

Dissertationes Forestales 54

Effects of recreational use and fragmentation on the
understorey vegetation and soil microbial communities of
urban forests in southern Finland

Minna Malmivaara-Lämsä

Department of Biological and Environmental Sciences
Faculty of Biosciences, University of Helsinki

Academic dissertation

To be presented, with the permission of the Faculty of Biosciences of the University of Helsinki, for public examination in Auditorium 311, Bulevardi 18, Helsinki, on February 1st 2008 at 12 o'clock noon.

Title: Effects of recreational use and fragmentation on the understorey vegetation and soil microbial communities of urban forests in southern Finland

Author: Minna Malmivaara-Lämsä

Dissertationes Forestales 54

Supervisors:

Professor Jari Niemelä, University of Helsinki, Finland

Docent Hannu Fritze, Finnish Forest Research Institute, Vantaa, Finland

Pre-Examiners:

Professor Rauni Strömmer, University of Helsinki, Finland

Associate Professor Margaret M. Carreiro, University of Louisville, USA

Opponent:

Doctor James Littlemore, Moulton College, UK

ISSN 1795-7389

ISBN 978-951-651-196-5 (PDF)

(2008)

Publishers:

Finnish Society of Forest Science

Finnish Forest Research Institute

Faculty of Agriculture and Forestry of the University of Helsinki

Faculty of Forestry of the University of Joensuu

Editorial Office:

Finnish Society of Forest Science

Unioninkatu 40A, 00170 Helsinki, Finland

<http://www.metla.fi/dissertationes>

Malmivaara-Lämsä, M. 2008. Effects of recreational use and fragmentation on the understorey vegetation and soil microbial communities of urban forests in southern Finland. *Dissertationes Forestales* 54. 39 p. Available at <http://www.metla.fi/dissertationes/df54.htm>

ABSTRACT

The impacts of fragmentation and recreational use on the hemiboreal urban forest understorey vegetation and the microbial community of the humus layer (the phospholipid fatty acid (PLFA) pattern, microbial biomass and microbial activity, measured as basal respiration) were examined in the greater Helsinki area, southern Finland. Trampling tolerance of 1) herb-rich OMT, 2) mesic MT, and 3) sub-xeric VT forests (in decreasing order of fertility) was studied by comparing relative understorey vegetation cover (urban/untrampled reference ratio) of the three forest types.

The trampling tolerance of forest vegetation increased with the productivity of the site (sub-xeric < mesic < herb-rich). Wear of understorey vegetation correlated positively with the number of residents (i.e., recreational pressure) around the forest patch. An increase of 15000 residents within a radius of 1 km around a forest patch was associated with ca. 30% decrease in the relative understorey vegetation cover. The cover of dwarf shrub *Vaccinium myrtillus* in particular decreased with increasing levels of wear. The cover of mosses in urban forests was less than half of that in untrampled reference areas. Cover of tree saplings, mainly *Sorbus aucuparia*, and some resilient herbs was higher than in the reference areas. In small urban forest fragments, broad-leaved trees, grasses and herbs were more abundant and mosses were scarcer than in larger urban forest areas. Thus, due to trampling and edge effects, resilient herb and grass species are replacing sensitive dwarf shrubs, mosses and lichens in urban forests.

Differences in the soil microbial community structure were found between paths and untrampled areas and the effects of paths extended more than one meter from the paths. Paths supported approximately 25-30% higher microbial biomass with a transition zone of at least 1 m from the path edge. However, microbial activity per unit of biomass was lower on paths than in untrampled areas. Furthermore, microbial biomass and activity were 30-45% lower at the first 20 m into the forest fragments, due to low moisture content of humus near the edge. The decreased microbial activity detected at forest edges and paths implies decreased litter decomposition rates, and thus, a change in nutrient cycling. Changes in the decomposition and nutrient supply may in turn affect the diversity and function of plant communities in urban forests.

Keywords: boreal forest vegetation, edge effects, phospholipid fatty acids, trampling, urban woodlands, wear

ACKNOWLEDGEMENTS

This work was carried out at Finnish Forest Research Institute (Metsäntutkimuslaitos, Metla) Vantaa Research Unit. I want to express my gratitude to the director Jari Varjo for providing excellent working facilities to me in the Unit.

The work was funded by the Academy of Finland (Finnish Biodiversity Research Programme, FIBRE), the Maj and Tor Nessling Foundation, University of Helsinki and the City of Helsinki, which are all acknowledged.

I would like to thank my supervisors Jari Niemelä and Hannu Fritze for their help and guidance during all these years. Jari, thank you for taking me into your group and introducing me theories of urban ecology. Hannu, your knowledge of soil microbiology made this work possible, and your good spirits and dynamic way to work were a great source of inspiration. I also thank Irja Löfström and Ilkka Vanha-Majamaa who first introduced me the ECOPLAN (Ecology and urban planning) project and helped me every way during the planning and preparation of the first paper.

I warmly thank all my other co-authors Leena Hamberg, Susanna Lehvävirta, Johan Kotze, Jari Liski and Elli Haapamäki for the pleasant cooperation. Leena, your help and support and all the conversations we had during the years sharing a room in Metla were essential.

The pre-examiners Rauni Strömmer and Margaret Carreiro gave valuable comments and helped to improve the summary and the manuscripts of the thesis. Also, I thank Fred Stoddard for the language revision.

Many people at Metla helped me with various things during the preparation of this thesis – thank you all for your help and for the pleasant working atmosphere. I thank Anneli Rautiainen and Miia Collander for their help in the laboratory analyses, Tiina Tonteri for her advice in performing GNMDS, Juhani Mäkinen, Hannu Rantanen, Ilkka Taponen and Johanna Saari for their help in tree stand measurements, Jyrki Jalonen for letting me use his data as a reference, Sari Elomaa and Anne Siika for preparing the figures and layout of this thesis.

Bob O’Hara and Hannu Rita from the University of Helsinki helped with the statistical analyses performed using R and with the study design used in paper IV, respectively.

Many thanks to the Green departments of Helsinki and Vantaa for letting me work in their forests.

Finally, I want to thank my dear friends and family for being there for me. Mother and father, I want to thank you for your love and support. You have always helped me - no matter how tired or tied up with other things you were. My special thanks go to my mother for taking care of Vilho for a whole year while I was working on this thesis. Many thanks also to Tarja, my mother-in-law, who helped during the summer weeks I had to spend working. Jaakko, thanks for your help and company in the field. Karri and Vilho, I can’t thank you enough for all your love, support and patience during these years.

I dedicate this work to my grandparents, fine people who have accomplished so much in their lives and who I greatly admire.

Vantaa, December 2007

Minna Malmivaara-Lämsä

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following articles and manuscripts, which are referred to by their Roman numerals.

- I Malmivaara Minna, Löfström Irja & Vanha-Majamaa Ilkka 2002. Anthropogenic effects on understorey vegetation in Myrtillus type urban forests in southern Finland. *Silva Fennica* 36, 367-381. <http://www.metla.fi/silvafennica/full/sf36/sf361367.pdf>
- II Malmivaara-Lämsä Minna, Hamberg Leena, Löfström Irja, Vanha-Majamaa Ilkka & Niemelä Jari 2007. Trampling tolerance of understorey vegetation in different hemiboreal urban forest site types in Finland (accepted for publication in *Urban Ecosystems*).
- III Malmivaara-Lämsä Minna & Fritze Hannu 2003. Effects of wear and above ground forest site type characteristics on the soil microbial community structure in an urban setting. *Plant and Soil* 256, 187-203. <http://www.springerlink.com/index/P67374707U008X25.pdf>
- IV Malmivaara-Lämsä Minna, Hamberg Leena, Haapamäki Elli, Liski Jari, Kotze Johan, Lehvävirta Susanna & Fritze Hannu 2007. Edge effects and trampling in boreal urban forest fragments - impacts on the soil microbial community (revised manuscript submitted to *Soil Biology & Biochemistry*).

Papers I, II and III are reprinted by kind permission from the publishers.

AUTHOR'S CONTRIBUTIONS

Minna Malmivaara-Lämsä participated in planning and designing of all four studies and she was responsible for data collection (I-IV), laboratory work (IV), data analyses (I-IV, except for the spatial analyses in paper IV which were performed by J. Liski and E. Haapamäki) and writing the papers (I-IV).

CONTENTS

ABSTRACT	3
ACKNOWLEDGEMENTS	4
LIST OF ORIGINAL PUBLICATIONS	5
AUTHOR'S CONTRIBUTIONS	5
1 INTRODUCTION	9
1.1 Urban forests	9
1.1.1 <i>Definition and characteristics</i>	9
1.1.2 <i>Why preserve forest ecosystems in urban areas?</i>	10
1.2 Ecological interactions between forest vegetation and soil microbes	10
1.3 Anthropogenic factors affecting forest ecosystems in urban areas	11
1.3.1 <i>Fragmentation</i>	12
1.3.2 <i>Recreational use</i>	12
1.4 Aims of the thesis	13
2 MATERIALS AND METHODS	14
2.1 Study areas	14
2.2 Vegetation inventories	14
2.3 Measures of recreational use and fragmentation.....	16
2.4. Wear classifications	16
2.5 Reference data (I and II).....	16
2.6 Trampling tolerance	17
2.7 Soil sampling.....	17
2.8 Microbiological and physico-chemical analyses (III and IV).....	17
2.9 Statistical analyses.....	19
3 RESULTS.....	20
3.1 Recreational use	20
3.1.1 <i>Effects of recreational use on understorey vegetation</i>	20
3.1.2 <i>Effects of recreational use on soil physico-chemical properties</i>	20
3.1.3 <i>Effects of recreational use on soil microbial community</i>	21
3.2 Fragmentation.....	22
3.2.1 <i>Effects of fragmentation on understorey vegetation</i>	22
3.2.2 <i>Effects of fragmentation on soil physico-chemical properties</i>	22
3.2.3 <i>Effects of fragmentation on soil microbial community</i>	22
4 DISCUSSION	23
4.1 Effects of recreational use on understorey vegetation.....	23
4.1.1 <i>Trampling tolerance of understorey vegetation</i>	23
4.1.2 <i>Effects of recreational use on understorey species composition</i>	24
4.1.3 <i>Tree layer characteristics and understorey vegetation composition</i>	25

4.2 Effects of recreational use on soil microbial community	26
4.2.1 <i>Effects of recreational use on microbial community structure</i>	26
4.2.2 <i>Effects of recreational use on microbial biomass</i>	26
4.2.3 <i>Effects of recreational use on microbial activity</i>	27
4.3 Effects of fragmentation on understorey vegetation.....	28
4.3.1 <i>Edge effects and understorey species composition</i>	28
4.3.2 <i>Eutrophication and understorey species composition</i>	28
4.4 Effects of fragmentation on soil microbial community.....	29
4.4.1 <i>Effects of fragmentation on microbial community structure</i>	29
4.4.2 <i>Effects of fragmentation on microbial biomass and microbial activity</i>	29
5 IMPLICATIONS	30
REFERENCES	31



Figure 1. Urban forest fragments in North Helsinki, Finland. (Photo: Antti Raassina)

1 INTRODUCTION

Forest fragmentation is increasing due to accelerating urbanisation, agricultural development, logging and road construction globally (Wade et al. 2003). Due to increasing number of urbanites, infilling inside city limits is increasing and cities are expanding in area. This development leads to further fragmentation of remnant forest ecosystems in urban areas. In Finland, urban forests have many recreational users, and thus, wear of vegetation caused by trampling is considerable (Lehvävirta and Rita 2002, Hamberg et al. 2007). However, knowledge about the effects of fragmentation and recreational use on forest ecosystems in urban areas is scarce. Changes in vegetation and soil structure have been reported (Bhaju and Ohsawa 1998, Florgård 2000, Lehvävirta and Rita 2002, Littlemore and Barker 2003, Hamberg et al. 2007), but the effects on the biological properties of the soil are not well known (but see Waltert et al. 2002).

We need to understand how stresses in urban forests influence ecological processes both above and below ground. Because ecological interactions between forest vegetation and soil microbes are pivotal, both parts of the ecosystem were examined in this study. The aim of this thesis was to elucidate the effects of fragmentation and recreational use on the state and composition of forest understorey vegetation and structure and function of forest soil microbial communities in hemiboreal urban forests in Finland. This information is needed for the purposes of urban planning and management with the aim of preserving indigenous forest ecosystems in urban areas.

1.1 Urban forests

1.1.1 Definition and characteristics

Here, urban forests are defined as forests with indigenous forest understorey vegetation (or remains of it) located within, or at the outskirts of, towns and cities (cf. Löfström 1987, Tyrväinen 1999, Lehvävirta 2005). Park-like areas with sown grassy understorey vegetation are not included here.

Urban forests in Finland vary in size from less than half a hectare within cities to tens or sometimes hundreds of hectares at the outskirts of cities (Fig. 1). Within the city of Helsinki, the majority of forest patches are less than two hectares in size (Saukkonen 2007). Urban forests are mainly managed for recreational use, but scenic values, protective abilities and biodiversity are also taken into account (Gundersen et al. 2005).

