









## ABSTRACT

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Sensitivity of soil decomposer communities to habitat fragmentation – an experimental approach

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The objectives of this thesis were (i) to experimentally investigate the effects of habitat fragmentation on soil decomposers, and (ii) to examine whether such studies of soil decomposer communities can be used as a tool to provide generally applicable information on the consequences of habitat fragmentation. Special emphasis was put on testing the utility of habitat corridors in mitigating the expected negative effects of fragmentation. The experiments were conducted both in the laboratory and in the field. The results show that the soil decomposer organisms are, in general, relatively insensitive to habitat fragmentation. However, some predatory and rare, non-predatory microarthropod species were an exception to this rule, being negatively affected by restricted habitat size. The functioning of corridors in alleviating fragmentation-induced effects was practically undetected. Despite this, corridors were shown to facilitate the colonisation of new habitats by both soil fauna and microbes, suggesting that the corridors may benefit a whole community instead of only one or a few species. It was also shown that resource quality is a fundamental factor in determining the abundance of soil decomposers in fragmented habitats. The present studies were novel in the sense that they investigated the responses of a wide variety of organisms, from basal resources to top predators. Although it is unlikely that the results can be straightforwardly extrapolated to larger scales, they nevertheless suggest that not all communities, and species therein, unanimously suffer from habitat fragmentation. On the other hand, the fragmentation responses of soil microarthropods may not differ that much from those of aboveground organisms operating at larger scales. The results of this thesis support the applicability of studying soil food webs as a tool for solving questions related to both applied and theoretical ecology.

Key words: Habitat corridors; habitat fragmentation; resource quality; soil fauna; soil food webs; soil microbes.

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## LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following articles, which are referred to in the text by their Roman numerals. Apart from original planning, I have personally performed a majority of the work (except in paper V). I have also written the first drafts of all articles, which were then completed in co-operation with the other authors.

- I Rantalainen, M.-L., Fritze, H., Haimi, J., Kiikkilä, O., Pennanen, T. & Setälä, H. 2004. Do enchytraeid worms and habitat corridors facilitate the colonisation of habitat patches by soil microbes? *Biology and Fertility of Soils* 39: 200-208.
- II Rantalainen, M.-L., Haimi, J. & Setälä, H. 2004. Testing the usefulness of habitat corridors in mitigating the negative effects of fragmentation: the soil faunal community as a model system. *Applied Soil Ecology* 25: 267-274.
- III Rantalainen, M.-L., Fritze, H., Haimi, J., Pennanen, T. & Setälä, H. Species richness and food web structure of soil decomposer community as affected by the size of habitat fragment and habitat corridors. Manuscript, submitted.
- IV Rantalainen, M.-L., Fritze, H., Haimi, J., Pennanen, T. & Setälä, H. Colonisation of newly established habitats by soil decomposer organisms: the effect of habitat corridors in relation to colonisation distance and habitat size. Manuscript, submitted.
- V Rantalainen, M.-L., Kontiola, L., Haimi, J., Fritze, H. & Setälä, H. Influence of resource quality on the composition of soil decomposer community in fragmented and continuous habitat. Manuscript, submitted.

# 1 INTRODUCTION

## 1.1 Background for the thesis

Dating back to the early 1980's, the "Soil Group" at the University of Jyväskylä has had a strong tradition of studying the organisms and processes of soils. Previous studies of the research group have investigated the responses of soil biota to various anthropogenic disturbances, such as fertilisation of forests (Huhta et al. 1986), forest management practices (Siira-Pietikäinen 2002) and use of pesticides (Martikainen 1998). Furthermore, the functional importance of soil organisms in affecting ecosystem processes has been under focus (Setälä 1990, Haimi 1993, Mikola 1997, Laakso 1998, Liiri 2001, Sulkava 2001, Nieminen 2002). The current thesis forms a logical continuum to the previous studies, concentrating on factors that can potentially affect the local diversity of soil organisms of coniferous forest floor, i.e. habitat fragmentation, habitat corridors and resource quality.

