Diversity of macrofungi and plants in Scots pine forests along an urban pollution gradient

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Abstract

Fungal and plant community structures were studied in mature Scots pine stands along an urban pollution gradient with four zones of pollution intensity around the city of Oulu, northern Finland. For fungi sporocarp inventories and characterization of ectomycorrhizal (ECM) morphotypes were used and for plants coverage analyses were made. Significant differences were found in community structure of macrofungi and plants along the gradient. The number of ECM species and their sporocarp production, especially those of Cortinarius spp., diminished towards the emission sources, whereas the fruiting of saprotrophic fungi increased close to the emission sources. Eight fruiting macrofungal species reflected the differences between the pollution zones. The species decreasing towards the emission sources were almost all ectomycorrhizal (Chroogomphus rutilus, Cortinarius anomalus, C. brunneus, C. gentilis, C. semisanguineus, Suillus variegatus), with only one species, Cantharellula umbonata considered as saprotrophic. In contrast, ectomycorrhizal Paxillus involutus proved to be pollution-tolerant. The diversity of ECM species was lowest at the most polluted zone while the diversity of plant species increased towards the emission sources. The diversity among ECM morphotypes and saprotrophic species did not differ between the zones. Close to the emission sources slowly growing plant species were displaced by species typical for more nutrient-rich forests, herbs and grasses being more abundant while the number of bryophyte species diminished and lichens were absent. The observed differences in fungal and plant communities are suggested to be results of long-term nitrogen-mediated changes and they support the hypothesis that nitrogen inputs lead to loss of fruiting ECM species.


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Introduction

The productivity of many northern ecosystems is limited by the supply of biologically available nitrogen. On the other hand, in many urban areas emissions of nitrogen from anthropogenic sources exceed natural inputs. Elevated N availability increases productivity and biomass accumulation (Tilman 1996), but generally reduces the biological diversity of ecosystems (Tilman 1987, Vitousek et al. 1997). The increase of limiting nutrients can drastically change species dominance in ecosystems (e.g. Vitousek et al. 1997, Wallenda & Kottke 1998, Lilleskov et al. 2001). Thus, the rises and the falls in diversity vary between different types of organisms (Gehring et al. 1998) depending on the sensitivity of the species for example to atmospheric ammonia (Fangmeier et al. 1994) and their capacity to compete under changed nutrient conditions (Kaye & Hart 1997).

Nitrogen deposition in the coniferous forests of Europe has generally been reported to decrease the number of ectomycorrhizal (ECM) species and the sporocarp production of ectomycorrhizal fungi (e.g. Ohenoja 1988, Brandrud 1995, Kärén & Nylund 1997). However, the main effect of N deposition has supposed to be on the relative abundance of ECM species rather than on the number of all ECM species (Kärén & Nylund 1997, Brandrud & Timmermann 1998).

Resource allocation into the production of sporocarps, mycorrhiza and/or mycelia varies among ECM species (Gardes & Bruns 1996). According to Wallenda & Kottke (1998) the ECM fungi, which are less affected by increased N availability, are ‘generalist’ species, forming a symbiosis with a wide range of tree species. On the other hand, excess nitrogen tends to have less harmful effect on the sporocarp production of saprotrophic than on that of ECM fungi (Ohenoja 1994, Peter et al. 2001).

Nitrogen enrichment can be expected to favour plants with high relative growth rates, which thus increase in abundance leading to the decline of slow-growing species and thus decreasing species diversity (Tilman 1996). However, the type of mycorrhiza (Allen et al. 1995) may regulate the diversity of plant species. In grasslands, mycorrhizal fungi have been found to affect plant communities indirectly by influencing the pattern and strength of plant competitive interactions (Smith et al. 1999). One would expect that by following succession plant species that benefit most from mycorrhizal symbiosis and their fungal associates would be at a selective advantage, and come to predominate in the plant community (Johnson et al. 1997, Hartnett & Wilson 1999).