In Helsinki, southern Finland, mesic, herb-rich and sub-xeric heath forests are the most abundant covering 40%, 23% and 10% of the total forest area of Helsinki (ca. 4000 ha), respectively (Tiina Saukkonen, pers. comm. 7 September, 2007). These forest types are dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) with a mixture of broad-leaved trees, such as *Betula pendula*, *B. pubescens*, *Populus tremula*, *Alnus incana* and *Sorbus aucuparia*. Most abundant species in the understorey vegetation are dwarf shrubs, *Vaccinium myrtillus* and *V. vitis-idaea*, and mosses, such as *Pleurozium shreberi*, *Dicranum polysetum* and *Hylocomium splendens*. The proportion of herbs, such as *Oxalis acetosella*, *Maianthemum bifolium* and *Trientalis europaea*, increases with increasing fertility of the forest type being the lowest in sub-xeric and the highest in herb-rich forest type.

In addition to natural disturbances and successional processes, diversity of vegetation in these forests has been greatly affected by humans. Intensive recreational use of the forests has a long history and recorded management of forests in Helsinki dates back to 1890s (Saukkonen 2007). The flora is most altered in forest patches near the city centre (Kurtto and Helynranta 1998). Many forest species are missing from there (even spruce and pine), and they have been replaced by cultural species more tolerant to anthropogenic disturbances.

1.1.2 Why preserve forest ecosystems in urban areas?

In Finland, ca. 75% of urban green areas are forests (e.g., Saukkonen 2007). They are important areas for recreation (running, walking, cycling, walking the dog, berry picking and mushroom gathering) and are highly appreciated green areas in residential districts (Tyrväinen 1999). They offer exciting areas for children's play and education (Florgård 2004, Florgård and Forsberg 2006), and may present urbanites' only contact to nature. Furthermore, they have positive effects on the health and psychological welfare of the residents (Frumkin 2003, Tzoulas et al. 2007).

Forests ameliorate urban microclimate by moderating temperatures and decreasing wind velocity (Oke 1989, McPherson et al. 1997). Forests and parks can be 5°C cooler than surrounding urban areas, and this cooling effect may extend 150 m into the surrounding urban area (Robert Brown, pers. comm. 27 September, 2006). Forest vegetation binds airborne nutrients and pollutants, and thus cleans the air in urban areas (Bobbink et al. 1998, Weathers et al. 2001).

Urban forests can be important reserves of biodiversity. In general, they are less intensively managed than commercial forests (Gundersen et al. 2005). For example, the proportion of broad-leaved trees and amount of coarse woody debris may be higher in urban forests than in commercial forests (Lehvävirta and Rita 2002, Maene 2005, Hamberg et al. 2007). Thus, promoting and preserving biodiversity in urban forests is one way to slow down the rapid rate of biodiversity loss (Alvey 2006).

Costs for development, maintenance and management of urban forests are low when compared to other green areas, such as parks (Florgård 2004). Management costs for urban forests in Helsinki in the year 2005 (490 €/ha) were only 5% of those for parks (10200 €/ha) (Saukkonen 2007). Thus, utilization of this existing mature indigenous vegetation as green areas in future development sites is economically advantageous (Florgård 2000).

1.2 Ecological interactions between forest vegetation and soil microbes

Trees are the main producers of organic matter in a forest ecosystem. They affect the understorey vegetation and the soil by the associated microclimate that is formed under them, and by their above- and below-ground litter (Kuusipalo 1983, Lahti and Väisänen 1987, Priha 1999). Canopy litterfall represents the major above-ground pathway by which carbon and nutrients are returned to the forest floor (Cole and Rapp 1981). In Norway spruce stands, mean annual total litterfall production (LF_{total}) in southern Finland ranged from 2200 to 4200 kg dry weight ha^{-1} (Saarsalmi et al. 2007) and in Scots pine stands, LF_{total} was 2300 kg ha^{-1} (Starr et al. 2005). The litter of trees and understorey vegetation determines the chemical characteristics of humus (Mikola 1985) and influences the composition of decomposer communities (Priha et al. 2001, Marschner et al. 2004, Aneja et al. 2006). Different types of soil organic matter have a different composition of soil microbes and soil animals. In boreal forests, acid forest soils

(mor humus, raw, acid, fibrous and poor in nutrients) are usually dominated by small mites, enchytraeid worms, springtails and a thriving fungal community (Killham 1994).

The forest soil microorganisms play a key role in the decomposition process and thus their function strongly influences nutrient cycling in the ecosystem. The functions of the microbial community (litter decomposition, mineralisation of carbon and nitrogen, nitrogen fixation, production of phytohormones) in turn determine the structure and function of plant communities (Van der Heijden 1998a, Hartnett and Wilson 1999). Mineralisation reactions are important to the productivity of forest ecosystems because the major fraction of nutrients such as nitrogen and phosphorus in most soils is in the organic form (Killham 1994).

Trees and dwarf shrubs actively translocate assimilation products into their mycorrhizas and exude photosynthetic assimilates out of roots into the rhizosphere (Grayston et al. 1996). Rhizodeposition of carbon (including root exudation) increases microbial biomass and activity in the rhizosphere and consequently influences plant growth. Mycorrhizas are formed by association between a plant root and a fungus and most vascular plants are involved in these associations (Killham 1994). Ectomycorrhizas of trees and other woody plants and endomycorrhizas, such as ericoid mycorrhizas of ericaceous plants and Vesicular Arbuscular Mycorrhizas of herbaceous plants, are essential in forest ecosystems as they contribute to the uptake of water and nutrients (nitrogen and phosphorus) by plants. Mycorrhizal development in turn is strongly influenced by the available concentrations of soil nutrients (phosphorus and nitrogen in particular), pH and soil moisture (Killham 1994), and thus may be sensitive to anthropogenic disturbances (see Waltert et al. 2002).

The indications of the vast diversity of uncultured life in soil (only 1–5% of the microorganisms observed under the microscope can be cultivated and characterized) have stimulated development of methods for culture-independent study of microbial communities (Torsvik and Øvreås 2002). Over the past 15 years fingerprinting techniques, such as phospholipid fatty acid (PLFA) analysis, denaturant gradient gel electrophoresis (DGGE) and terminal restriction fragment length polymorphism (T-RFLP), and some modifications of these techniques have become popular in studying changes in the whole microbial community structure. These techniques provide information on the species composition, and they can be used to compare common species present in samples. PLFA analysis, used in this study, has been considered a fast and reliable method for initial detection of the overall changes in the microbial community structure (Frostegård 1995). However, only the relative abundances of some microbial groups (i.e. fungi, actinobacteria, gram-positive and -negative, methanotrophs) can be determined as most of the individual PLFAs are common in all microbial cells (Frostegård 1995, Bååth et al. 1998).

1.3 Anthropogenic factors affecting forest ecosystems in urban areas

Forests in urban environments are under stress due to fragmentation, pollution and wear of understorey vegetation and soil caused by recreational use. Effects on vegetation are reflected in soil microbial communities and vice versa. Due to the stresses, vegetation composition and cover may change (Bhujji and Ohsawa 1998, Flørgård 2000, Lehvävirta and Rita 2002, Littlemore and Barker 2003, Hamberg et al. 2007) and ecosystem functions, such as decomposition, mineralization of nitrogen, and nitrification, may be reduced in urban forests (see Goudie 1990). However, urban stresses may have complex interactions in urban forest ecosystems. They may have both negative effects and positive effects on ecosystem functions (see McDonnell et al. 1997). For example, positive effects of heat island phenomenon and

the presence of alien earthworms overrode the negative effects of heavy metal pollution and caused increased litter decomposition in urban forests of New York City (Pouyat et al. 1997). However, it is difficult to generalize as studies of urban ecosystems in different geographical areas and vegetation zones are scarce.

1.3.1 Fragmentation

Fragmentation has several effects, one of them being an increase in the proportion of the edge zone, with changes in microclimate and accompanying changes in plant species composition (Ranney et al. 1981, Chen et al. 1993, Murcia 1995, Hamberg et al. 2007). Given that the forest edges are warmer, windier and receive more light than forest interiors (Chen et al. 1993), the proportion of light-demanding and drought-resistant plant species will increase (Ranney et al. 1981). Depth of an edge zone varies from tens to hundreds of meters into a forest fragment depending on vegetation type, edge structure and edge orientation (Matlack 1993a, Chen et al. 1993, Murcia 1995, Didham and Lawton 1999, Huggard and Vyse 2002). Changed environmental conditions in small forest fragments and isolation of the patches are factors decreasing survival of indigenous forest species and changing species composition, as species better adapted to the new conditions of the surrounding matrix may colonize the patches and eventually replace the indigenous forest species (Lovejoy and Oren 1981, Gilbert 1989). Soils at the forest edges are affected by the vegetation changes and atmospheric deposition of pollutants and nutrients, and may thereby become more fertile than forest interiors (Thimonier et al. 1992, Weathers et al. 2001, Hamberg et al. 2007). Changes in the microclimate, the vegetation and the soil are likely to cause changes in the soil microbial community (Fig. 2).

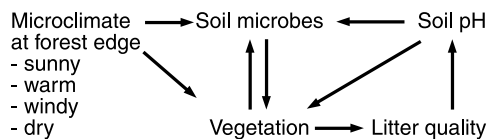


Figure 2. Edge effects in fragmented forests.

1.3.2 Recreational use

Trampling damages vegetation by decreasing vegetation cover, biomass, height and species richness and diminishing forest tree regeneration (Liddle 1997, Lehvävirta and Rita 2002, Ros et al. 2004). Sensitive species disappear first and more tolerant species remain and may eventually replace sensitive ones. Trampling creates suitable habitats for pioneer species in the community (Gilbert 1989).

Resistance (ability to withstand/resist trampling damages) and resilience (ability to recover from trampling) of component plant species determine the trampling tolerance of different plant communities (Cole and Bayfield 1993, Cole 1995, Tolvanen et al. 2001). The growth form and the morphology of plant species determine to a great extent their resistance to trampling (Liddle 1997). Herbs with large and thin leaves found in fertile vegetation types as well as lichens of dry vegetation types low in fertility habitats, e.g. on rocky terrains, are fragile (Kellomäki and Saastamoinen 1975, Liddle 1997). Vegetation types with the understorey vegetation of low productivity are most easily damaged due to their slow rate

of regeneration after disturbance (Kellomäki and Saastamoinen 1975, Cole 1987, Liddle 1997, Rydgren et al. 1998). In boreal forests, the relationship between the site fertility and the trampling tolerance of the understorey vegetation was found to be curvilinear: the trampling tolerance of the vegetation on the poorest (*Cladonia* type) and the richest (herb-rich) sites was lower than that of the sites of medium fertility (Kellomäki and Saastamoinen 1975). However, the richest sites were more tolerant than the poorest. If trampling is extremely intense and prolonged, even the most tolerant species will die and the humus layer will gradually erode, exposing mineral soil and tree roots prone to additional trampling damage.

In addition to vegetation damage, soil properties are also affected by trampling. In the early phases of trampling, wear of vegetation and concomitant changes in litter quality may lead to changes in the quality of soil organic matter and pH (Liddle 1997). Litter cover decreases during long-term trampling disturbance (Legg and Schneider 1977) and this may lead to loss of soil organic matter. Loss of vegetation may reduce root exudation and thus carbon substrates essential for microbial communities in the rhizosphere (Killham 1994). Due to the loss of understorey vegetation, microclimate on paths may be drier and warmer than under untrampled vegetation (Liddle and Moore 1974), possibly creating an edge effect. Soil macropore space and infiltration rates decrease and bulk density and run-off increase due to trampling (Legg and Schneider 1977, James et al. 1979, Stohlgren and Parsons 1986). Soil compaction causes deficiencies in oxygen, water and nutrient availability and may reduce mineralisation of organic matter and thereby restrict plant growth (Grable 1971, Kemper et al. 1971, Liddle 1997). Trampling also affects vegetation indirectly through changes in soil properties (Bhuju and Ohsawa 1998, Florgård 2000), and changes in both vegetation and soil are likely to adversely affect forest soil microbial communities (Liddle 1997, Zabinski and Gannon 1997, Ohtonen and Väre 1998) (Fig. 3).

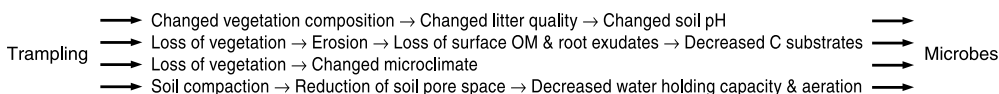


Figure 3. Effects of trampling on the vegetation, soil and microbial community. OM = organic matter.

1.4 Aims of the thesis

The aims of this thesis were to study

- 1) the effects of recreational use and fragmentation on (a) cover, and (b) species composition of understorey vegetation in urban forests (I, II),
- 2) whether the understorey vegetation of urban forests varying in fertility (herb-rich, mesic and sub-xeric) differ in trampling tolerance (II), and
- 3) the effects of recreational use and fragmentation on (a) forest soil microbial community structure, microbial biomass, and (c) microbial activity in urban forests (III, IV).

In study I, it was hypothesized that changes in understorey species composition and cover due to the effects of trampling and fragmentation would occur. These effects were expected to be largest in small forest fragments with numerous residents in the vicinity.

In study II, it was hypothesized, based on the results of Kellomäki and Saastamoinen (1975), that trampling tolerance of understorey vegetation of the forest types studied would increase curvilinearly with increasing fertility; sub-xeric forest type having the lowest and mesic forest type having the highest trampling tolerance.

In study III (based on the results of study I), wear of the understorey vegetation (changes in the cover and species composition) was expected to influence the soil microbial community in mesic urban forests.