## 1.2 Habitat fragmentation

Habitat fragmentation, generally defined as the loss of an organism's natural habitat, accompanied with an increase in isolation of the remaining habitat areas (Collinge 1996), constitutes a major and universally occurring threat to the biodiversity of various terrestrial ecosystems (Sih et al. 2000). Even though habitat fragmentation can be caused by natural phenomena, such as fires and floods, the predominant culprit nowadays is the unceasing sprawl of urban and agricultural areas (Collinge 1996, Vitousek et al. 1997). The disappearance, shrinkage and deterioration of natural habitats often induce diminution or even total extinction of the original populations, leading to substantially lowered diversity of the community. Due to its high prevalence, studying the effects of

habitat fragmentation on different populations has gained substantial attention among ecologists – from both theoretical and empirical points of view (reviewed by Collinge 1996, Harrison & Bruna 1999, Tscharntke & Kruess 1999, Debinski & Holt 2000, Drake et al. 2002, Steffan-Dewenter & Tscharntke 2002). Whilst gathering information on the consequences of habitat fragmentation in different ecosystems is crucial, the ultimate goal of this research has been to accumulate knowledge to improve conservation of the remaining habitats and populations therein (Quinn & Harrison 1988, Burkey 1989, Hanski 1994, Burkey 1995, Collinge 1996, Cabeza & Moilanen 2001).

The concept of scale is one of the central tenets in modern ecology (Menge & Olson 1990, Levin 1992) and it is also a major issue when habitat fragmentation is concerned (Andrén 1994). It is well acknowledged that both temporal and spatial scale of fragmentation can considerably direct fragmentation processes (Sih et al. 2000). For instance, an abrupt habitat change may be more likely to lead to extinctions than a subtle change occurring at a longer time-scale, which offers time for the organisms to adapt. Concerning the effects of spatial scale, large fragments are usually predicted to have a more species-rich community than small fragments. To begin with, such a positive species-area relationship (Rosenzweig 1995) may simply result from a sheer sampling effect (random sample hypothesis; Connor & McCoy 1979, Andrén 1996). Fragment size may also determine the rate of species extinctions following fragmentation (relaxation effect; Diamond 1972, Gonzalez 2000), with large fragments offering generally better probabilities for long-term survival of species/populations than small ones (Burkey 1989, 1995). Small fragments often harbour small populations predicted to be especially vulnerable to extinctions caused by e.g. demographic or environmental stochasticity (Burkey 1995). Large fragments are also more likely to become (re)colonised than small fragments (MacArthur & Wilson 1967).

It should be noted that the concept of “spatial scale of fragmentation” embodies also variables other than size of the fragment. Such variables are the shape, location and distance of the fragment to other habitat areas. Nevertheless, most studies on habitat fragmentation have recognised habitat size as the major determinant for species’ persistence (Collinge 1996). Size effects are often explained by the high proportion of edge in relation to area in small fragments, which are consequently more vulnerable to “edge effects” than large fragments. Edge effects may induce changes in both physical and biotic conditions of the fragments (Saunders et al. 1991, Murcia 1995, Fagan et al. 1999), rendering them, in the worst case, uninhabitable for some species.

Spatial configuration of the remaining habitat areas, combined with the quality of the surrounding matrix (Fahrig 2001) defines the degree of their isolation, which is a fundamentally important factor in determining the effects of habitat fragmentation (Andrén 1994, 1996). The importance of isolation lies with its effect on the ability of a given organism to disperse between habitat areas (Gustafson & Gardner 1996), ultimately determining the fate of local populations inhabiting the fragmented landscapes. It is hypothesized that