Scots pine forests on anthropogenic pollution gradient around the industrialized city of Oulu, northern Finland, have been studied since 1987. The gradient is formed by emissions originating from pulp mills and a fertilizer factory, heating and traffic. The project has included studies on ECM symbiosis, soil fauna, the amount and activity of soil microorganisms and certain physicochemical parameters of the forest humus layer (e.g. Markkola & Ohtonen 1988, Ohtonen & Markkola 1989, Ohtonen et al. 1990, 1992, Ohtonen 1994, Markkola et al. 1995). According to the earlier studies the thickness of forest humus layer, total N, total S and heavy metal concentration in the forest humus layer increased towards the emission sources whereas C/N ratio and soil respiration rate decreased (Ohtonen & Markkola 1989, Ohtonen et al. 1990, Ohtonen 1994). The objectives of the present study were to determine whether there are differences in the fungal and plant community structures in Scots pine...
forests along this gradient. It was hypothesized that 1) the species richness and diversity of ECM fungi decreases along the pollution gradient, and 2) plant species with high growth rates become more abundant.

Materials and Methods

Study area

The study area is located in the middle boreal vegetation zone (Ahti et al. 1968) around the city of Oulu in northern Finland (65°00'N, 25°30'E). The area is characterized by nutrient-poor mineral soil. The study sites were chosen in dry-dryish pine stands in different pollution zones determined by reference to the sulfur concentration in the pine needles – zone I: not measured, zone II: <1100, zone III: 1100–1300, and in the zone IV: >1300 µg g⁻¹ (Karhu 1986). The outermost zone I, was located 25–40 km from the emission sources; zone II, 10–25 km; zone III, 2–10 km and zone IV, 0.5–2 km from the emission sources (Fig. 1). Totally 20 study sites were chosen in mature Scots pine stands in terms of similarity in vegetation, stand properties and pH of the forest humus layer, five sites per zone.

The principal emissions in the area have decreased during the last decade. The NOₓ emissions have decreased to one third, while SO₂ emissions have decreased to half of the level in the late 1980s (Fig. 2; Anonymous 2001). The mean (1982–1990) wet deposition of SO₄-S was 13.1 kg ha⁻¹ year⁻¹ in zone IV and 6.2 kg ha⁻¹ year⁻¹, while deposition of NO₃-N was 2.3 kg ha⁻¹ year⁻¹ in the zone IV and 1.4 kg ha⁻¹ year⁻¹ in zone III (Anonymous 1991). The wet deposition in 2000 in Oulu municipality was 3.0 kg SO₄-S ha⁻¹ year⁻¹ and 1.6 kg NO₃-N ha⁻¹ year⁻¹ (Anonymous 2001). The wet deposition data is not available for zones I and II.

Nitrogen concentration in forest humus layer was 14.4, 16.5, 19.1 and 20.3 mg g⁻¹ OM, and S concentration in forest humus layer was 2.12, 2.61, 3.08 and 3.58 µg g⁻¹ OM in zones I, II, III and IV, respectively (Markkola et al. 1995). To check whether there still exists the observed N gradient in the forest humus layer one soil sample (seven soil cores 3 cm in diameter) per site were taken from the zones I and IV in November 2000 for analyzing the thickness of the forest humus layer, pH, total and ammonium-nitrogen.

Fungal species composition and ECM morphotypes

Species composition of macrofungi (excluding the wood-dwelling Aphyllophorales) were inventoried at each site within a 50-m radius once in 1987, four times in each year 1988, 1989 and 1990, and once again in 1997. The fungal species were divided into taxonomic and ecological (ectomycorrhizal, saprotrophic and parasitic) groups (Hansen & Knudsen 1992). The sporocarp production was studied by collecting the sporocarps of ECM and saprotrophic fungi along a 50 m² transect (25 m × 2 m) in the middle of the study circle, one per site, identified to species, group or genus level, and the number of sporocarps were counted. The surveys were made twice in September 1988 and twice in both August and September in 1989 and 1990.