In study IV, it was hypothesized that the microbial community would change along a gradient from 1) the forest edge to the forest interior, with accompanying changes in vegetation and soil chemistry, and 2) from paths to untrampled areas. Microbial activity and biomass (especially the biomasses of bacteria and actinomycetes) were expected to be adversely affected by trampling, to increase with increasing distance from paths, and to decrease with increasing levels of wear (see Liddle 1997, Zabinski and Gannon 1997, Ohtonen and Väre 1998). Based on the results of the study III, pH and the C/N ratio were expected to be important determinants of the soil microbial community.

2 MATERIALS AND METHODS

2.1 Study areas

All studies were conducted in the greater Helsinki area, southern Finland, in the hemiboreal vegetation zone (Ahti et al. 1968). Altogether 85 urban forest stands of varying size (0.5-1600 ha) were selected for the studies (Fig. 4). Mesic *Vaccinium myrtillus* type (MT) biotopes were chosen for the studies I, III and IV. Trampling tolerance of 1) herb-rich *Picea abies* and broad-leaved tree dominated *Oxalis acetosella* - *Vaccinium myrtillus* type (OMT), 2) mesic *Picea abies*, *Pinus sylvestris* and *Betula pendula* dominated MT, and 3) sub-xeric *Pinus sylvestris* dominated *Vaccinium vitis-idaea* type (VT) in the decreasing order of fertility (Cajander 1926, Kuusipalo 1996) were compared in study II (see Table 1 for the number of forest stands and biotopes in each study). The age of dominant trees was over 80 years and forest management practises had not been employed in these forests during the last five years. The topography of the sites was level. The soil type was podsol developed on moraine and the humus form was mor (VT, MT) or mull-like (OMT).

In study IV, urban forest edges facing south to west were selected in order to maximize the edge effects (maximum radiation and the prevailing wind direction in the study area). The forest edge was defined as a line along the outermost mature trees of a fragment. All edges were more than ten years old and bordered artificially covered areas, mostly residences and asphalt roads.

2.2 Vegetation inventories

Understorey vegetation of selected stands was mapped in order to identify internally homogenous OMT, MT and VT biotopes. For vegetation inventories a 100 m² sample plot (or two if the biotope size was > 1 ha) was chosen in the centre of each biotope used for the study (I-III). Within each sample plot, 1 m² sub-plots located 4 m in the direction of all principal compass points from the centre point of the sample plot were used in the understorey vegetation

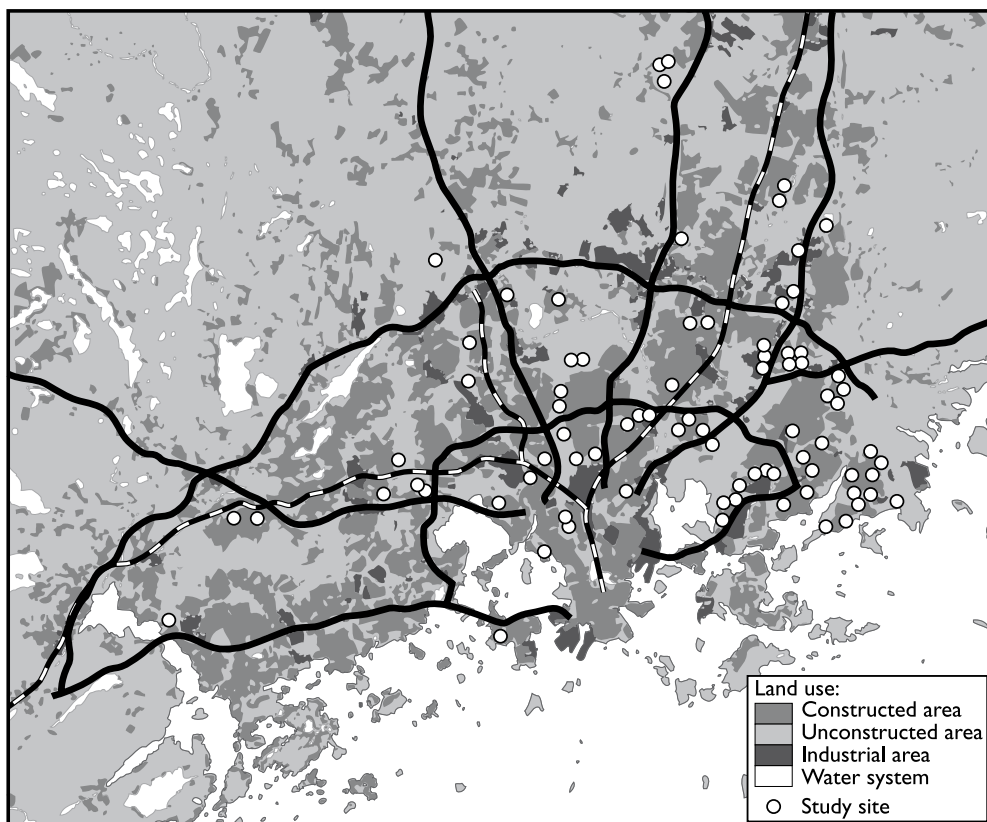


Figure 4. Map of the greater Helsinki area, southern Finland, showing the location of study sites (I-IV). Main roads are marked with solid lines and railroads with striped lines. The scale is approximately 1:350 000.

Table 1. Number of stands and biotopes in studies I-IV.

	Study I	Study II	Study III	Study IV
Stands	40*	40*+11	40*	34
Biotopes				
-MT	69	75	67	34
-OMT	-	40	-	-
-VT	-	40	-	-

* indicated stands are the same.

inventories. The cover of plant species and litter on the sub-plots were estimated visually by using a scale of 0.25–100% with cover values above 10% estimated in 5% intervals: 0.25, 0.5, 1, 2, 3, 5, 10, 15, 20 ... 90, 95, 100. All understorey vegetation species, including tree saplings under 50 cm in height, with the exception of liverworts and lichens were determined to the species level. In study IV the data on percentage covers of understorey vegetation (inventoried in 0.5 m² sized sample plots by Hamberg et al. 2007) were used as background information.

Furthermore, measurements were taken of basal area, volume and number of stems per ha of coniferous and broad-leaved trees (dbh > 5 cm) and cover of shrubs and tree saplings (height > 50 cm and dbh < 5 cm) in each 100 m² sample plot (I-III) and used as measures of tree density and tree species composition. In study IV, summed breast height diameter of all trees (inventoried in 50 m² circular plots by Hamberg et al. 2007) was used as background information.

2.3 Measures of recreational use and fragmentation

Total area of paths, area of exposed mineral soil and thickness of humus layer within the 100 m² sample plots were used as measures of trampling (I-III). In study IV, wear class of paths was used as a measure of trampling (see *Wear classifications*, below). Distance from the nearest forest edge was used as a measure of fragmentation (I-IV). In addition, data on number of residents within distances of 1 and 2 km, and number of children in schools and kindergartens within distance of 300 m from centre points of the sample plots collected from resident registers were used as measures of recreational use (I-III).

2.4 Wear classifications

Wear classifications were used to study the effect of increasing amount of recreational use on the vegetation composition and soil microbial communities within the urban forests studied. In study I, biotopes were classified into five classes according to the level of wear: 1) undeteriorated, 2) slightly deteriorated, 3) deteriorated, 4) highly deteriorated, and 5) totally worn-away vegetation (modified after Holmström 1970). In study III, the same biotopes were divided into three path area classes: 1) no paths, 2) path area ≤ 5 m², and 3) path area > 5 m² per 100 m² sized sample plot. In study IV, paths were classified according to the four levels of wear described by Lehvävirta (1999); 1 = lightly worn (visible effects of wear, vegetation damaged but only slightly reduced in cover), 2 = moderately worn (visible effects of wear, vegetation damaged and reduced in cover but not completely worn away), 3 = heavily worn (generally no vegetation on the path, humus layer not worn away, rocks and tree roots sometimes uncovered), and 4 = very heavily worn (bare mineral soil or a deeply worn humus layer, no vegetation remaining, and rocks and tree roots often uncovered).

2.5 Reference data (I and II)

The urban understorey vegetation data was compared to data from untrampled reference areas in order to study the effects of trampling and other anthropogenic disturbances on the cover and composition of the vegetation (I and II). The reference data of the same forest types (OMT, MT, VT) and of the same age (ca. 80 years) was collected from commercial forests in southern Finland during the Eighth National Forest Inventory in 1985 (Finnish Forest Research Institute, unpublished data). Data of Jalonen and Vanha-Majamaa (2001) collected from commercial forests of the same site type (MT) and same age was used as a second reference in study I. The reference areas were located in the same vegetation zone as the urban forests studied. The upper canopy layers of OMT and MT forests in reference areas were denser than those of urban forests (number of stems/ha was higher) and the cover of

small broad-leaved trees (height > 0.5 m and dbh < 5 cm) was ca. 80% lower in the reference areas than in the urban forests (Table 5 in study II). Otherwise the major difference between urban forests and the reference areas was the number of residents in the surroundings, which was expected to correlate with the amount of recreational use and the concomitant wear of vegetation.

2.6 Trampling tolerance

As there are characteristic differences in the OMT, MT and VT field and ground layer vegetation (Fig. 1 in study II), relative understorey vegetation cover (urban/reference ratio) was used in comparing the trampling tolerance of the forest types. The urban/reference ratio shows the state of wear of the urban understorey vegetation compared to vegetation in untrampled reference areas. A value < 1 indicates wear of understorey vegetation; the smaller the value the more worn the vegetation.

2.7 Soil sampling

Soil samples were taken from the organic humus layer by using a steel soil corer of 5.8 cm diameter. In study III, 16 humus subsamples were collected from the 100 m² sample plots described above (see *Vegetation inventories*). Altogether 76 pooled humus samples were obtained. In study IV, six humus subsamples were taken from each 0.5 m² sample plot on paths (representing four levels of wear, namely lightly, moderately, heavily and very heavily worn), next to them (at 0.45 m) and 1.2–4 m away from them, at approximate distances of 0, 15, 30, and 60 m from the forest edge (Fig. 5A). In practice, distance from the forest edge ranged from 0 to 80 m. The subsamples were pooled to form a composite sample for each 308 sample plots. Furthermore, corresponding samples were collected 10 cm apart in a small-scale spatial sampling over two paths (105 and 120 samples) and an untrampled area (100 samples) in study IV (Fig. 5B). Visible green plant material, large roots, soil animals and mineral soil particles were removed. The samples were sieved (2.8 mm mesh) and frozen (-20°C) within a few days of collection.

2.8 Microbiological and physico-chemical analyses (III and IV)

Microbial community structure was determined by using the phospholipid fatty acid (PLFA) method. The phospholipid fatty acids (PLFAs) were extracted from 5 ml of weighed fresh humus (IV) or from 1 g fresh weight (III and IV) (Frostegård et al. 1993, modified by Pennanen et al. 1999). The fatty acid methyl esters were separated by gas chromatography (Hewlett Packard 5890) equipped with a flame ionisation detector and a HP-5 (phenylmethyl silicone) capillary column, 50 m in length, using He (30 ml min⁻¹) as a carrier gas. The peak areas were quantified by adding methyl nonadecanoate (19:0) as an internal standard, and the peaks were identified using HP ChemStation software.

In total, 39 PLFAs were identified and their amounts in nmol g⁻¹ dry matter (d. m.) were used to indicate the total microbial biomass. The sum of PLFAs considered to be predominantly of bacterial origin (i15:0, a15:0, 15:0, i16:0, 16:1 ω 9, 16:1 ω 7t, i17:0, a17:0, 17:0, cy17:0, 18:1 ω 7, and cy19:0) was chosen as an index of the bacterial biomass, and the quantity of

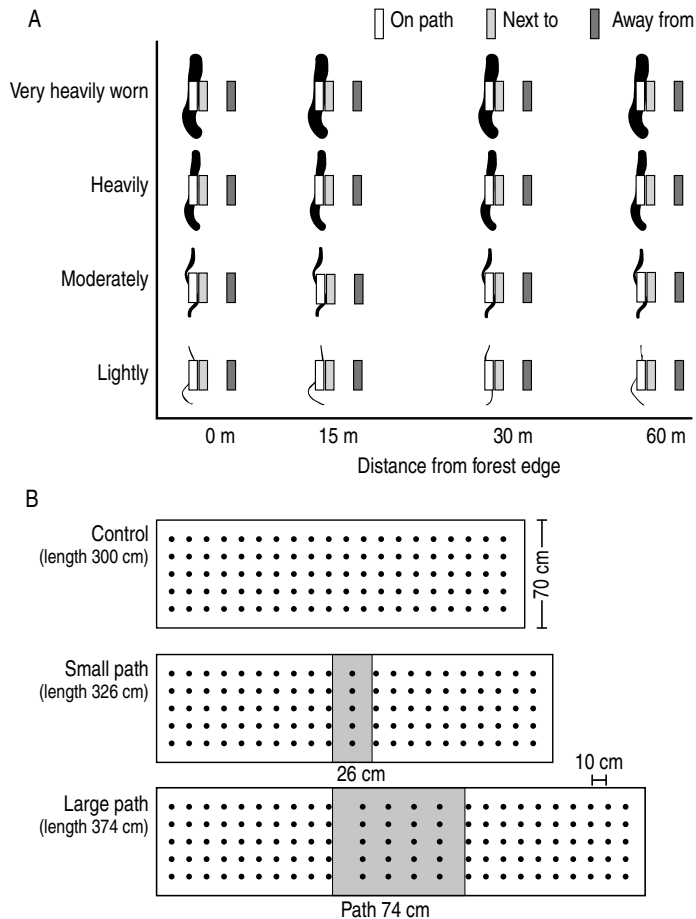


Figure 5. (A) Sampling design used to test the effects of forest edge and paths and **(B)** small-scale effect of paths on the forest soil microbial community (IV).