immigrants dispersing from other habitat areas can increase the persistence time of the local population and even save it from extinction by increasing the population size (Hanski 1999). This hypothesis has been termed the “rescue effect” (Brown & Kodric–Brown 1977) and has been studied mainly theoretically in the light of the metapopulation (and –community) concept (Burkey 1989, Anderson & Danielson 1997, Hanski 1999, Jordán 2000). Metapopulations are regional populations consisting of many small local populations, which go extinct frequently, but the simultaneous establishment of new local populations by dispersing individuals can maintain the metapopulation structure indefinitely (Hanski 1999). Despite the fairly sound theoretical background, the actual functioning of the rescue effect has been empirically demonstrated only rarely (Clinchy 1997; but see Gilbert et al. 1998, Gonzalez et al. 1998, Hanski 1999, Coffman et al. 2001, Gonzalez & Chaneton 2002).

The negative effects of habitat fragmentation have been shown to relate to a wide variety of taxonomic groups of organisms, from microarthropods to large mammals. Importantly, it is the characteristics of the organism in question that ultimately determine its responses to fragmentation (Tracy & George 1992, Andrén 1996, Andreassen et al. 1998, Davies & Margules 1998). On the other hand, there are some attributes, such as large body size, high trophic status, rarity, habitat specificity and low dispersal capacity, which have been shown in various groups of organisms to correlate with high vulnerability to habitat fragmentation (e.g. Kruess & Tschardt 1994, De Vries et al. 1996, Burkey 1997, Davies et al. 2000, Kotze & O’Hara 2003).

### **1.3 Habitat corridors**

Habitat corridors, i.e. linear strips of habitat connecting habitat areas (Beier & Noss 1998; see Hess & Fischer 2001 for further definitions), have been offered as a means to mitigate the negative effects of fragmentation and particularly, of isolation. The habitat corridors should provide (i) a dispersal pathway for species unable to utilise the unattractive matrix for dispersal (habitat specialists; Tiebout & Anderson 1996, Haddad et al. 2003) or (ii) a safer dispersal route as compared to the matrix, thus increasing the survival probability of dispersers (Forman & Godron 1981). Consequently, the presence of corridors has been predicted to induce (or strengthen) the rescue effect, thus maintaining the populations and/or diversity of species inhabiting the connected fragments (Burkey 1989, Hanski 1999) or alternatively, reducing the time required for organisms to recolonise currently uninhabited patches (Hess 1994). On the other hand, corridors could bring about severe negative implications, such as spread of diseases (Hess 1994) and increase in the mortality rate of dispersers due to low quality of the corridor as a habitat (Henein & Merriam 1990). The

risk of predation in the presence of corridors may also increase (Simberloff et al. 1992).

Despite the criticism, it is generally accepted that corridors are beneficial for populations inhabiting fragmented habitats. The corridor hypothesis has been widely theorized and modelled and has also been a subject of various experiments (reviewed by Rosenberg et al. 1997, Beier & Noss 1998, Debinski & Holt 2000, Niemelä 2001). However, as the experiments have produced vague and even contrasting results, the actual usefulness of habitat corridors still largely remains a matter of controversy. The most convincing evidence supporting the importance of corridors comes from experiments operating at relatively small scales (e.g. Gilbert et al. 1998, Gonzalez et al. 1998, Gonzalez & Chaneton 2002), whereas experiments conducted at larger scales, considered more relevant to nature conservation, have often failed to demonstrate plausibly the applicability of corridors (Rosenberg et al. 1997; but see Tewksbury et al. 2002, Haddad et al. 2003). These failures are due largely to practical difficulties in setting up experiments with proper replication and sufficient spatio-temporal scale in relation to the characteristics of the organisms studied (Debinski & Holt 2000). Therefore, the use of small-scale model systems may well be a relevant way to shed light on the corridor issue (Burkey 1997, Gonzalez 2000) despite the fact that extrapolating the results of small-scale studies to larger scales is rarely straightforward (e.g. Carpenter 1996, Drake et al. 1996, Lawton 1999, Mönkkönen & Reunanen 1999, Haddad et al. 2000, Noss & Beier 2000). It has been proposed that no single "right" scale exists at which ecological processes are to be studied (Levin 1992). This indicates that things happening at small scales may bring about valuable predictions of similar phenomena taking place at larger scales (Lawton 1999). Whatever the scale, it is essential to select it properly in relation to the traits (e.g. body size, dispersal capacity) of the organisms studied.