Fig. 1. The Oulu district was divided into four zones according to the sulphur concentration of the Scots pine needles in 1984, which was in the zone I: not measured, zone II: <1100, zone III: 1100–1300, and in the zone IV: >1300 µg g⁻¹ (Karhu 1986). a) The study site location in the zones. b) Mean wind directions 1987–2000 (Anonymous 2001).
Morphotypes of ectomycorrhizas were characterized in September 1987 from Scots pine root samples (five per site) taken with a soil corer (3 cm in diameter) from the total depth of the forest humus layer at random points on a circle within a radius of 5 m from the mid-point of the site. The mean depth of the forest humus layer (SD in parentheses) was 3.8 (1.0), 4.4 (0.5), 6.6 (2.2) and 7.1 (0.6) cm in zones I–IV, respectively (Markkola et al. 1995). The morphotyping of ECM roots of pine was done under a stereomicroscope, and the types were divided into 18 different groups by colour of the mantle, type of ramification and hyphal connections (Markkola & Ohtonen 1988, Ohtonen et al. 1990).

Plant cover

Cover values of higher plants, bryophytes and lichens were estimated from ten randomly selected 1 m² quadrates per site in June–August 1989 using a percentage scale of + (transformed to value 0.25 for computation), 0.5, 1, 2, 3, 4, 5, 10, 15, 20, ..., (5% intervals), 100. The means for each site were calculated and for data analysis the plants were divided into six groups, i.e. bryophytes, lichens, herbs, grasses, shrubs and tree saplings (height <2 m).

Diversity indices

Diversity of fungal and plant communities were analysed using two indices (Hubálek 2000): 1) species richness ($S$) as the total number of species in a study site, and 2) the reciprocal (1/$D$) of Simpson's lambda $D = \sum(p_i)^2$, where $p_i$ is the proportion of species $i$ of the total number of sporocarps of all fungal species in the 50 m² transects, or mean coverage of each plant species as a proportion of all plant species in the study site. The indices were also calculated for ECM and saprotrophic fungi separately, and the ECM morphotypes in Scots pine fine roots.

Statistics

We tested all dependent variables for normality of distribution (Shapiro-Wilk's test) and homogeneity of variances (Levene's test). Transformations were made to normalize the distribution of the reciprocal Simpson's indices. One-way ANOVA or Kruskal-Wallis test were employed to test whether the variables differed between the zones. Pair-wise comparisons between zones were made using Tukey's or Bonferroni test. Comparison of the present data with soil parameters (data published by Ohtonen et al. 1989, 1990, Markkola et al. 1995) was made using the components of a principal component analysis with quartimax/varimax rotation and Pearson's correlation. Principal component analysis (PCA) was used for grouping variables, since most soil parameters were intercorrelated. Quartimax rotation with Kaiser normalization was used to gain the best result. SPSS 10.1 for Windows 1998 was used for statistical analysis chosen according to Sokal & Rohlf (1995) and Tabachnick & Fidell (1996).

Indicator species analysis (Dufréne & Legendre 1997) was made to find the species that would reflect the differences along the gradient. Indicator values for fungal species collected from the 50 m² transects in 1988–1990 were calculated using PC-ORD for Windows 1997. The significance of the observed maximum indicator value for species was tested by Monte Carlo test (1000 permutations). The mean cumulative fruiting was calculated for the indicator species found in the analysis.

Results

Fungal community

The fungal diversity recorded in 1987–1990 at forest sites (50 m radius) consisted of 168 taxa, most of them being Basidiomycetes. Most species belonged to the Agaricales (68% of the total number of species), followed by Boletales (11%) and Russulales (11%). Aphyllophorales were represented by 4%, and the rest of the species were Lycoperdales (2%) and Ascomycota (2%). The identified species were placed into three main ecological groups: ectomycorrhizal (97 species), saprotrophic (72 species) and facultatively parasitic (Galerina sp., Lyophyllum sp., Armillaria sp.).