18:2 ω 6 was used as an indicator of fungal biomass (Frostegård and Bååth 1996). PLFAs 16:1 ω 7t, 16:1 ω 7c, cy17:0, 18:1 ω 7 and cy19:0 were taken to represent Gram-negative bacteria (Wilkinson 1988, Zogg et al. 1997), and the branched, saturated PLFAs 10Me16:0, i15:0, a15:0, i16:0, i16:1, i17:0, a17:0, br17:0 and 10Me17:0 to represent Gram-positive bacteria (O’Leary and Wilkinson 1988, Zogg et al. 1997). The sum of PLFA 10Me16, 10Me17 and 10Me18 was used as an indicator of actinomycetes (Kroppenstedt 1985, Brennan 1988, Zelles et al. 1994) and the quantity of PLFA 16:1 ω 5 was used as an indicator of arbuscular mycorrhiza (Olsson et al. 1995).

Basal respiration rate was measured as the amount of CO₂ evolved in 24 and 48 h as described by Pietikäinen and Fritze (1995) and used to determine microbial activity. Weighed fresh humus samples, 15 ml in volume (IV), or fresh humus samples equalling 2 g d.m. (III), or fresh humus samples equalling 2, 1.5 or 1 g d.m. depending on the volume of the sample (spatial sampling in IV) were used in the analyses.

The physico-chemical variables of the humus layer: $\text{pH}_{\text{H}_2\text{O}}$, 0.1 M BaCl_2 extractable cations (Al, B, Ca, Cd, Cu, Fe, K, Mg, Mn, Na, P, Zn), titrated acidity (H^+), base saturation (BS), cation exchange capacity (CEC), C, N, and C/N ratio, were determined according to the methods of Tamminen and Starr (1990). The dissolved organic carbon (DOC) and nitrogen (DON), which could be eluted into 100 ml water from 2 g d.m. humus by shaking for 2 h at 200 rpm was measured, after filtering the solution through a S&S 589³ filter paper, with an Analytic Jenan MULTI-NC in study III.

2.9 Statistical analyses

A Generalized Additive Mixed Model (GAMM) was used to test hypotheses concerning trampling tolerance of the forest types and to quantify the effects of factors thought to affect the cover of understorey vegetation (II). In study IV, GAMMs were used in order to reveal the magnitude and extent of the effects of forest edges and paths on microbial biomass and microbial activity. The R statistical software was used to run the GAMMs (R Development Core Team 2005).

Global Non-Metric Multi-Dimensional Scaling (GNMDS) was used to relate differences in vegetation and soil microbial community structure to the level of wear (I and III) and to study the effects of forest edges and paths on microbial community structure (IV). The Bray-Curtis coefficient was used as a dissimilarity measure and Permutation tests were used in the vector fitting procedure (Oksanen et al. 2005).

Principal Component Analysis (PCA) and sample scores along the first principal component (PC1) were used to summarize the microbial community structure in the spatial analysis (IV). To characterise and illustrate spatial variability in these scores and other variables analysed, geostatistical methods were used (Isaaks and Srivastava 1989). Variograms were calculated per sample plot, and exponential equations were used to explore the degree and range of spatial autocorrelation within the plot. Block kriging with the equations fitted to the variograms was used to interpolate the values of the variables inside the plots, and maps were drawn of these interpolated values.

One-way analysis of variance (ANOVA), along with Tukey's HSD test, or the non-parametric Kruskal-Wallis test were used in comparing vegetation composition between wear classes and between urban forests and reference areas (I), and in comparing PLFAs, microbial biomass and microbial activity between path area classes (III). In study II, either t-tests or nonparametric Mann-Whitney tests were used when comparing vegetation composition between urban and reference forests.

3 RESULTS

3.1 Recreational use

3.1.1 Effects of recreational use on understorey vegetation

Wear of understorey vegetation and area of paths correlated positively with the number of residents (indicating recreational pressure) around a forest patch (I, II). An increase of 15000 residents within a radius of 1 km around a forest patch was associated with ca. 30% decrease in the relative understorey vegetation cover of OMT, MT and VT urban forests (II). The relative cover of understorey vegetation was highest in herb-rich OMT, lower in mesic MT and lowest in sub-xeric VT. Thus, the trampling tolerance of understorey vegetation increased with increasing fertility of the forest type: OMT proved to be most tolerant, MT intermediately tolerant and VT least tolerant of the three forest types. The cover of ground layer in the three urban forest types was less than half of that in untrampled reference areas. Hence, total cover of understorey vegetation in the urban forests was also lower than that of the same forest types in the reference areas.

Typical MT forest species, namely dwarf shrubs (e.g. *Vaccinium myrtillus* and *V. vitis-idaea*), mosses (e.g. *Pleurozium schreberi* and *Dicranum polysetum*) and herbs (e.g. *Melampyrum pratense* and *Trientalis europaea*), were more frequent and/or abundant in untrampled (wear class 1) than in trampled (wear classes 2 and 3) urban forests (Table 2A) (I). Fewer species (e.g. *Pohlia nutans* and *Sorbus aucuparia*) were more frequent and/or abundant in trampled than in untrampled areas (Table 2B). Cover of grasses (in total) did not increase with the increasing levels of wear. Some mesic species, such as *Convallaria majalis* and *Melica nutans*, occurred also in trampled areas (I).

In general, when compared to percentage covers in the reference areas, covers of mosses (e.g. *Pleurozium schreberi*, *Dicranum polysetum* and *Hylocomium splendens*), lichens, and dwarf shrubs, especially *Vaccinium vitis-idaea*, were lower in the urban forests (I, II). In contrast, covers of tree saplings (mainly *Sorbus aucuparia*) and of some herbs and ferns (e.g. *Melampyrum pratense*, *Trientalis europaea* and *Pteridium aquilinum*) were higher in the urban forests than in the reference areas (II). *Brachythecium oedipodium* and *Pohlia nutans* were more abundant in the urban forests than in the reference areas but the cover of grasses did not differ between the areas (I, II).

3.1.2 Effects of recreational use on soil physico-chemical properties

Soil pH and BS were higher in areas with more than 5 m² paths per 100m² (path area class 3) than in areas with no paths (path area class 1) (III). The pH was 0.3 units higher on than next to paths, and increased with increasing levels of wear with a difference of almost 0.1 pH unit between wear classes of paths (IV). BS was almost 10% higher at heavily and very heavily worn (wear classes 3 and 4) than at lightly and moderately worn (wear classes 1 and 2) paths (IV). DOC, DON, N and other soil physico-chemical variables tested were not affected by recreational use (III).

Table 2. (A) Species with higher mean cover percentage or frequency in untrampled (wear class 1) than in trampled urban forests. **(B)** Species with higher mean cover percentage or frequency in trampled (wear classes 2 and 3) than in untrampled urban forests (I). Species in decreasing order of cover percentage and frequency.

(A) Untrampled urban forests	
Cover%	Frequency
<i>Vaccinium myrtillus</i>	<i>Vaccinium vitis-idaea</i>
<i>Pleurozium schreberi</i>	<i>Descampsia flexuosa</i>
	<i>Trientalis europaea</i>
	<i>Luzula pilosa</i>
	<i>Dicranum polysetum</i>
	<i>Melampyrum pratense</i>
	<i>Plagiothecium laetum</i>
	Hepaticae
	<i>Dicranum majus</i>
	<i>Hylocomium splendens</i>
	<i>Linnaea borealis</i>
	<i>Polytrichum commune</i>
	<i>Carex globularis</i>
	<i>Cladonia</i> spp.
	<i>Populus tremula</i>
	<i>Sphagnum angustifolium</i>
(B) Trampled urban forests	
Cover%	Frequency
<i>Sorbus aucuparia</i>	<i>Brachythecium oedipodium</i>
	<i>Pohlia nutans</i>
	<i>Plagiothecium curvifolium</i>
	<i>Pinus sylvestris</i>
	<i>Agrostis capillaris</i>

3.1.3 Effects of recreational use on soil microbial community

Changes in microbial community structure (PLFA pattern) were associated with the effects of recreational use on vegetation and soil (III). Variation in the microbial community structure correlated with variation in the tree species (broad-leaved tree/conifer) ratio, understorey species composition and soil chemistry, mainly pH and C/N ratio (III, IV). Wear of vegetation (especially dwarf shrubs) significantly affected the PLFA pattern (III). Absolute amounts of nine PLFAs out of 39 were significantly lower in areas with more than 5 m² paths per 100 m² (path area class 3) than in areas with no paths (path area class 1). PLFA pattern differed between paths and untrampled areas (IV). Path edge effect on the microbial community structure extended more than one meter from the paths. Spatial autocorrelation of the PLFA

pattern within an untrampled area extended to 0.7 m while on and next to paths this range was 1.5 m.

Microbial biomass (Gram-positive bacteria, fungi, actinomycetes and arbuscular mycorrhiza) were significantly affected by distance from the path (IV). Paths supported approximately 25–30% higher microbial biomass than untrampled areas with a transition zone of at least 1 m from the path edge. The ratio of fungal to bacterial biomass (F/B) was higher on paths than next to them and higher at heavily and very heavily worn paths (wear classes 3 and 4) than at lightly and moderately worn ones (classes 1 and 2).

Microbial activity, measured as basal respiration, was lower in areas with more than 5 m² paths per 100 m² (path area class 3) as compared to areas with no paths (path area class 1) (III). However, the activity was higher at moderately worn paths (wear class 2) than at lightly and very heavily worn paths (classes 1 and 4) (IV).

3.2 Fragmentation

3.2.1 Effects of fragmentation on understorey vegetation

Forest size was associated with understorey species composition and correlated with tree species composition (but not with the level of wear) (I). Broad-leaved trees along with light-demanding and drought-resistant understorey species, such as grasses, and some ruderal species (e.g. *Senecio vulgaris*, *Rubus idaeus*, *Taraxacum species*, *Hieracium sylvaticum* and *Veronica officinalis*) were more abundant in small forest fragments. Cover of litter in small forest fragments was high, and cover of mosses and other shade demanding interior species was low.

3.2.2 Effects of fragmentation on soil physico-chemical properties

Soil pH and BS were higher at forest edges and correlated positively with the number of broad-leaved trees and the cover of grasses (III, IV). Soil pH decreased by 0.7 units from 4.8 at the forest edge to between 4.0–4.2 at distances 20 m and further into the forests, while humus moisture increased from approximately 20% to 35–40% at the same distances (IV). C/N ratio, as well as C, N, K, CEC, H⁺, Fe and Al, increased with increasing distance from the forest edge and correlated positively with the number of conifers and cover of mosses.

3.2.3 Effects of fragmentation on soil microbial community

Microbial community structure (PLFA pattern) changed due to the effects of fragmentation on vegetation (III, IV). The PLFA pattern differed slightly between distances of 0–10 m and over 50 m from the forest edge (IV). Variation in PLFA pattern was associated with edge-interior gradients in vegetation and soil chemistry (III, IV). Changes in the microbial community structure correlated strongly with changes in soil pH and C/N ratio (III, IV).

Microbial biomass (Gram-positive and Gram-negative bacteria, fungi, actinomycetes and arbuscular mycorrhiza) and microbial activity (basal respiration rate) were significantly affected by distance from the edge, soil pH and C/N ratio (IV). They were 30–45% lower near the forest edge, increasing up to 20 m from the edge where they reached the level characteristic for the forest interior. Humus moisture explained a significant amount of variation in microbial responses to distance from the edge.

4 DISCUSSION

The results showed that recreational use and fragmentation (including edge effects) greatly affected understorey vegetation in the urban forests studied. In addition to forest site type, species composition and abundance of understorey vegetation were influenced by number of recreational users, forest size and the related broad-leaved tree/conifer ratio and soil chemistry. Most probably, air-borne pollution and forest management practices also affect understorey vegetation in urban forests. Furthermore, soil microbial community structure, as well as microbial biomass and activity in urban forests were affected by recreational use and fragmentation, and by related changes in the broad-leaved tree/conifer ratio, understorey species composition and soil properties, mainly pH, C/N ratio and soil moisture. In the following, the effects of these anthropogenic factors on vegetation, soil properties and microbial communities in the studied urban forests will be discussed.

4.1 Effects of recreational use on understorey vegetation

4.1.1 *Trampling tolerance of understorey vegetation*

The number of residents reflects well the recreational pressure placed on understorey vegetation: the greater the number of residents, the lower the cover of vegetation and larger the area of paths. In forests with 6500–8000 residents in the surroundings (within a radius of 1 km), the relative cover of understorey vegetation was 85% of that in forests without residents in the surroundings, whereas 15000 residents around a forest patch decreased the relative understorey vegetation cover to 70%. The loss of understorey vegetation is not surprising because people in urban areas tend to use forests near them on a daily basis (Jaatinen 1973, Sievänen 1987, Arnberger 2006). Children in particular use forests < 100 m from their homes (Florgård and Forsberg 2006).