The ambiguousness of the experimental evidence on the applicability of corridors may also result from the interdependency between the characteristics of the organism (e.g. size, mobility, habitat specificity) and the properties of the corridors (e.g. width, habitat quality) (Andreassen et al. 1996). The spatial configuration of the corridor-patch systems may also be of great importance (Collinge 1998). Moreover, it has been suggested that the responses of organisms to the presence of habitat corridors are strictly species-specific (Hobbs 1992, Beier & Noss 1998; but see Tewksbury et al. 2002, Hudgens & Haddad 2003), which would inevitably render the use of model systems fruitless. However, as nature conservation rarely is about preserving one or just a few species but the entire community, it is worthwhile to collect generally applicable information on the utility of habitat corridors for organisms with different kinds of life-history traits.

## 1.4 Why study habitat fragmentation using soil organisms?

The effects of habitat fragmentation on soil decomposer organisms have remained largely unexplored (but see Didham 1998, Gilbert et al. 1998, Gonzalez et al. 1998, Gonzalez & Chaneton 2002, Wardle et al. 2003), even though the critical functioning of decomposers in the processes in soils could give special value to such information (Wardle et al. 2003). Besides narrowing this gap in knowledge, my intention was to use the soil decomposer community as a tool for studying the responses of communities to habitat fragmentation. The soil decomposer communities possess many attributes that render them a noteworthy tool for use in studies of this kind (see also Wright & Coleman 1993).

First, soil food webs include a wide variety of organisms with different sets of life-history traits. For instance, active dispersal capacities of soil organisms appear to vary greatly, ranging from relatively mobile predatory mites and large collembolans (Siepel 1994) to fairly immobile nematodes and soil bacteria (Dighton et al. 1997). Furthermore, soil food webs are composed of various trophic positions, with a large variation in both body size and spatial distribution of the taxa. Consequently, soil communities offer a great opportunity to look for special traits that could render a given species vulnerable to fragmentation. Second, not only the soil decomposer communities, but also their habitat can be manipulated fairly easily. Small size and short life cycles of most of the organisms make it possible to construct properly replicated experiments with relevant spatial and temporal scales, thus avoiding scale-related complications typical to many previous experiments (Debinski & Holt 2000, Davies et al. 2001). Habitat size and distance to other habitat areas also can be adjusted relatively easily. Finally, the effects can be studied at various levels of the community hierarchy, from species to community and even ecosystem level (Wardle et al. 2003).

The soil decomposer community is responsible for mineralising nutrients bound to dead organic matter (Petersen & Luxton 1982, Wardle 2002), thereby representing an irreplaceable component in the functioning of entire ecosystems (Copley 2000). It is possible, albeit a controversial issue (Ekschmitt & Griffiths 1998, Setälä et al. 1998), that fragmentation-induced changes in the composition of the soil community, such as lowered species diversity, could hamper the functioning of not only soils, but also the entire ecosystem. In any case, there are some key functional groups or keystone species in soils whose responses to habitat fragmentation are likely to be mirrored in the functioning of the whole community (Didham et al. 1996).

Large-scale changes in landscapes, such as those caused by forest management practices, may intuitively appear irrelevant from the soil organisms' point of view. However, forestry practices, such as harrowing the soil, can cause fragmentation of the forest floor at scales relevant to the soil biota (Siira-Pietikäinen et al. 2003). In previous studies, comparable small-scale

fragmentation has been shown to affect negatively the species diversity of moss-inhabiting arthropod communities (Gilbert et al. 1998, Gonzalez et al. 1998, Gonzalez & Chaneton 2002), consisting of the same key groups of fauna as the communities in soils. Bearing in mind the indispensable role of soil decomposers in ecosystem processes, it is of interest to study their responses to small-scale habitat change *per se*, not only their responses as model communities.