![Fig. 2. Emissions of NO, and SO₂ in the years 1987–2000 in most polluted zone IV, Oulu municipal, Finland (Anonymous 2001).](image-url)
1997, we found 25 additional species (13 ectomycorrhizal and 12 saprotrophic), which were not fruiting during the earlier inventories. Almost all new species in 1997 were found in the most polluted zone IV, ten new ectomycorrhizal and all new saprotrophic species. The species richness of ECM fungi in transects differed significantly between the zones ($F_{3,16} = 20.9$, $p < 0.000$), being higher in the less polluted zones I and II than in the more polluted zones III and IV in pair-wise comparisons (Fig. 3a). There were no significant differences between the zones in the numbers of the saprotrophic species ($F_{3,16} = 1.8$, $p = 0.182$, Fig. 3a). If all species recorded within a 50-m-radius were taken into consideration, the differences in species richness between the zones remained similar to those obtained in the transects in either ecological group ($F_{3,16} = 12.5$, $p = 0.001$; $F_{3,16} = 2.3$, $p = 0.121$, respectively). The reciprocal of Simpson’s diversity index for all fungal species and fruiting ECM species in transects was lowest in the most polluted zone (Table 1). In pair-wise comparisons, the zone IV differed significantly from other zones when comparison was made using index values consisting of all fungal species. The difference in index values for ECM species was significant only between the zones II and IV. The reciprocal of Simpson’s index for fruiting saprotrophic species and ECM morphotypes did not differ significantly.

Only one fungal species, *Lactarius rufus* (Scop.: Fr.) Fr., was found at all twenty sites. The sporocarp production of *L. rufus* was slightly, but not significantly, increasing towards the emission sources. In the indicator species analysis we found 14 species, which were most abundant at either end of the gradient. Number of sporocarps of eight of them (Fig. 4) differed significantly between the zones in the Kruskal-Wallis analysis. The sporocarp production of the ECM species *Chroogomphus rutilus* (Schaeff.: Fr.) O.K. Mill. (H$_3 = 9.3$, $p = 0.025$), Cortinarius anomalus (Fr.: Fr.) Fr. (H$_3 = 8.2$, $p = 0.042$), *C. brunneus* (Pers.: Fr.) Fr. (H$_3 = 15.3$, $p = 0.002$), *C. gentilis* (Fr.) Fr. (H$_3 = 10.5$, $p = 0.005$), *C. semisanguineus* (Fr.) Gillet (H$_3 = 8.6$, $p = 0.035$) and *Suillus variegatus* (Sw.: Fr.) Kuntze (H$_3 = 12.9$, $p = 0.005$) and one saprotrophic species, *Cantharellula umbonata* (J.F. Gmel.: Fr.) Singer (H$_3 = 12.9$, $p = 0.005$), decreased towards the pollution sources. On the contrary, ectomycorrhizal *Paxillus involutus* (Batsch: Fr.) Fr. (H$_3 = 10.1$, $p = 0.018$) increased towards the pollution sources.

**Plant community**

Totally 41 plant species were identified. *Pleurozium schreberi* (Brid.) Mitt., *Hylocomium splendens* (Hedw.) Schimp., *Dicranum polysetum* Sw. and...
D. scoparium Hedw. dominated in the ground layer, and Vaccinium vitis-idaea L., V. myrtillus L. and Empetrum nigrum L. in the field layer of the three less polluted zones (I–III). Three species (Deschampsia flexuosa (L.) Trin., Luzula pilosa (L.) Willd. and Pohlia nutans (Hedw.) Lindb.) were found in all zones. The number of lichen, herb and shrub species differed between the zones (F3,16 = 9.6, p = 0.001; F3,16 = 5.8, p = 0.007; F3,16 = 4.3, p = 0.021, respectively; Fig. 3b).