According to some studies, small forest patches and forest edges are the most worn areas due to active recreational use (Kellomäki and Wuorenrinne 1979, Guirado et al. 2006). However, in this study neither the distance from forest edge nor the forest size correlated with the wear of understorey vegetation. This may be because some patches attract more people than others. They may be of scenic beauty, as rocky outcrops and different water elements are attractive to recreational users (Hammitt and Cole 1998). The most heavily worn patches are easy to access, easy to walk in and they are often used as shortcuts, e.g. between home and bus stop or school and sports field. There are also heavily worn areas in larger forests in the proximity of constructed paths actively used for recreation. In Finland, there are only few restrictions on the use of urban forests for recreational purposes. Thus, people often move off the ‘official’ paths, especially if these are poorly managed (see Hammitt and Cole 1998) or when they are orienteering, picking berries or gathering mushrooms.

The present results support the view that the trampling tolerance of forest vegetation increases with the productivity of the site. Trampling tolerance of sub-xeric VT was lower than that of mesic MT and herb-rich OMT, which is consistent with the results of Kellomäki and Saastamoinen (1975), Liddle (1975b) and Tolvanen et al. (2001). Herb-rich OMT proved to be most tolerant of the three forest types, which was against expectations based on the findings of Kellomäki and Saastamoinen (1975). They suggested that the trampling tolerance of OMT might be lower than that of MT because of the abundance of sensitive herb species. However, the high proportion of herbs in relation to dwarf shrubs may actually be the reason

for high trampling tolerance of OMT since herbs are more resilient, i.e. recover faster after trampling, than dwarf shrubs (Cole 1995). Furthermore, regeneration after disturbance is fastest in OMT, the forest type with the highest productivity (see Cole 1987, Liddle 1997, Rydgren et al. 1998). Nutrient load in urban areas may accelerate the regeneration of OMT vegetation since fast growing grass and herb species are abundant. Thus, it appears that resilience rather than resistance of plant species determines the tolerance of vegetation during a long-term trampling disturbance (see also Cole 1995).

A further contribution to the apparently higher trampling tolerance of OMT may be the vegetation structure of OMT itself. The number of small trees and shrubs in OMT is higher than in MT and VT (Table 5 in study II), which may restrict recreational use in OMT or at least concentrate it mainly on existing paths (Lehvävirta 1999). It is easier to walk in lower and sparser VT vegetation dominated by dwarf shrubs and mosses, which may lead to more dispersed use and more extensive wear of VT sites (Roovers et al. 2006).

4.1.2 Effects of recreational use on understorey species composition

Typical forest species, such as dwarf shrubs and mosses, suffered from trampling and few tolerant species benefited from it. Sensitive species survived in patches of untrampled vegetation, but on paths, only the most tolerant species survived and were dwarfed. Hamberg et al. (2007) found that the effects of trampling were most severe on paths but that light effects occurred also in seemingly untrampled areas. For example, they found that the cover and/or frequency of mosses and *Vaccinium myrtillus* were affected off the paths as well as on them, which is in accordance with the present results. In addition to direct mechanical effects of trampling, changes in soil chemistry may also have affected species composition on paths and trampled areas where the soil pH and BS were higher than in untrampled areas (III, IV). This may also explain the increase of mesic species observed in trampled areas.

The most pronounced effect of trampling in urban forests seemed to be the overall decrease in the cover of ground layer vegetation. In general, the trampling tolerance of mosses and particularly lichens is low (Kellomäki and Saastamoinen 1975, Nylund et al. 1979, Florgård 2000, Hamberg et al. 2007). *Dicranum polysetum*, *Hylocomium splendens*, and *Pleurozium schreberi*, in particular, decreased in the present set of urban forests, probably due to their slow rate of recovery after trampling. For example, *H. splendens* recovers slowly after disturbance because it lacks a soil-buried propagule bank (Jonsson 1993). Furthermore, microclimate in highly trampled urban forests may be suboptimal for mosses because paths and their surroundings are usually drier and warmer than areas of intact vegetation (Liddle 1997). For example, *H. splendens* is highly sensitive to changes in microclimate, especially to lowered availability of moisture (Busby et al. 1978, Callaghan et al. 1978).

The cover of dwarf shrubs, especially evergreen *Vaccinium vitis-idaea*, was low in the urban forests studied. The cover of *V. myrtillus* decreased with increasing levels of wear, indicating its sensitivity to trampling. In general, dwarf shrubs are sensitive to trampling because their regenerative buds are located above ground (Cole 1995, Liddle 1997), and vegetative regrowth after disturbance takes several years (Rydgren et al. 1998, Hautala et al. 2001), which makes recovery almost impossible in frequently trampled areas.

Trampling creates openings in the forest floor and provides opportunities for pioneer species or species originating outside the forest to establish (Hamberg et al. 2007). In urban forests studied, small tree saplings (< 50 cm in height), especially *Sorbus aucuparia*, were common probably because they benefited from free growing space created by moderate trampling. The openings established in the ground layer may especially enhance the regeneration of tree

saplings from seeds (Kuuluvainen 1994, Rydgren et al. 1998). In addition, trampling, cutting and the removal of saplings may increase vegetative growth of *S. aucuparia* from root suckers (Kullman 1986, Zerbe 2001). Lehvävirta and Rita (2002) also found that anthropogenic disturbance had some positive effect on aspen, birch and rowan saplings in urban forests.

This study showed that resilient species (e.g. *Pteridium aquilinum*, *Trientalis europaea* and *Melampyrum pratense*) thrived in urban forests. These species are not resistant to trampling but they are able to recover well after trampling disturbance (Lehtilä and Syrjänen 1995, Littlemore and Barker 2003). *M. pratense* has a good ability to recover from damage by compensatory growth (Lehtilä and Syrjänen 1995). *T. europaea* may benefit from free growing space created by trampling because its clonal spreading after disturbance is fast (Hiirsalmi 1969, Rydgren et al. 1998). Furthermore, the present results showed that the pioneer moss species *Pohlia nutans* has increased in urban forests. It efficiently colonizes bare humus after trampling disturbance, by germinating from a soil-buried propagule bank (Jonsson 1993, Koponen 1994, Rydgren et al. 1998). Grasses are known to be resilient species as they regenerate fast after disturbance, and thus, it has been suggested that trampling may increase their proportion in the vegetation (Liddle 1975a, Kellomäki 1977, Nylund et al. 1979, Tolvanen et al. 2001). However, the present results and results of Hamberg et al. (2007) showed that trampling did not increase the proportion of grasses in hemiboreal urban forests.

4.1.3 Tree layer characteristics and understorey vegetation composition

Upper canopy layers of urban forests were more open than in reference forests, probably because forest management in urban areas does not aim at a high production of timber as is the case in commercial forests (Gundersen et al. 2005). Furthermore, recreational users prefer open, clean and safe-looking forests (Tyrväinen et al. 2003), which has consequences for forest management decisions in urban areas.

Forest management practices, e.g. thinning to create more open and less shady forests, as well as undergrowth cuttings that increase vegetative growth of *Sorbus aucuparia* (Kullman 1986, Zerbe 2001), may explain the increased cover of small broad-leaved trees (height > 50 cm and dbh < 5 cm) found in these urban forests. In addition, exclusion of moose from urban forests may have an effect on tree species composition because moose mainly browse *Sorbus aucuparia*, *Populus tremula* and *Salix caprea* saplings (Andren and Angelstam 1993). In addition, fragmentation and eutrophication of urban forests may also have been beneficial for broad-leaved trees (discussed below). Consequently, urban forests may change towards domination by broad-leaved trees.

Changes in tree stand characteristics, such as tree density and ratio of broad-leaved trees to conifers, affect understorey vegetation composition (Kuusipalo 1983, 1985, Mikola 1985, Lahti and Väisänen 1987). In the present study, the percentage of broad-leaved trees (of all trees) was a good explanatory variable for total understorey vegetation cover. The cover increased with increasing percentage of broad-leaved trees, which is in accordance with previous studies (Mikola 1985, Lahti and Väisänen 1987). Under broad-leaved trees (e.g. *Betula pendula* and *B. pubescens*), soil fertility is higher and light and temperature conditions are more optimal for fast-growing and light-demanding herb and grass species, which increase in cover (Mikola 1985). The cover of litter, which increased with increasing amount of broad-leaved trees, was also an important determinant of understorey vegetation. The cover of mosses decreases with increasing amounts of litter (Mikola 1985, Lahti and Väisänen 1987, Hamberg et al. 2007). Thus, in the future mosses may gradually disappear and herbs and grasses may become dominant in urban forests.

4.2 Effects of recreational use on soil microbial community

4.2.1 *Effects of recreational use on microbial community structure*

By sampling systematically over study sites as well as by sampling directly on paths and in their vicinity, differences in microbial community structure (PLFA pattern) and activity caused by trampling were found. As the results showed, the most pronounced and obvious impact of recreational use occurred on paths where vegetation and soil changes are inevitable (Cole 1995). However, effects of trampling on microbial community structure and microbial biomass extended more than one meter from the paths. This may be caused by light trampling off the paths by both recreationists and their dogs, and fouling by dogs which inflicts changes in vegetation and soil pH. Microclimatic changes on paths may also occur and they may affect surrounding vegetation (Liddle 1997). Effects of trampling on covers and frequencies of plant species (especially mosses) have been shown to extend several meters off the paths (Hamberg et al. 2007). These changes may explain the effects observed in the soil microbial community in this study.

Differences discovered in PLFA pattern and microbial biomass between paths and untrampled areas were mainly attributable to differences in humus pH. Indeed, microsite variation in soil pH is the most relevant determinant of microbial community (Killham 1994). The present results showed that a spatial autocorrelation of PLFA pattern in an untrampled control area extended approximately 0.7 m, which implies that patches of the similar PLFA pattern reflect the zone of influence of dwarf shrubs and other boreal forest understorey vegetation (Ettema and Wardle 2002). Some studies report patches extending from one to several meters and relate the results to the zone of influence and positioning of single trees (Pennanen et al. 1999, Saetre and Bååth 2000). According to the present results, trampling disrupts the small-scale heterogeneity in the soil microbial community, since patch sizes of the similar microbial community on paths and next to them were two times larger than in the untrampled area. This disruption of small-scale spatial heterogeneity may influence spatial patterns of decomposition, nutrient supply and root herbivory, and thus the spatial structure and diversity of plant communities (Ettema and Wardle 2002). Furthermore, spatial changes in the functions of mycorrhizal fungi may hinder re-establishment and growth of plants in trampled areas (Reeves et al. 1979, Van der Heijden et al. 1998b, Hartnett and Wilson 1999, Kozłowski 1999, Waltert et al. 2002).

4.2.2 *Effects of recreational use on microbial biomass*

All microbial biomasses were higher on paths and immediately next to paths, although microbial activity and biomass (especially the biomasses of bacteria and actinomycetes) were expected to be adversely affected by trampling, to increase with increasing distance from paths, and to decrease with increasing levels of wear (Liddle 1997, Zabinski and Gannon 1997, Ohtonen and Väre 1998). pH levels on paths were 0.3 units higher than in untrampled areas, which is in accordance with other studies conducted in acid soils (reviewed by Liddle 1997). This may explain the higher microbial biomass observed, because the biomasses of bacteria, actinomycetes and arbuscular mycorrhiza are all known to increase with increasing soil pH (Frostegård et al. 1993, Bååth et al. 1995).

Soil pH on paths may be higher because 1) trampling diminishes vegetation cover and changes the amount and quality of litter on paths, e.g., reducing the amount of acidic litter

including needles and mosses, causing changes in soil organic matter and pH; 2) the humus layer on paths is eroded and in some areas almost completely removed and, thus mixed with exposed mineral soil. Mineral soils further down the soil profile have typically higher pH than the humus layer (Pietikäinen et al. 1999, Fritze et al. 2000); 3) amount of dog excrement on paths and next to them may be high and urease and other N-mineralising activities in soil tend to raise pH. In the vicinity of urea and animal wastes, the soil pH may be several units higher than in the bulk soil (Killham 1994).

In addition to the increase in pH, other mechanisms can also explain the higher microbial biomass on paths. Due to trampling, litter on paths may be pulverized and thus become more easily decomposable (see Liddle 1997, Ros et al. 2004), thereby contributing to an enhanced microbial biomass. Compaction may reduce predation by protozoa and nematodes in the soil because it causes a reduction in the number of soil pores $> 30 \mu\text{m}$ in neck diameter (Killham 1994, Breland and Hansen 1996). In contrast, the number of small pores (neck diameter $< 3 \mu\text{m}$) inhabited by microbes may increase (Breland and Hansen 1996). Furthermore, root exudation of plants, which stimulates microbial growth, has been shown to increase with increasing mechanical impedance (Boeuf-Tremblay et al. 1995).

4.2.3 *Effects of recreational use on microbial activity*

Microbial activity decreases due to loss of vegetation and/or soil compaction caused by trampling (Liddle 1997, Zabinski and Gannon 1997, Ohtonen and Väre 1998, Breland and Hansen 1996). According to Efremov and Novikova (2003), enzymatic activity and microbial biomass decrease with an increase in soil bulk density during recreational use. Furthermore, compaction of soil increases soil anaerobiosis and consequently decreases microbial activity (Hubbell and Gardner 1948, Liddle 1997, Hammitt and Cole 1998, Jordan et al. 2003). The present results showed that microbial activity was lower in trampled areas (with more than 5% coverage of paths) than in areas with no paths. However, the results did not confirm the hypothesis that microbial activity would be lower on paths than further away from them. Thus, anaerobiosis may not be severe in the present study probably because the organic humus layer is not very easily compacted (Hammitt and Cole 1998).