## 1.5 Habitat change and resource quality

The smaller the habitat fragment is, the less likely it is to contain a full set of resources needed by a given organism to complete its life cycle. Therefore, the aspect of resource quality and availability in habitat fragments can have a guiding role in affecting the sustainability of the fragment-inhabiting populations. This parallels to the hypothesis on the positive species-area relationship being explained by an increase in habitat diversity with increasing area (Connor & McCoy 1979).

Detrital food webs are generally considered to be strictly (Pimm 1982) or largely donor-controlled (Wardle 2002), indicating that it is mainly the availability of resources that restricts the population growth of soil decomposers. Following this prediction, increasing the quantity of resources has been proven to have strong positive effects on the local abundances of soil organisms, propagating even up to the top predatory level (e.g. Chen & Wise 1999, Ponsard et al. 2000). However, the local species richness of decomposer communities appears to be determined mainly by the quality and variety of available resource types rather than resource quantity (Giller 1996, Hansen & Coleman 1998, Sulkava & Huhta 1998). It has been suggested that the diversity of basal resources in a habitat may determine the diversity of the next trophic level(s) by affecting the extinction and colonisation processes occurring in the habitat (Moore & De Ruiter 1997). Diversity of resources may, for example, allow the establishment and continuous coexistence of species that would otherwise compete for the same resource, i.e. excluding the possibility of competitive exclusion of species (Tilman 1999). Even though the extent of competition for resources amongst soil organisms is still largely unknown (Giller 1996, Maraun et al. 2003), it appears that the quality of resources available in a habitat fragment may be a fundamental factor in determining the composition of the resident soil community.

## 1.6 Aims and main hypotheses of the thesis

In this thesis, my objective was to explore experimentally the responses of various members of the soil decomposer community, from microbes to mesofauna, to habitat fragmentation. The effects of habitat corridors and fragment size on the populations of soil organisms inhabiting fragmented habitats were specifically under focus. The effect of resource quality on the diversity of soil organisms was also assessed. The main hypotheses were:

- (i) Habitat fragmentation leads to reduced species richness of soil organisms by inducing extinctions of populations originally present in the fragments. Fragment size determines the species richness of the local community and the persistence of populations, with small fragments having a higher extinction rate than large fragments.
- (ii) Habitat corridors aid in the dispersal of soil organisms between the habitat areas, thus a) maintaining the populations and species diversity of the soil decomposer communities in fragmented habitats (rescue effect), or alternatively, b) facilitating the colonisation of new, previously unpopulated habitats by soil organisms.
- (iii) Both the effects of habitat size and corridors are dependent on the characteristics of the organisms, with e.g. predators and species with rare occurrence being especially vulnerable to reduced habitat size.
- (iv) Quality of resources in the habitat fragments has a profound influence on the composition of a local soil community: fragments with high quality resources can maintain a more species rich community with larger populations than those with resources of low quality.

## **2 MATERIALS AND METHODS**

### **2.1 General design of the experiments**

In each of the five experiments, the general set-up consisted of patches of raw coniferous forest humus, representing habitats for the soil organisms studied. These patches were embedded in mineral soil (except for half of the patches in V; see the section 2.2.2), aimed to function as an inhabitable or non-preferred matrix for a majority of soil biota. Thus, the experimental systems (mineral soil and humus patches) were expected to represent fragmented habitats for the patch-inhabiting soil organism communities. At the start of the experiments, the humus patches were either populated with soil fauna and microbes (II, III, V) or were unpopulated (I, IV). In experiments studying the effects of habitat corridors (I-IV), the amount of habitat (raw humus) was kept constant between the systems with and without corridors. This set-up excluded the possibility of corridor effects being caused by additional habitat area (or space) introduced with the corridors. The duration of all experiments was long enough to include several generations of most of the soil organisms studied.