Certain species (e.g. Trientalis europaea L., Rubus idaeus L., Sorbus aucuparia L.) were observed more often in the zones III and IV than in the outermost zones I and II. The coverage of herbs differed significantly between the zones (H3 = 12.4, p = 0.006). In the pair-wise comparisons coverage of herbs in the zone IV differed significantly from that in zones I, II and III (p = 0.003, 0.004 and 0.014, respectively). The coverage of bryophytes and shrubs were greater in zone I than IV (p = 0.021 and p = 0.045, respectively). There were also differences in the coverage of lichens (H3 = 10.8, p = 0.013) and grasses (H3 = 9.5, p = 0.023). Lichens were absent from the more polluted zones III and IV. The coverage of grasses was significantly greater in the zone IV than in zones I and II (p = 0.007 and 0.016, respectively).

In contrast to the fungal community, the plant diversity measured by reciprocal Simpson's index increased significantly towards the more urban zones (Table 1). The zones I and II differed significantly from zones III and IV (I vs. III, p = 0.029; I vs. IV, p = 0.003; II vs. III, p = 0.034; II vs. IV, p = 0.004, respectively). The data was too small to calculate relevant index values for different plant groups.

### Table 1. Reciprocal Simpson index (1/D) for all fungal species and for ECM and saprotrophic species based on sporocarp inventories, and for all plant species in the zones along an urban pollution gradient. For definition of zones see Fig. 1. Means and standard deviation in parentheses (five sites per zone). Transformed data (ln [value + 0.1]) tested by ANOVA (df = 3). Values within the species group with the same letter are not significantly different (p < 0.05, Tukey). ns = not significant.

<table>
<thead>
<tr>
<th>Zone</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>All fungal species</td>
<td>8.37a</td>
<td>10.63a</td>
<td>8.59a</td>
<td>4.00b</td>
<td>7.55</td>
<td>0.002</td>
</tr>
<tr>
<td>ECM fungal species</td>
<td>6.60a</td>
<td>6.58a</td>
<td>6.27a</td>
<td>2.68b</td>
<td>3.91</td>
<td>0.029</td>
</tr>
<tr>
<td>ECM morphotypes</td>
<td>1.93a</td>
<td>2.17a</td>
<td>1.79a</td>
<td>1.62a</td>
<td>1.09</td>
<td>ns</td>
</tr>
<tr>
<td>Saprophytic species</td>
<td>4.92a</td>
<td>3.16a</td>
<td>4.88a</td>
<td>3.30a</td>
<td>1.86</td>
<td>ns</td>
</tr>
<tr>
<td>All plant species</td>
<td>1.42a</td>
<td>1.43a</td>
<td>2.81a</td>
<td>3.56b</td>
<td>9.32</td>
<td>0.001</td>
</tr>
</tbody>
</table>

Relation of fungal and plant species to soil parameters

The differences in the soil parameters between the zones were similar when comparing parameters measured in 1987 to those measured again in 2000. One study site in both zones could not be used and therefore the earlier data from those sites was not used in the calculations. The thickness and the concentration of total N in forest humus layer differed significantly in 1987 (Zone I: 3.5 cm and IV: 7.2 cm, t = −6.8, p = 0.001; zone I: 15 mg N g⁻¹ OM and IV: 21 mg N g⁻¹ OM; t = −5.9, p = 0.001) and 2000 (Zone I: 4.0 cm and IV: 6.8 cm, t = −4.0, p = 0.007; Zone I: 9.4 mg N g⁻¹ OM and IV: 19 mg N g⁻¹ OM; t = −5.0, p = 0.003). The difference in pH and in the concentration of ammonium nitrogen in the forest humus layer were not significant in either of the years, although the ammonium concentration was 3–4 times higher in more polluted urban sites (zone IV) than in zone I in both of the years 1987 and 2000.

The first rotated PCA component explained 40.3% of the total variance grouping seven parameters (by decreasing eigenvalues: thickness of forest humus layer, N H₄-N, pH, total N, total S in the forest humus layer which increased along the gradient, and soil respiration, C/N in forest humus layer which decreased along the pollution gradient). The second component explained 33.5% of the total variance grouping four parameters (by decreasing eigenvalues: concentration of V, Cr, Cu and Zn in forest humus layer). The third component explained 8.6% of the total variance, but consisted of only one parameter, Pb concentration in the forest humus layer. The first component forms an nitrogen and sulphur pollution index while the second component forms a heavy metal index.