Interestingly, moderately worn paths exhibited higher microbial activity (basal respiration rates) than lightly and very heavily worn paths in this study. These findings agree with those of Ros et al. (2004) who showed that microbial biomass carbon and microbial activity as well as several enzymatic activities increased with increasing intensity of trampling, being highest at moderate levels of trampling. They suggested that trampling increased incorporation of plant remains into soil and thus increased soil organic carbon content and hence available enzyme substrates (see also Liddle 1997, Hammitt and Cole 1998). Another reason for increased microbial activity could be stress inflicted on the microbial populations by trampling, as overall metabolic activity has been shown to increase in stress conditions (Killham 1985). Furthermore, paths are usually warmer than the surroundings covered by vegetation (Liddle 1997), which may increase microbial activity to a certain level, at least if soil moisture is sufficient (Killham 1994).

As Killham (1985) pointed out, the effects of environmental stresses on microbial functions should be evaluated by using metabolic quotient (usually calculated as respired C/biomass C) rather than by microbial activity *per se*, because the metabolic quotient is a more sensitive indicator of change (see also Ohtonen 1994). Therefore, basal respiration rate/total microbial biomass was calculated for the present set of study plots and it was found that the value

was significantly lower on paths than in areas more than 1.5 m away from them, 0.0056 and 0.0073 respectively ($p < 0.001$). Thus, the findings suggest that trampling inflicts stress on soil microbial community.

4.3 Effects of fragmentation on understorey vegetation

4.3.1 Edge effects and understorey species composition

Vegetation in small forest fragments was characterized by an abundance of broad-leaved trees, grasses and herbs, which increased the amount of leaf litter on the ground. Hamberg et al. (2007) also found that species adapted to sunny, warm and dry conditions, such as grasses, were abundant while sensitive forest species, such as dwarf shrubs and mosses, were scarce at urban forest edges in Helsinki. They showed that the effects of edge on the understorey vegetation extended at least up to 50 m into the forests. Forest edges receive more light and are warmer and drier than forest interiors (Chen et al. 1993, 1995). The present results showed that soil moisture near the edge was only half of that in the forest interior. Thus, microclimate is too dry for mosses (Huggard and Vyse 2002) and probably also for other interior species at forest edges. Furthermore, mosses tend to withdraw from areas with an abundance of litter as found at forest edges in this study (Lahti and Väisänen 1987). Thus, mosses may be scarce or almost absent in small urban forest fragments with large proportion of edge zone. In contrast, some species, such as light demanding *Pteridium aquilinum* and *Melampyrum pratense*, which are abundant in urban forests studied, may benefit from the abundance of broad-leaved trees and open canopy structure in small forest fragments and in the proximity of forest edges (Hämet-Ahti et al. 1998, Tonteri 2000).

4.3.2 Eutrophication and understorey species composition

Soil pH and BS were higher and C/N ratio was lower at the forest edges than in the interiors in this study. Broad-leaved trees, grasses and herbs abundant at forest edges have a fertilizing effect on the soil through their above and below ground litter and root activities (see Mikola 1985, Priha 1999). In addition, forest edges act as concentrators of air-borne pollutants and nutrients, e.g. nitrogenous compounds (Bobbink et al. 1998, Weathers et al. 2001). Furthermore, local residents often dump garden waste at forest edges bordering their gardens (Matlack 1993b, Saukkonen 2007), which may locally increase soil nutrient levels at the edges and increase nutrient-demanding herb and grass species there.

Nitrogen load may increase soil fertility and cause decreases in the proportions not only of bryophytes and lichens but also of dwarf shrubs, while causing an increase in the proportion of herbs and grasses in forest vegetation (Kuusipalo 1996). For example, low covers of *Pleurozium schreberi* and *Hylocomium splendens* in urban forests and especially at forest edges may partly be due to nitrogen load and acid deposition in urban areas (Dirkse and Martakis 1992, Mäkipää 2000a, b). The present results indicated the presence of eutrophication caused by nitrogen load especially in VT, where the cover of herbs increased and the covers of dwarf shrubs, mosses and lichens decreased. However, this phenomenon could not be confirmed in the urban forests studied since soil N levels at the forest edges were not detectably higher than in the interiors. Pollutant concentrations in Finland are generally low. When compared to other European air quality monitoring results (5208 measurements in 25 countries in 2000), Finland was the country with the nitrogen dioxide concentrations, only 55% of the European

average (Anttila et al. 2003). Thus, the effects on forest vegetation may be less severe than in more polluted areas in Europe.

4.4 Effects of fragmentation on soil microbial community

4.4.1 Effects of fragmentation on microbial community structure

Variation observed in the structure of the humus microbial community (PLFA pattern) reflected differences in the vegetation (mainly the ratio of broad-leaved trees to conifers) between the forest edge and its interior. Broad-leaved trees and associated herbs and grasses were abundant at the forest edges and conifers and mosses in the forest interiors (see Hamberg et al. 2007). This change in vegetation was associated with an increase in pH and nutrient levels and a decrease in the C/N ratio of the humus layer near the forest edges, thus affecting the microbial community structure in a way similar to that shown here.

4.4.2 Effects of fragmentation on microbial biomass and microbial activity

Increases in soil pH and fertility have been reported to cause increases in the biomasses of Gram-negative bacteria, arbuscular mycorrhiza and actinomycetes and microbial activity (Frostegård et al. 1993, Bååth et al. 1995, Pietikäinen and Fritze 1995, Pennanen et al. 1999, Saetre 1999, Priha et al. 2001). However, in the present study biomasses of all microbial groups as well as microbial activity (measured as basal respiration) increased with increasing distance from the edge, irrespective of soil pH and fertility. The low levels of microbial biomass and microbial activity near the forest edge were attributable to low moisture content of humus. There is a positive correlation between soil biological activity and soil water content (Killham 1994). Soil microbes, bacteria in particular, are sensitive to water stress as they require an aqueous environment.

Soil moisture was negatively affected up to a distance of 20 m from south- to west-facing urban forest edges studied, which is 10 m more than at a northern edge in Sicamous Creek, British Columbia (Huggard and Vyse 2002), and approximately 30 m less than at open southern and western edges of mixed-mesophytic forest fragments in east-central Illinois (Gehlhausen et al. 2000). In the present study, humus moisture was 40-45% lower at the edge than in the forest interior, which is twice the percentage difference reported by Huggard and Vyse (2002). Macroclimate, edge orientation, edge structure and the landform or plant community type adjacent to the studied plant community can explain differences in microclimatic conditions between various edge environments/forest edges (Chen et al. 1993, 1995, Didham and Lawton 1999, Gehlhausen et al. 2000, Harper et al. 2005). In this study, abrupt urban forest edges bordered by artificially covered and/or built areas, received maximum radiation and wind. Wind penetration of forest edges increases evaporation and accentuates the drying effects of the sun (Saunders et al. 1991). In addition, urban land-use affects soil hydrology by increasing the surface runoff of rainwater and may create drought conditions due to drainage and impermeable surfaces such as asphalt roads and residential areas.

Microclimatic variables, particularly soil moisture content and temperature, seem to determine microbial activities in different edge environments (see Chen et al. 1999). According to preliminary results of Edmonds et al. (2000) litter decomposition rates were greater near a southwest-facing edge than in interiors of Douglas-fir forests in western Washington probably

owing to high soil moisture and temperatures. In Scotland, where native pine woodlands have expanded onto moorland soils, microbial biomass and basal respiration were higher in peaty and wet soils near the forest edge where pH and soil moisture content were higher than in the interior (Chapman et al. 2003). The present study suggests that low moisture content of humus may reduce microbial biomass and basal respiration at urban forest edges and highlights the importance of soil moisture for microbial activity.

The decreased microbial activity detected implies decreased litter decomposition rates, and thus, a change in ecosystem nutrient cycling at urban forest edges (see Pennanen 2001). Consequential changes in nutrient supply may affect structure and diversity of plant communities (Ettema and Wardle 2002). Changes in the biomass and activity of mycorrhizal fungi may reduce seedling regeneration (e.g. Waltert et al. 2002). These impacts complicate future maintenance of indigenous plant species in urban forest remnants.

5 IMPLICATIONS

Since trampling tolerance of vegetation increases with site fertility, I recommend promoting the use of more durable herb-rich forest type by constructing paths and guiding recreational use on these sites while protecting sub-xeric forest types by restricting recreational use of these sites that are particularly sensitive to trampling. For example, natural barriers, like fallen logs and thickets of shrubs and small trees, can be used to restrict trampling in sensitive areas (see Lehvävirta 1999). However, the larger the number of residents around a forest patch the more deteriorated the understorey vegetation will be, irrespective of site fertility. Thus, the number of forests left within and at the outskirts of cities should be large enough and, as mentioned above, sites should be managed to ameliorate the effects of recreational use.

There are paths in almost every forest fragment in Helsinki and the number of residents within a radius of 1–2 kilometers around a fragment correlates positively with the area of paths. On average, paths account for 5% of the forest area and their zone of influence (at least 1 m on both sides of a path) adds considerably to the area where small-scale spatial variation of the soil microbial community is disrupted and the microbial activity per unit of biomass is decreased. Vegetation on paths is almost totally worn away and light changes in vegetation can be detected up to 8 m away from paths (Hamberg et al. 2007). In Finland, there are only few restrictions on the use of urban forests for recreational purposes. Thus, people often move off the ‘official’ paths especially if these are poorly managed (see Hammitt and Cole 1998). This disperses the effects of trampling on the forest floor. Therefore, a well-designed and managed path network could efficiently concentrate the use of urban forest on fewer paths, and thus a smaller area.

According to the present results, the effects of forest edge on soil microbial biomass and activity penetrate 20 meters into urban forest patches from south to west facing edges. The effects on microbial community structure (PLFA pattern) penetrate even further – 50 meters – into forests similar to the effects on understorey vegetation in Helsinki (Hamberg et al. 2007). Thus, if a circular shape of an urban forest fragment and 20–50 m edge zone is used in calculations, 58–99% of a forest fragment 1 ha in size, 37–76% of a fragment 3 ha in size, and 29–64% of a fragment 5 ha in size are influenced by edge effects (Table 3). In these edge zones, microbial biomass and activity are considerably reduced, suggesting decreased

Table 3. Percentage of edge zones 20 and 50 m in depth in circular forest areas of different sizes.

Forest size (ha)	Edge zone 20 m (%)	Edge zone 50 m (%)
1	58	99
3	37	76
5	29	64
10	21	48

litter decomposition rates, and thus a change in ecosystem nutrient cycling (Pennanen 2001). In Helsinki, there are only four larger forest areas (Haltiala, Viikin Vanhankaupunginlahti, Uutela, Mustavuori) which are not totally affected by edge effects if a 50–100 m edge zone in all edge orientations is presumed (Saukkonen 2007). Although forest patches may be large enough, they may be suboptimal in shape. Narrow patches are totally affected by edge effects and consequently changed in soil microbial community and vegetation. The proportion of edge zone is smallest in circular patches. Thus, in addition to the quantity of patches and their quality (forest type), both size and shape of a fragment left within urban development should be taken into account when planning future residential areas.

REFERENCES

- Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968. Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici* 5: 169-211.
- Alvey, A.A. 2006. Promoting and preserving biodiversity in the urban forest. *Urban Forestry & Urban Greening* 5: 195-201.
- Andren, H. & Angelstam, P. 1993. Moose browsing on Scots Pine in relation to stand size and distance to forest edge. *Journal of Applied Ecology* 30(1): 133-142.
- Aneja, M.K., Sharma, S., Fleischmann, F., Stich, S., Heller, W., Bahnweg, G., Munch, J.C. & Schloter, M. 2006. Microbial colonization of beech and spruce litter - influence of decomposition site and plant species litter on the diversity of microbial community. *Microbial Ecology* 52: 127-135.
- Anttila, P., Alaviippola, B. & Salmi, T. 2003. Air quality in Finland - monitoring results in relation to the guideline and limit values and comparisons with European concentration levels (in Finnish with an English summary). Finnish Meteorological Institute, Publications on Air Quality No. 33.
- Arnberger, A. 2006. Recreation use of urban forests: An inter-area comparison. *Urban Forestry & Urban Greening* 4: 135-144.
- Bhujji, D.R. & Ohsawa, M. 1998. Effects of nature trails on ground vegetation and understorey colonization of a patchy remnant forest in an urban domain. *Biological Conservation* 85: 123-135.
- Bobbink, R., Hornung, M. & Roelofs, J.G.M. 1998. The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *Journal of Ecology* 86: 717-738.