### **2.2 Micro- and mesocosm experiments (I, II)**

The aim of the microcosm experiment (I) was to investigate the colonisation of new, previously unpopulated habitat patches by soil microbes, in either presence or absence of habitat corridors and soil fauna (enchytraeid worms). The worms were hypothesised to function as vectors for microbe dispersal; enchytraeid worms have been shown previously to be a functionally important group in coniferous forest soils (Laakso & Setälä 1999, Setälä et al. 2000). The microcosms used were transparent plastic containers with a volume of 15 L. The habitat patch systems established in these microcosms consisted of a central

patch, functioning as a source of colonisers, and four satellite patches, functioning as colonisable new habitats. The corridors, when present, connected the central patch to the satellite patches (see I, Fig. 1). The patches and corridors consisted of sterile (autoclaved) humus and were embedded in sterilised mineral soil. At the beginning of the experiment, the central patches were inoculated with 8 taxa of saprophytic fungi, 5 taxa of soil bacteria and 3 taxa of ectomycorrhizal fungi. In half of the microcosms, the central patches received also enchytraeid worms. A Scots pine (*Pinus sylvestris* L.) seedling was planted in each patch to study the functioning of the decomposer community. Colonisation of the satellite patches by the inoculated microbial taxa and tree growth in the patches were followed for 16 months, including two growing periods and three samplings of the satellite patches.

The objective of the mesocosm experiment (II) was to investigate whether the presence of habitat corridors maintains the abundance and/or species richness of soil fauna in a fragmented habitat. The mesocosms (open systems) were round plastic containers with a volume of 15 L. The habitat patch systems established in these mesocosms consisted of four slightly homogenised but non-sterilised habitat patches, each 20 cm<sup>2</sup> in area. The humus corridors, when present, connected the patches to each other (see II, Fig. 1). To obtain conditions as close to natural as possible, yet avoiding dispersal of soil organisms from the surroundings into the mesocosms (potentially obscuring the corridor effect), the mesocosms were placed on the roof of the Department of Biological and Environmental Science building in Jyväskylä. During the winter, the mesocosms were kept in an incubation chamber, where simulated winter conditions were created. Development of the micro- and mesofaunal communities originally present in the humus patches was followed for 12 months, with three samplings of the habitat patches and corridors.

## 2.3 Field experiments (III-V)

### 2.3.1 Experimental sites

The field site at Muhos, Central Finland (63°43'N, 26°02'E) (III, IV), was a 65-year old forest stand dominated by Scots pines. The field layer vegetation was dominated by *Vaccinium vitis-idaea* L. and *Empetrum nigrum* L. and the ground layer was dominated by *Pleurozium schreberi* (Brid.) Mitt. The raw humus layer at the site was approximately 5 cm thick. For the experiments, an area of 50 m x 50 m of the forest was manually clear-felled (see cover picture).

The field site at Uurainen, Central Finland (62°32'N, 25°35'E) (V) was an abandoned sandpit, surrounded by a mature forest stand dominated by Scots pines. The dominating species in the field and ground layers of the forest were the same as at the Muhos field site. The raw humus layer of the forest soil was approximately 4 cm thick.

### 2.3.2 Set-up of the experiments

The aim of the first experiment at Muhos (III) was to investigate (i) the effect of fragment size on the abundance and species richness of soil organisms and (ii) the possible role of habitat corridors in maintaining the populations. The experiment was established at the forest clearing by removing the organic soil layer from areas of three different sizes (25 cm x 25 cm, 77.5 cm x 77.5 cm and 236 cm x 236 cm), thus exposing the underlying mineral soil. The habitat fragment-corridor systems, composed of sieved but non-sterilised humus, were established in the squares, the size of the systems being proportional to the size of the squares. The sizes of the fragments were 2 cm<sup>2</sup>, 20 cm<sup>2</sup> and 200 cm<sup>2</sup> in the small, medium-sized and large squares, respectively. In each square, there were four humus fragments that were either disconnected or connected to each other with corridors (see III, Fig. 1). The development of the decomposer communities (from microbes to mesofauna) in the fragments was followed for 2.5 years, with 3 samplings of the habitat fragments and corridors.