The comparison between Quartimax rotated components and fungal parameters (Table 2) showed that the reciprocal of Simpson's index for both ECM fungi and morphotypes, and the number of ECM species correlated with the first principal component, which indicates N and S pollution, the number of these species decreasing with increasing pollution index. Similar trends were seen with fungal indicator species some of them decreasing with increasing pollution. However, one indicator species, Paxillus involutus, showed quite the opposite trend as did also a number of saprotrophic species.

The reciprocal of Simpson's index for plant species showed positive correlation with both first and second PCA axes (Table 2). The coverage of herbs and grasses correlated positively with component 2, an index for heavy metal level, whereas lichens and bryophytes correlated significantly negatively with component 1, an index for N and S pollution.
Discussion

Fungal community

The number of fruiting ectomycorrhizal (ECM) species decreased while fruiting saprotrophic species were slightly increasing towards the emission sources with increasing thickness of forest humus layer and total N concentration in this layer. Especially, the number of Cortinarius species decreased towards the emission sources. This is in agreement with observations that high N load in the soil is reflected by a loss of number and relative abundance of fruiting ECM species in coniferous forests (e.g. Ohenoja 1994, Brandrud 1995, Kårén & Nylund 1997, Jonsson et al. 2000, Peter et al. 2001, Lilleskov et al. 2001), while excess nitrogen does not seem to affect the species richness of saprophytes (Ohenoja 1994, Peter et al. 2001). Decreasing trends in fruiting of many ECM fungi have been found not only with increasing nitro-

Table 2. Pearson's correlation of the fungal and plant data with axis 1 (thickness of organic layer, NH4–N, pH, soil respiration, ratio total C:total N, total N, total S in organic layer) and axis 2 (concentration of V, Cr, Cu and Zn in organic layer) of a principal component analyses of mature Scots pine communities under acidification (SO4; Shaw et al. 1992, Såstad & Jenssen 1993) and N fertilization (Ohenoja 1994) treatments. On the contrary, Lilleskov et al. (2001) grouped L. rufus with nitrophilic species, because its sporocarp production decreased due to long-term N addition.

<table>
<thead>
<tr>
<th>Coverage of plant groups</th>
<th>Lichens: -0.496</th>
<th>Bryophytes: -0.734</th>
<th>Herbs: 0.296</th>
<th>Grasses: 0.368</th>
<th>Shrubs: -0.235</th>
<th>Tree saplings: 0.251</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pearson's correlation</td>
<td>4</td>
<td>6 (2003)</td>
<td></td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>
Nutrient cycling in forest ecosystems.

Pathways as those between decomposers and plants in ECM and saprotrophic fungi are as important as those between decomposers and mycorrhizal fungi are. In the aboveground communities, though, the Simpson’s index showed significant decrease in diversity, while it failed to do so in belowground communities. Peter et al. (2001) found that the impact of nitrogen on belowground ECM diversity was slight, but there was a change in ECM fungal communities seen both above- and belowground. However, excess nitrogen has been reported to affect less the formation of mycorrhizas than sporocarp production. Wallander (1995, Kårén & Nylund 1997, Jonsson et al. 2000, Peter et al. 2001).