- Boeuf-Tremblay, V., Plantureux, S. & Guckert, A. 1995. Influence of mechanical impedance on root exudation of maize seedlings at two development stages. *Plant and Soil* 172: 279-287.
- Breland, T.A. & Hansen, S. 1996. Nitrogen mineralization and microbial biomass as affected by soil compaction. *Soil Biology & Biochemistry* 28: 655-663.
- Brennan, P. 1988. Mycobacterium and other actinomycetes. In: Ratledge, C. & Wilkinson, S.G. (eds.). *Microbial Lipids*, Vol. 1. Academic Press, London. p. 203-298.
- Busby, J.R., Bliss, L.C. & Hamilton, C.D. 1978. Microclimate control of growth rate and habitats of the boreal forest mosses, *Tomenthypnum nitens* and *Hylocomium splendens*. *Ecological Monographs* 48: 95-110.
- Bååth, E., Frostegård, Å., Pennanen, T. & Fritze, H. 1995. Microbial community structure and pH response in relation to soil organic matter quality in wood-ash fertilized, clear-cut or burned coniferous forest soils. *Soil Biology & Biochemistry* 27: 229-240.
- , Frostegård, Å., Díaz-Raviña, M. & Tunlid, A. 1998. Microbial community-based measurements to estimate heavy metal effects in soil: the use of phospholipid fatty acid patterns and bacterial community tolerance. *Ambio* 27: 58-61.
- Cajander, A.K. 1926. The theory of forest types. *Acta Forestalia Fennica* 29(3): 1-108.
- Callaghan, T.V., Collins, N.J. & Callaghan C.H. 1978. Photosynthesis, growth and reproduction of *Hylocomium splendens* and *Polytrichum commune* in Swedish Lapland. *Oikos* 31: 73-88.
- Chapman, S.J., Campbell, C.D., Fraser, A.R. & Puri, G. 2003. Native woodland expansion: soil chemical and microbiological indicators of change. *Soil Biology & Biochemistry* 35: 753-764.
- Chen, J., Franklin, J.F. & Spies, T.A. 1993. Contrasting microclimates among clearcut, edge and interior of old-growth Douglas-fir forest. *Agricultural and Forest Meteorology* 63: 219-237.
- , Franklin, J.F. & Spies, T.A. 1995. Growing season microclimatic gradients extending into old-growth Douglas-fir forests from clearcut edges. *Ecological Applications* 5: 74-86.
- , Saunders, S.C., Crow, T.R., Naiman, R.J., Brososke, K.D., Mroz, G.D., Brookshire, B.L. & Franklin, J.F. 1999. Microclimate in forest ecosystem and landscape ecology. *BioScience* 49: 288-297.
- Cole, D.N. 1987. Effects of three seasons of experimental trampling on five montane forest communities and a grassland in Western Montana, USA. *Biological Conservation* 40: 219-244.
- 1995. Experimental trampling of vegetation. II. Predictors of resistance and resilience. *Journal of Vegetation Science* 32: 215-224.
- & Bayfield N.G. 1993. Recreational trampling of vegetation: standard experimental procedures. *Biological Conservation* 63: 209-215.
- Cole, D.W. & Rapp, M. 1981. Elemental cycling in forest ecosystems. In: Reichle, D.E. (ed.). *Dynamic properties of forest ecosystems*. Cambridge University Press, International Biological Programme 23. p. 341-409.
- Didham, R.K. & Lawton, J.H. 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. *Biotropica* 31: 17-30.
- Dirkse, G.M. & Martakis, G.F.P. 1992. Effects of fertilizer on bryophytes in Swedish experiments on forest fertilization. *Biological Conservation* 59: 155-161.
- Edmonds, R.L., Marra, J.L., Barg A.K. & Sparks, G.B. 2000. Influence of forest harvesting on soil organisms and decomposition in western Washington. USDA Forest Service General Technical Report PSW-GTR-178. p 53-71.

- Efremov A.L. & Novikova N.V. 2003. Biological peculiarities of soils under coniferous forest plantations in the recreation zone of the town of Mogilev (in Russian with an English summary). *Pochvovedenie* 10: 1228-1234.
- Ettema, C.H. & Wardle, D.A. 2002. Spatial soil ecology. *Trends in Ecology & Evolution* 17: 177-183.
- Florgård, C. 2000. Long-term changes in indigenous vegetation preserved in urban areas. *Landscape and Urban Planning* 52: 101-116.
- 2004. Remaining original natural vegetation in towns and cities – Introduction. *Urban Forestry & Urban Greening* 3: 1-2.
- & Forsberg, O. 2006. Residents' use of remnant natural vegetation in the residential area of Järvafältet, Stockholm. *Urban Forestry & Urban Greening*, 5: 83-92.
- Fritze, H., Pietikäinen, J. & Pennanen, T. 2000. Distribution of microbial biomass and phospholipid fatty acids in Podzol profiles under coniferous forest. *European Journal of Soil Science* 51: 565-573.
- Frostegård, Å. 1995. Phospholipid fatty acid analysis to detect changes in soil microbial community structure. PhD thesis. Department of Ecology, University of Lund.
- , Bååth, E. & Tunlid, A. 1993. Shifts in the structure of soil microbial communities in limed forest as revealed by phospholipid fatty acid analysis. *Soil Biology & Biochemistry* 25: 723-730.
- & Bååth, E. 1996. The use of phospholipid fatty acid analysis to estimate bacterial and fungal biomass in soil. *Biology and Fertility of Soils* 22: 59-65.
- Frumkin, H. 2003. Healthy places: exploring the evidence. *American Journal of Public Health* 93: 1451-1456.
- Gehlhausen, S.M., Schwartz, M.W. & Augspurger, C.K. 2000. Vegetation and microclimatic edge effects in two mixed-mesophytic forest fragments. *Plant Ecology* 147: 21-35.
- Gilbert, O.L. 1989. *The ecology of urban habitats*. University Press, Cambridge. 369 p.
- Goudie, A. 1990. *The human impact on the natural environment*. The MIT Press Cambridge, Massachusetts. 388 p.
- Gable, A.R. 1971. Effects of compaction on content and transmissions of air in soils. In: Barnes, K.K., Carleton, W.M., Taylor, H.M., Throckmorton, R.I. & Vanden Berg, G.E. (eds.). *Compaction of agricultural soils*. American Society of Agricultural Engineers, St Joseph. p. 154-164.
- Grayston, S.J., Vaughan, D. & Jones, D. 1996. Rhizosphere carbon flow in trees in comparison with annual plants: the importance of root exudation and its impacts on microbial activity and nutrient availability. *Applied Soil Ecology* 5: 29-56.
- Guirado, M., Pino, J. & Rodà, F. 2006. Understorey plant species richness and composition in metropolitan forest archipelagos: effects of forest size, adjacent land use and distance to the edge. *Global Ecology and Biogeography* 15: 50-62.
- Gundersen, V., Frivold, L. H., Löfström, I., Jørgensen, B.B., Falck, J. & Øyen, B.-H. 2005. Urban woodland management – the case of 13 major Nordic cities. *Urban Forestry & Urban Greening* 3: 189-202.
- Hamberg, L., Lehvävirta, S., Malmivaara-Lämsä, M., Rita, H. & Kotze, D.J. 2007. The effects of habitat edges and trampling on understorey vegetation in urban forests in Helsinki, Finland. *Applied Vegetation Science*, in press. Online version available at: <http://www.opuluspress.se>.
- Hammitt, W.E. & Cole, D.N. 1998. *Wildland recreation: ecology and management*. John Wiley and Sons, New York. 361 p.

- Hartnett, D.C. & Wilson, G.W.T. 1999. Mycorrhizae influence plant community structure and diversity in tall-grass prairie. *Ecology* 80: 1187-1195.
- Harper, K.A., MacDonald, S.E., Burton, P.J., Chen, J., Brosfoske, K.D., Saunders, S.C., Euskirchen, E.S., Roberts, D., Jaiteh, M.S. & Esseen P.-A. 2005. Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology* 19: 768-782.
- Hautala, H., Tolvanen, A. & Nuortila, C. 2001. Regeneration strategies of dominant boreal forest dwarf shrubs in response to selective removal of understorey layers. *Journal of Vegetation Science* 12: 503-510.
- Hiirsalmi, H. 1969. *Trientalis europaea* L.: A study of the reproductive biology, ecology and variation in Finland. *Annales Botanici Fennici* 6: 119-173.
- Holmström, H. 1970. Eräiden Etelä-Suomen vapaa-aika-alueiden kasvillisuuden kulutuskestävyyden tutkimus (in Finnish). Uudenmaan seutukaavaliitot, Lounais-Suomen seutukaavaliitto, Helsinki. 53 p.
- Hubbell, D.S. & Gardner, J.L. 1948. Effects of aeration, compaction, and water-logging on soil structure and microflora. *Journal of the American Society of Agronomy* 40: 832-840.
- Huggard, D.J. & Vyse, A. 2002. Edge effects in high-elevation forests at Sicamous Creek. *Silviculture*. Extension note 62, 1-8. Ministry of Forests, Forest Science Program, British Columbia.
- Hämet-Ahti, L., Suominen, J., Ulvinen, T. & Uotila, P., eds. 1998. *Retkeilykasvio* [Field flora of Finland]. Finnish Museum of Natural History, Botanical Museum, Helsinki.
- Isaaks, E.H. & Srivastava, R.M. 1989. *Applied geostatistics*. Oxford University Press, New York. 561 p.
- Jatinen, E. 1973. Recreational use of Helsinki's forests. *Folia Forestalia* 186.
- Jalonen, J. & Vanha-Majamaa, I. 2001. Immediate effects of four different felling methods on mature boreal spruce forest understorey vegetation in southern Finland. *Forest Ecology and Management* 146: 25-34.
- James, T.D.W., Smith, D.W., Mackintosh, E.E., Hoffman, M.K. & Monti P. 1979. Effects of camping recreation on soil, jack pine, and understorey vegetation in a northwestern Ontario park. *Forest Science* 25: 333-349.
- Jonsson, B.G. 1993. The bryophyte diaspore bank and its role after small-scale disturbance in a boreal forest. *Journal of Vegetation Science* 4: 819-826.
- Jordan, D., Ponder, F. Jr. & Hubbard, V.C. 2003. Effects of soil compaction, forest leaf litter and nitrogen fertilizer on two oak species and microbial activity. *Applied Soil Ecology* 23: 33-41.
- Kellomäki, S. 1977. Deterioration of forest ground cover during trampling. *Silva Fennica* 11(3): 153-161.
- & Saastamoinen, V.-L. 1975. Trampling tolerance of forest vegetation. *Acta Forestalia Fennica* 147: 1-22.
- & Wuorenrinne, H. 1979. On factors effecting on deterioration of urban forests (in Finnish with an English summary). *Silva Fennica* 13(2): 177-183.
- Killham, K. 1985. A physiological determination of the impact of environmental stress on the activity of microbial biomass. *Environmental pollution* 38: 283-294.
- 1994. *Soil Ecology*. Cambridge University Press, Cambridge. 242 p.
- Kemper, W.D., Stewart, B.A. & Porter, L.K. 1971. Effects of compaction on soil nutrient status. In: Barnes, K.K., Carleton, W.M., Taylor, H.M., Throckmorton, R.I. & Vanden Berg, G.E. (eds.). *Compaction of agricultural soils*. American Society of Agricultural Engineers, St Joseph. p. 178-189.

- Koponen, T. 1994. Lehtisammalten määrittäysopas [Moss identification guide]. Helsingin yliopiston kasvitieteen laitoksen monisteita 139, Helsinki.
- Kozłowski, T.T. 1999. Soil compaction and growth of woody plants. *Scandinavian Journal of Forest Research* 14: 596-619.
- Kroppenstedt, R.M. 1985. Fatty acid and menaquinone analysis of actinomycetes and related organisms. In: Goodfellow, M. & Minnikin, D.E. (eds.). *Chemical Methods in Bacterial Systematics*. Academic Press, London. p. 173-199.
- Kullman, L. 1986. Temporal and spatial aspects of subalpine populations of *Sorbus aucuparia* in Sweden. *Annales Botanici Fennici* 23: 267-275.
- Kurto, A. & Helynranta, L. 1998. Helsingin kasvit. Kukkivilta kiviltä metsän syliin [Flora of Helsinki. From flowering stones to forest floor]. City of Helsinki Environment Centre & Helsinki University Press, Helsinki. 400 p.
- Kuuluvainen, T. 1994. Gap disturbance, ground microtopography, and the regeneration dynamics of boreal coniferous forests in Finland: a review. *Annales Zoology Fennici* 31: 35-51.
- Kuusipalo, J. 1983. Distribution of vegetation on mesic forest sites in relation to some characteristics of the tree stand and soil fertility. *Silva Fennica* 17(4): 403-418.
- 1985. An ecological study of upland forest site classification in southern Finland. *Acta Forestalia Fennica* 192: 1-77.
- 1996. Suomen metsätyypit [Forest site types in Finland]. Kirjayhtymä, Helsinki. 144 p.
- Lahti, T. & Väisänen, R.A. 1987. Ecological gradients of boreal forests in South Finland: an ordination test of Cajander's forest site type theory. *Vegetatio* 68: 145-156.
- Legg, M.H. & Schneider, G. 1977. Soil deterioration on campsites: northern forest types. *Soil Science Society of America Journal* 41: 437-441.
- Lehtilä, K. & Syrjänen, K. 1995. Compensatory responses of two *Melampyrum* species after damage. *Functional Ecology* 9: 511-517.
- Lehvävirta, S. 1999. Structural elements as barriers against wear in urban woodlands. *Urban Ecosystems* 3: 45-56.
- 2005. Urban woodland ecology – methodological perspectives and empirical studies. PhD thesis. Department of Biological and Environmental Sciences, University of Helsinki, Finland. 8 p. + 7 papers.
- & Rita, H. 2002. Natural regeneration of trees in urban woodlands. *Journal of Vegetation Science* 13: 57-66.
- Liddle, M.J. 1975a. A selective review of the ecological effects of human trampling on natural ecosystems. *Biological Conservation* 7: 17-36.
- 1975b. A theoretical relationship between the primary productivity of vegetation and its ability to tolerate trampling. *Biological Conservation* 8: 251-255.
- 1997. *Recreation ecology: The ecological impact of outdoor recreation and ecotourism*. Chapman & Hall, London. 639 p.
- & Moore, K.G. 1974. The microclimate of sand dune tracks: the relative contribution of vegetation removal and soil compression. *Journal of Applied Ecology* 2: 1057-1068.
- Littlemore, J. & Barker, S. 2003. The ecological response of forest ground flora and soils to experimental trampling in British urban woodlands. *Urban Ecosystems* 5: 257-276.
- Lovejoy, T.E. & Oren, D.C. 1981. The minimum critical size of ecosystems. In: Burgess, R.L. & Sharpe, D.M. (eds.). *Forest island dynamics in man-dominated landscapes*, *Ecological studies* 41. Springer-Verlag, New York. p. 7-12.
- Löfström, I. 1987. Taajamametsien hoito (in Finnish). *Folia Forestalia* 693: 1-53.