In the second experiment at the Muhos field site (IV), the goal was to investigate the potential of soil decomposer organisms to colonise new, previously sterilised and thus non-populated habitat patches under field conditions. The roles of habitat corridors, habitat patch size and colonisation distance in determining the colonisation success specifically were under focus. The experiment consisted of circles (120 cm in diameter) of uncovered mineral soil, into which originally sterile (autoclaved) humus patches were embedded. There were three different types of patches: (1) large ones situated relatively far from the surrounding intact forest soil (main source area of colonisers), (2) small ones situated far from the source area and (3) small ones situated close to the source area (see IV, Fig. 1). The patches were either disconnected or connected with habitat corridors, composed of originally sterile humus, to the intact forest soil. Colonisation of the patches by soil decomposer organisms (from microbes to mesofauna) was followed for 2.5 years, with three samplings of the patches during the experiment.

The experiment at the Urainen field site (V) studied the influence of resource quality on the diversity of the soil decomposer community in both fragmented and continuous habitat. The experiment was established by embedding sieved, non-sterilised humus patches of different resource quality (pure homogenised humus, humus with needle litter or humus with both needle and leaf litter) into either mineral soil of the sandpit (fragmented habitat) or natural forest soil (continuous habitat). Development of the decomposer communities (from microbes to mesofauna) in the patches was followed for 12 months, with 2 samplings of the patch materials. In addition, the activity of possible epigeic colonisers of the patches in the study area was studied using pitfall traps. The occurrence of possible edaphic colonisers in the soil surrounding the patches was studied using soil core samples (taken from both sandpit and forest soil).

## 2.4 Analyses

### 2.4.1 Biological and physicochemical analyses

Soil animals (enchytraeid worms, nematodes, mites and collembolans) were extracted from the soil samples using appropriate standard extraction methods (I-V). Enchytraeid worms were counted (I-V) and their biomass was estimated (II, III, V). Nematodes were counted, identified to genus level and divided to different feeding groups (II-V). Mites and collembolans were counted and identified to species level, when possible (II-V).

The number of microbial taxa (species) in the originally sterile humus patches (I, IV) was analysed using a 16S and 18S ribosomal DNA-based PCR-DGGE molecular method (Vainio & Hantula 2000, Pennanen et al. 2001). The composition of the microbial community (microbial biomass; III-V) was determined using a PLFA (phospholipid fatty acids) method (Frostegård et al. 1993, Pennanen et al. 1999). Since a majority of soil fauna depend on microbes for nutrition, the microbial data were used not only for studying the effects of treatment factors on the microbes but also as a possible explanatory factor for the responses of soil animals.

Physicochemical properties measured from the experimental soil samples were soil moisture (I-V) and soil pH<sub>H2O</sub> (I, IV).

### 2.4.2 Statistical analyses

Since the samples were taken at subsequent samplings from the same micro- and mesocosms (I, II), or from the same patch-corridor systems (III, IV) or patches (V), analysis of variance (ANOVA) for repeated measurements were used in analysing the data. In the case of significant interactions between the main test factors, simple effects tests were applied (Zar 1999). The data were transformed to log (x+1) whenever necessary to improve their fit to the assumptions of parametric testing. Differences in the composition of microbial (as indicated by the PLFA-analysis) and microarthropod communities between the treatment levels were studied using principal component analysis (PCA; III, V).