Though our and several other studies show that N inputs can cause changes in ECM fungal communities, the proximal mechanisms for the changes are unclear (Brandrud & Timmermann 1998, Lilleskov & Bruns 2001). The decrease in production of sporocarps of ECM fungi may be related to a reduction in number of species forming sporocarps or to factors that disturb the development of sporocarps (Kårén & Nylund 1997). One probable mechanism for the reduction in sporocarp yield is that increased N availability stimulates shoot growth of the plant instead of carbon allocation to the fungal symbionts. Certainly, excess of N affects the pattern of carbon allocation to fungal structures (Wallander & Nylund 1992, Brandrud & Timmermann 1998). Wallander (1995) proposes that the fungus itself, rather than the plant, modifies the carbon allocation patterns to fit with the N supply. This ability varies among ECM fungal species depending on their capacity to assimilate N and their sensitivity to harmful levels of N (Wallander 1995). On the other hand, trees may be able to reduce allocation to ECM fungi with abundant external structures effective in N absorption (such as Cortinarius and Suillus, species actually found to decrease in our study also) in case of excess N supply. In a recent study, Leake et al. (2001) showed that C allocation to external ECM mycelium was reduced in the presence of a wood-decomposer fungus. For example, this observation raises a question about the possible increase in competition for carbon between ECM and saprotrophic fungi in our study sites with high nitrogen load. This may even be related with elevated sporocarp production of saprotrophic fungi in these sites compared to ECM fungi. In their new model, Lindahl et al. (2002) propose that antagonistic interactions involving nutrient transfer between decomposers and mycorrhizal fungi are as important pathways as those between decomposers and plants in nutrient cycling in forest ecosystems.

Plant community

The nitrogen deposition in zone IV was relatively low (2.3 kg NO\textsubscript{3}-N ha\textsuperscript{-1} year\textsuperscript{-1}; Anonymous 1991) compared to minimum critical load found in boreal forests of Nordic countries (1.3 kg N ha\textsuperscript{-1} year\textsuperscript{-1}; Rosén et al. 1992). This still means that the harmful effects of nitrogen on vegetation were possible. Most of our study sites were located relatively close to inhabited areas. However, the anthropogenic pressure increased towards the city centre, and thus the intensity of disturbance and landscape fragmentation was higher in zones III and IV compared to zones I and II. The forest stands in the city close to the emission sources were typically small patches, which made the canopy quite open. As both nutrient and light availability were higher than in forests in more natural state, the conditions could be expected to favour plants with relative high growth rates. For example, Vaccinium vitis-idaea, which was dominating in less polluted zones, seemed to be displaced by herbs and grasses (such as D. flexuosa) along the gradient. Similar reductions in shrubs were observed after N-fertilization (Sipola 1994) and acidification (Såstad & Jenssen 1993) and N enrichment have generally been found to decrease plant species richness (Bobbink et al. 1998, Vanha-Majamaa & Reinikainen 2000). Several studies also report a positive correlation between D. flexuosa domination of the ground flora of coniferous forests and the level of N deposition (e.g. Rosén et al. 1992, Mäkipää 1994).

In a feedback model, Bever et al. (1997) suggested that the soil microbial community may be involved in the maintenance of plant species diversity. At first step, a plant or populations of plants change the composition of the soil community; secondly, this change in turn affects the rate of growth of the plant or population. In our study area, the major shift in the ground layer from shrubs to herbs and concomitant increase in litter production certainly participated the increase in thickness of humus layer in addition to decreased decomposition rate (Ohtonen 1994). Consequently, this may have affected the competition between ECM symbiotic plants and plants with other main types of mycorrhiza, such as arbuscular-mycorrhizal grasses. Moreover, the increase in litter deposition and changes in chemical composition of litter may have improved conditions for saprophytic fungi.

Conclusion

The observed differences in fungal and plant communities along the local pollution gradient could be explained mainly by the level of nitrogen and sulphur concentration in the forest humus layer despite the rel-
atively low present deposition levels. Nitrogen-mediated changes in ECM fungal communities may have long-term ecological significance since they may further affect the capacity of their plant symbionts, i.e., long-living trees, to grow in the changing forest ecosystems. The present study area provides an interesting forum for long-term experiments focusing on changes in community and population level. Despite that the industrial emissions have been cut down during the last decades, the N load of traffic origin has not decreased and the accumulation of N can be seen in thick humus layer. This nitrogen load is still affecting the vegetation and fungal communities in urban middle boreal forests.

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