- Maene, S. 2005. Dead wood in urban forests in Helsinki, Finland. MSc thesis, Department of Biological and Environmental Sciences, University of Helsinki, Finland. 45 p.
- Marschner, P., Crowley, D & Yang, C.H. 2004. Development of specific rhizosphere bacterial communities in relation to plant species, nutrition and soil type. *Plant and Soil* 261: 199-208.
- Matlack, G.R. 1993a. Microenvironment variation within and among forest edge sites in the eastern United States. *Biological Conservation* 66: 185-194.
- 1993b. Sociological edge effects: Spatial distribution of human impact in suburban forest fragments. *Environmental Management* 17: 829-835.
- McDonnell, M.J., Pickett, S.T.A., Groffman, P., Bohlen, P., Pouyat, R.V., Zipperer, W.C., Parmelee, R.W., Carreiro, M.M. & Medley, K. 1997. Ecosystem processes along an urban-to-rural gradient. *Urban Ecosystems* 1: 21-36.
- McPherson, E.G., Nowak D., Heisler, G., Grimmond, S., Souch, C., Grant, R. & Rowntree, R. 1997. Quantifying urban forest structure, function, and value: the Chicago Urban Forest Climate Project. *Urban Ecosystems* 1: 49-61.
- Mikola, P. 1985. The effect of tree species on the biological properties of forest soil. National Swedish Environmental Protection Board, Rapport 3017. 27 p.
- Murcia, C. 1995. Edge effect in fragmented forests: implication for conservation. *Trends in Ecology & Evolution* 10: 58-62.
- Mäkipää, R. 2000a. *Pleurozium schreberi*. In: Reinikainen, A., Mäkipää, R., Vanha-Majamaa, I. & Hotanen, J.-P. (eds.). *Kasvit muuttuvassa metsäluonnossa [Changes in the frequency and abundance of forest and mire plants in Finland since 1950]*. Tammi, Helsinki. p. 251-253.
- 2000b. *Hylocomium splendens*. In: Reinikainen, A., Mäkipää, R., Vanha-Majamaa, I. & Hotanen, J.-P. (eds.). *Kasvit muuttuvassa metsäluonnossa [Changes in the frequency and abundance of forest and mire plants in Finland since 1950]*. Tammi, Helsinki. p. 248-250.
- Nylund, M., Nylund, L., Kellomäki, S. & Haapanen, A. 1979. Deterioration of forest ground vegetation and decrease of radial growth of trees on camping sites. *Silva Fennica* 13: 343-356.
- Ohtonen, R. 1994. Accumulation of organic matter along a pollution gradient: application of Odum's theory of ecosystem energetics. *Microbial Ecology* 27: 43-55.
- & Väre, H. 1998. Vegetation composition determines microbial activities in a boreal forest soil. *Microbial Ecology* 36: 328-335.
- Oke, T.R. 1989. The micrometeorology of the urban forest. *Philosophical Transactions of the Royal Society of London* 324: 335-349.
- Oksanen, J., Kindt, R. & O'Hara, R.B. 2005. *vegan: Community Ecology Package* version 1.6-9. Available at: <http://cc.oulu.fi/~jarioksa/>.
- O'Leary, W. & Wilkinson, S. 1988. Gram-Positive bacteria. In: Ratledge, C. & Wilkinson, S.G. (eds.). *Microbial Lipids*, Vol. 1. Academic Press, London. p. 117-202.
- Olsson, P.-A., Bååth, E., Jakobsen, I. & Söderström, B. 1995. The use of phospholipid and neutral lipid fatty acids to estimate biomass of arbuscular mycorrhizal fungi in soil. *Mycological Research* 99: 623-629.
- Pennanen, T. 2001. Microbial communities in boreal coniferous forest humus exposed to heavy metals and changes in soil pH - a summary of the use of phospholipid fatty acids, Biolog® and ³H-thymidine incorporation methods in field studies. *Geoderma* 100: 91-126.

- , Liski, J., Bååth, E., Kitunen, V., Uotila, J., Westman, C.J. & Fritze, H. 1999. Structure of the microbial communities in coniferous forest soils in relation to site fertility and stand development stage. *Microbial Ecology* 38: 168-179.
- Pietikäinen, J. & Fritze, H. 1995. Clear-cutting and prescribed burning in coniferous forest: comparison of effects on soil fungal and total microbial biomass, respiration activity and nitrification. *Soil Biology & Biochemistry* 27: 101-109.
- , Vaijärvi, E., Ilvesniemi, H., Fritze, H. & Westman, C.J. 1999. Carbon storage of microbes and roots and the flux of CO₂ across a moisture gradient. *Canadian Journal of Forest Research* 29: 1197-1203.
- Pouyat, R.V., McDonnell, M.J. & Pickett, S.T.A. 1997. Litter decomposition and nitrogen mineralization in oak stands along an urban-rural land use gradient. *Urban Ecosystems* 1: 117-131.
- Priha, O. 1999. Microbial activities in soils under Scots pine, Norway spruce and silver birch. PhD thesis. Finnish Forest Research Institute, Research Papers 731. 50 p. + 6 papers.
- , Grayston, S.J., Hiukka, R., Pennanen, T. & Smolander, A. 2001. Microbial community structure and characteristics of the organic matter in soils under *Pinus sylvestris*, *Picea abies* and *Betula pendula* at two forest sites. *Biology and Fertility of Soils* 33: 17-24.
- Ranney, J.W., Bruner, M.C. & Levenson, J.B. 1981. The importance of edge in the structure and dynamics of forest islands. In: Burgess, R.L. & Sharpe, D.M. (eds.). *Forest island dynamics in man-dominated landscapes*, Ecological studies 41. Springer-Verlag, New York. p. 67-95.
- R Development Core Team 2005. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Reeves, F.B., Wagner, D., Moorman, T. & Kiel, J. 1979. The role of endomycorrhizae in revegetation practices in the semi-arid West I. A comparison of incidence of mycorrhizae in severely disturbed vs. natural environments. *American Journal of Botany* 66: 6-13.
- Roovers, P., Dumont, B., Gulinck, H. & Hermy, M. 2006. Recreationists' perceived obstruction of field and shrub layer vegetation. *Urban Forestry & Urban Greening* 4: 47-53.
- Ros, M., Garcia, C., Hernandez, T., Andres, M. and Barja A. 2004. Short-term effects of human trampling on vegetation and soil microbial activity. *Communications in Soil Science and Plant Analysis* 35: 1591-1603.
- Rydgren, K., Hestmark, G. & Økland, R. 1998. Revegetation following experimental disturbance in a boreal old-growth *Picea abies* forest. *Journal of Vegetation Science* 9: 763-776.
- Saarsalmi, A., Starr, M., Hokkanen, T., Ukonmaanaho, L., Kukkola, M., Nöjd, P. & Sievänen, R. 2007. Predicting annual canopy litterfall production for Norway spruce (*Picea abies* (L.) Karst.) stands. *Forest Ecology and Management* 242: 578-586.
- Saetre, P. 1999. Spatial patterns of ground vegetation, soil microbial biomass and activity in a mixed spruce-birch stand. *Ecography* 22: 183-192.
- & Bååth, E. 2000. Spatial variation and patterns of soil microbial community structure in a mixed spruce-birch stand. *Soil Biology & Biochemistry* 32: 909-917.
- Saukkonen, T. 2007. Helsingin kaupungin luonnonhoidon linjaus (in Finnish with an English summary). Helsingin kaupungin rakennusviraston julkaisut xx/2007. 60 p. Available at: http://www.hel.fi/wps/wcm/resources/file/ebd87d46401c032/luonnonhoito_012.pdf.
- Saunders, D.A., Hobbs, R.J. & Margules, C.R. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5: 18-32.

- Sievänen, T. 1987. Experiences of forest recreation in another culture: A comparison between Finland and Minnesota. *Scandinavian Forest Economics* 29: 49-56.
- Starr, M., Saarsalmi, A., Hokkanen, T., Merilä, P. & Helmisaari, H.-S. 2005. Models of litterfall production for Scots pine (*Pinus sylvestris* L.) in Finland using stand, site and climate factors. *Forest Ecology and Management* 205: 215-225.
- Stohlgren, T.J. & Parsons, D.J. 1986. Vegetation and soil recovery in wilderness campsites closed to visitor use. *Environmental Management* 10: 375-380.
- Tamminen, P. & Starr, M.R. 1990. A survey of forest soil properties related to soil acidification in southern Finland. In: Kauppi, P., Anttila, P. & Kenttämies, K. (eds.). *Acidification in Finland*. Springer-Verlag, Berlin. p. 234-251.
- Thimonier, A., Dupouey, J.L. & Timbal, J. 1992. Floristic changes in the herb-layer vegetation of a deciduous forest in the Lorraine Plain under the influence of atmospheric deposition. *Forest Ecology and Management* 55: 149-167.
- Torsvik, V. & Øvreås, L. 2002. Microbial diversity and function in soil: from genes to ecosystems. *Current Opinion in Microbiology* 5: 240-245.
- Tolvanen, A., Forbes, B., Rytönen, K. & Laine, K. 2001. Regeneration of dominant plants after short-term pedestrian trampling in subarctic plant communities. In: Wielgolaski, F.E. (ed.). *Nordic Mountain Birch Ecosystems. Man and the Biosphere Series Volume 27*, UNESCO, Paris, and Parthenon Publishing, Carnforth. p. 359-368.
- Tonteri, T. 2000. *Melampyrum pratense*. In: Reinikainen, A., Mäkipää, R., Vanha-Majamaa, I. & Hotanen, J.-P. (eds.). *Kasvit muuttuvassa metsäluonnossa [Changes in the frequency and abundance of forest and mire plants in Finland since 1950]*. Tammi, Helsinki. p. 202-204.
- Tyrväinen, L. 1999. Monetary valuation of urban forest amenities in Finland. PhD thesis. Finnish Forest Research Institute, Research Papers 739. 51 p. + 4 papers.
- , Silvennoinen, H. & Kolehmainen, O. 2003. Ecological and aesthetic values in urban forest management. *Urban Forestry & Urban Greening* 1: 135-149.
- Tzoulas, K., Korpela, K., Venn, S., Yli-Pelkonen, V., Kazmierczak, A., Niemelä, J. & James, P. 2007. Promoting ecosystem and human health in urban areas using Green Infrastructure: a literature review. *Landscape and Urban Planning* 81: 167-178.
- Van der Heijden, M.G.A., Klironomos J.N., Ursic, M., Moutoglis, P., Streitwolf-Engel, R., Boller, T., Wiemken, A. & Sanders, I.R. 1998a. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* 396: 69-72.
- , Boller, T., Wiemken, A. & Sanders, I.R. 1998b. Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. *Ecology* 79: 2082-2091.
- Wade, T.G., Riitters, K.H., Wickham, J.D. & Jones, K.B. 2003. Distribution and causes of global forest fragmentation. *Conservation Ecology* 7(2): 7. [Online journal]. Available at: <http://www.consecol.org/vol7/iss2/art7>.
- Waltert, B., Wiemken, V., Rusterholtz, H.-P., Boller, T. & Baur, B. 2002. Disturbance of forest by trampling: Effects on mycorrhizal roots of seedlings and mature trees of *Fagus sylvatica*. *Plant and Soil* 243: 143-154.
- Weathers, K.C., Cadenasso, M.L. & Pickett, S.T.A. 2001. Forest edges as nutrient and pollutant concentrators: potential synergisms between fragmentation, forest canopies, and the atmosphere. *Conservation Biology* 15: 1506-1514.
- Wilkinson, S.G. 1988. Gram-negative bacteria. In: Ratledge, C. & Wilkinson, S.G. (eds.). *Microbial Lipids, Vol. 1*. Academic Press, London. p. 299-488.
- Zabinski, C.A. & Gannon, J.E. 1997. Effects of recreational impacts on soil microbial communities. *Environmental Management* 21: 233-238.

- Zelles, L., Bai, Q.Y., Ma, R.X., Rackwitz, R., Winter, K. & Beese, F. 1994. Microbial biomass, metabolic activity and nutritional status determined from fatty acid patterns and polyhydroxybutyrate in agriculturally-managed soils. *Soil Biology & Biochemistry* 26: 439-446.
- Zerbe, S. 2001. On the ecology of *Sorbus aucuparia* (Rosaceae) with special regard to germination, establishment and growth. *Polish Botanical Journal* 46: 229-239.
- Zogg, G., Zak, D., Ringelberg, D., Macdonald, N., Pregitzer, K. & White, D. 1997. Compositional and functional shifts in microbial communities due to soil warming. *Soil Science Society of America Journal* 61: 475-481.