horizons (Marschner 1995). As mentioned previously, *C. geophilum* also possesses proteolytic enzymes to mobilise organically bounded nitrogen (Dahlberg et al. 1997) and is rather N-dependent for growth (Eaton and Ayres 2002).

As mentioned in the introduction, the impacts of clear-cutting on mycorrhizal communities are varied (Cline et al. 2005; Jones et al. 2003), but it appears likely that a shift in humus forms induced by clear-cuttings would have long lasting impacts on ECM community structure. The loss of specific ECM due to changing humus forms could have important functional consequences, not just for the host plants but for the ecosystem as a whole, due to an altered ability of nutrient release by ECM. High ECM diversity has been proposed to increase plant productivity (Read and Perez-Moreno 2003; van der Heijden and Sanders 2002). Additional to the decrease in ECM diversity after clear-cuts (Cline et al. 2005) and the impaired nutrient availability in the remaining alkaline A-horizon (Baier 2004), the shift in humus forms with an altered ECM community on reforestation sites might explain the failure of artificial plantations of spruce.

This study was a first attempt to use the exploration type classification as an indication of differential resource utilisation. Therefore, investigation of the relevance of exploration types and their vertical distribution in pure organic humus layers over solid limestone with high gradients of different nitrogen forms (organically bound vs dissolved) on various data sets should be a focus of future studies. Such an approach is necessary to complement detailed studies of ECM community composition and the structure of ECM groups varying in resource requirement.

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## Appendix

### Ectomycorrhizal material

The isolated ECM are kept as voucher specimens in M (Holmgren et al. 1990): Germany, Bayern, Marquartstein, Rottauer Alm 47°48′00″N, 12°22′30″E, 1,050 m above sea level.

*Amphinema byssoides* (Pers.) J.Erikss. AMP-01: JI 154, leg. 09.10.02—JI 226, leg. 09.10.02—JI 074, leg. 03.08.02—JI 119, leg. 26.08.02—JI 103, leg. 26.08.02—JI 105, leg. 26.08.02—JI 064, leg. 03.08.02—JI 085, leg. 03.08.02—JI 245, leg. 09.10.02—JI 203, leg. 09.10.02—JI 127, leg. 26.08.02—JI 264, leg. 09.10.02.—*Cenococcum geophilum* Fr. CEN-01: JI 076, leg. 03.08.02—JI 082, eg. 03.08.02—JI 091, leg. 26.08.02—JI 065, leg. 03.08.02—JI 02, leg. 26.06.02.—*Chroogomphus* sp. CHR-00: JI 059, leg. 03.08.02—JI 057, leg. 03.08.02.—*Chroogomphus helveticus* (Singer) Moser CHR-01: JI 050, leg. 03.08.02—JI 220, leg. 09.10.02—JI 222, leg. 09.10.02.—*Chroogomphus helveticus* CHR-02: JI 081, leg. 03.08.02—JI 051, leg. 03.08.02—JI 258, leg. 09.10.02—JI 169, leg. 09.10.02—JI 093, leg. 26.08.02—JI 111, leg. 26.08.02.—*Cortinarius* sp. COR-00: JI 040, leg. 03.08.02—JI 078, leg. 03.08.02—JI 185, leg. 09.10.02—JI 187, leg. 09.10.02—JI 190, leg. 09.10.02—JI 276, leg. 09.10.02—JI 171, leg. 09.10.02—JI 174, leg. 09.10.02—JI 098, leg. 26.08.02—JI 107, leg. 26.08.02—JI 133, leg. 26.08.02—JI 136, leg. 26.08.02—JI 121, leg. 26.08.02—JI 196, leg. 09.10.02.—*Craterellus tubaeformis* (Bull.)Quél. CRA-01: JI 255, leg. 09.10.02 —JI 173, leg. 09.10.02—JI 210, leg. 09.10.02—JI 215, leg. 09.10.02—JI

219, leg. 09.10.02.—*Dermocybe* sp. DER-00: JI 253, leg. 09.10.02—JI 227, leg. 09.10.02—JI 228, leg. 09.10.02—JI 233, leg. 09.10.02—JI 237, leg. 09.10.02—JI 238, leg. 09.10.02—JI 240, leg. 09.10.02—JI 241, leg. 09.10.02—JI 118, leg. 26.08.02—JI 080, leg. 03.08.02—JI 049, leg. 03.08.02—JI 259, leg. 09.10.02—JI 162, leg. 09.10.02—JI 184, leg. 09.10.02—JI 186, leg. 09.10.02—JI 189, leg. 09.10.02—JI 256, leg. 09.10.02—JI 275, leg. 09.10.02—JI 170, leg. 09.10.02—JI 211, leg. 09.10.02—JI 212, leg. 09.10.02—JI 216, leg. 09.10.02—JI 095, leg. 26.08.02—JI 140, leg. 26.08.02—JI 100, leg. 26.08.02—JI 131, leg. 26.08.02—JI 132, leg. 26.08.02—JI 135, leg. 26.08.02—JI 272, leg. 09.10.02—JI 181, leg. 09.10.02—JI 110, leg. 26.08.02—JI 125, leg. 26.08.02—JI 126, leg. 26.08.02—JI 054, leg. 03.08.02—JI 055, leg. 03.08.02—JI 069, leg. 03.08.02—JI 159, leg. 09.10.02—JI 265, leg. 09.10.02—JI 267, leg. 09.10.02.—*Hebeloma* sp. HEB-00: JI 073, leg. 03.08.02—JI 043, leg. 03.08.02—JI 045, leg. 03.08.02—JI 047, leg. 03.08.02—JI 117, leg. 26.08.02—JI 262, leg. 09.10.02—JI 053, leg. 03.08.02—JI 038, leg. 03.08.02—JI 161, leg. 09.10.02—JI 194, leg. 09.10.02 —*Hydnellum* sp. HYD-00 *Inocybe* sp. INO-01: JI 052, leg. 03.08.02—JI 163, leg. 09.10.02—JI 099, leg. 26.08.02—JI 088, leg. 03.08.02—JI 152, leg. 09.10.02—JI 204, leg. 09.10.02—JI 207, leg. 09.10.02.—*Inocybe sp*. INO-02: JI 179, leg. 09.10.02—JI 246, leg. 09.10.02.—*Lactarius* sp. LAC-00: JI 153, leg. 09.10.02—JI 188, leg. 09.10.02—JI 198, leg. 09.10.02—JI 150, leg. 09.10.02—JI 122, leg. 26.08.02—JI 130, leg. 26.08.02—JI 063, leg. 03.08.02.—*Lactarius deterrimus* Gröger LAC-01: JI 141b, leg. 26.08.02—JI 183, leg. 09.10.02—JI 067, leg. 03.08.02—JI 060, leg. 03.08.02—JI 083, leg. 03.08.02—JI 250, leg. 09.10.02—JI 200, leg. 09.10.02—JI 208, leg. 09.10.02—JI 034, leg. 03.08.02—JI 035, leg. 03.08.02—JI 039, leg. 03.08.02.—*Lactarius* sp. LAC-02: JI 257, leg. 09.10.02—JI 273, leg. 09.10.02—JI 269, leg. 09.10.02—JI 270, leg. 09.10.02.—*Ramaria* sp. RAM-00: JI 271, leg. 09.10.02—JI 178, leg. 09.10.02—JI 113, leg. 26.08.02—JI 056, leg. 03.08.02—JI 036, leg. 03.08.02.—*Russula* sp. RUS-00: JI 180, leg. 09.10.02.—*Russula* cf. *densifolia* Secr. ex Gillet RUS-01: JI 124, leg. 26.08.02—JI 037, leg. 03.08.02—JI 032, leg. 26.06.02.—*Russula* cf. *sanguinea* (Bull.)Fr. RUS-02: JI 172, leg. 09.10.02.—*Russula* cf. *vinosa* Lindblad RUS-03: JI 086, leg. 03.08.02.—*Sebacina* sp. SEB-01 *Tomentella* sp. TOM-00: JI 145, leg. 26.08.02—JI 149, leg. 26.08.02—JI 089, leg. 03.08.02—JI 202, leg. 09.10.02—JI 025, leg. 26.06.02—JI 023, leg. 26.06.02.—*Tomentella* cf. *pilosa* (Burt)Bourd. &Galz.TOM-01: JI 155, leg. 09.10.02—JI 230, leg. 09.10.02—JI 232, leg. 09.10.02—JI 070, leg. 03.08.02—JI 071, leg. 03.08.02—JI 079, leg. 03.08.02—JI 066, leg. 03.08.02—JI 244, leg. 09.10.02—JI 248, leg. 09.10.02—JI 151, leg. 09.10.02—JI 209, leg. 09.10.02—JI 112, leg. 26.08.02.—*Tomentella* sp. TOM-02: JI 260, leg. 09.10.02—JI 144, leg. 26.08.02—JI 143, leg. 26.08.02.—*Tomentella* sp. TOM-03: JI 168, leg. 09.10.02—JI 166, leg. 09.10.02—JI 213, leg. 09.10.02—JI 217, leg. 09.10.02—JI 224, leg. 09.10.02.—*Tomentella* sp. TOM-04: JI 129, leg. 26.08.02.—*Tomentella* sp. TOM-05: JI 148, leg. 26.08.02—JI 142, leg. 26.08.02—JI 139, leg. 26.08.02—JI 084, leg. 03.08.02—JI 263, leg. 09.10.02.—*Tomentella* sp. TOM-06: JI 242, leg. 09.10.02—JI 223, leg. 09.10.02—JI 225, leg. 09.10.02—JI 243, leg. 09.10.02—JI 205, leg. 09.10.02—JI 193, leg. 09.10.02—JI 197a, leg. 09.10.02—JI 197b, leg. 09.10.02.—*Tomentella* sp. TOM-07: JI 234, leg. 09.10.02—JI 191, leg. 09.10.02—JI 274, leg. 09.10.02—JI 251, leg. 09.10.02.—*Tomentella* sp. TOM-08: JI 206, leg. 09.10.02—JI 160, leg. 09.10.02.—*Tomentella* sp. TOM-09: JI 077, leg. 03.08.02—JI 148b, leg. 26.08.02—JI 261, leg. 09.10.02—JI 094, leg. 26.08.02—JI 138, leg. 26.08.02—JI 102, leg. 26.08.02—JI 109, leg. 26.08.02—JI 137, leg. 26.08.02—JI 114, leg. 26.08.02—JI 128, leg. 26.08.02—JI 068, leg. 03.08.02—JI 195, leg. 09.10.02.—*Tuber* sp. TUB-00: JI 247, 09.10.02.—*Tuber* cf. *borchii* Vittad. TUB-01: JI 249, 09.10.02—JI 199, 09.10.02—JI 123, 26.08.02.—*Tuber* cf. *melanosporum* Vittad. TUB-02: JI 041, 03.08.02.

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