### **3 RESULTS AND DISCUSSION**

#### **3.1 Soil decomposer community as affected by fragmentation and fragment size (II, III, V)**

##### **3.1.1 Responses of soil fauna**

The hypothesis that habitat fragmentation has negative effects on species richness and abundance of soil fauna remained virtually unsupported in the current experiments. In the mesocosms (II), the abundance of enchytraeid worms and the abundance and species richness of microarthropods in the humus patches even increased during the experiment. However, this can result largely from exceptionally favourable conditions in the artificial mesocosm environment (Carpenter 1996, Setälä et al. 1991). Additionally, results of the field experiments (III, V) also suggest that even relatively small-scaled habitat fragmentation is not likely to induce extinctions in the soil decomposer community – apart from the initial sampling effect (Connor & McCoy 1979, Andrén 1996). In other words, most of the soil fauna appear to be well adapted to living in a restricted habitat patch. Previous studies have shown that soil faunal communities are relatively resistant to environmental changes, such as forest management practices (Setälä et al. 2000, Siira-Pietikäinen et al. 2001), and to isolation from the surrounding forest soil (Nieminen & Setälä 1998). My results give further support to the idea that soil fauna is generally insensitive to habitat change and isolation. However, the lack of negative responses to fragmentation was not totally uniform across different faunal groups. While e.g. microarthropods were, in general, relatively tolerant to reduced habitat size, the taxon richness and/or abundance of nematodes tended to decrease in the fragments.

The low vulnerability of soil fauna to negative effects of habitat fragmentation can be attributed to the following factors. First, even a small volume of soil may embody abundant resources for the small-sized soil

organisms, promoting their survival in small habitat fragments. The predominantly generalist feeding habits of soil fauna (Giller 1996, Maraun et al. 2003, Setälä et al. 2004) probably enabled efficient use of limited resources in the fragments, which received no energy inputs during the experiments. Due to the aggregated distribution of resources in natural forest soils (Lavelle & Spain 2001), soil animals – at least those incapable of long-distance dispersal – could also be inherently adapted to living within a habitat patch. Moreover, it has been suggested that the species-rich local soil decomposer communities are strongly interactive and “saturated”, being thus largely independent of the processes occurring at a larger regional scale (Setälä et al. 2004). This property could render the communities also resistant to habitat fragmentation, provided that conditions in the fragments remain sufficiently favourable. On the other hand, the response of nematodes is likely to be explained by environmental conditions, since as aquatic organisms they were particularly sensitive to the relatively low moisture of the fragmented soils. Further, the fragments inevitably lacked living plant roots that may function as an important source of resources for nematodes in natural soils (Wright & Coleman 1993, Lavelle & Spain 2001).

Also, the effects of fragment size (III) on the species richness of soil fauna only partly followed my expectations. The hypothesis that species richness increases with increasing fragment size was verified, indicating that the general species-area relationship (MacArthur & Wilson 1967, Rosenzweig 1995) holds also for soil faunal communities inhabiting fragmented habitats (see also Wardle et al. 2003). However, this relationship probably results from the sampling effect, causing a difference in the species number between the size classes already at the very beginning of the experiment. A more interesting aspect of the responses of the fauna during the experiment relates to the post-fragmentation relaxation process (Diamond 1972, Gonzalez 2000), i.e. the development of their communities – especially that of microarthropods. Contrary to my predictions and previous observations that the rate of extinctions is negatively correlated with habitat size (MacArthur & Wilson 1967, Burkey 1995), species richness of microarthropods decreased in the medium-sized and large fragments during the experiment but not in the small ones. A closer examination of the responses of the separate microarthropod groups revealed that the species that became extinct were collembolans. A plausible explanation for the sensitivity of collembolans, as compared to e.g. oribatid mites, can be the observed relatively high proportion of rare species (occurring in <10% of the fragments) among the collembolans. Rare species have frequently been shown to be especially vulnerable to negative effects of habitat fragmentation in aboveground milieus (e.g. Golden & Crist 1999, Davies et al. 2000, Summerville & Crist 2001). In the present study, due to the obvious sampling effect, rare species were probably not present in the small fragments even at the start of the experiment. Alternatively, due to the typically rapid initial loss of species in small habitat patches (Gonzalez 2000, Ovaskainen & Hanski 2002), some species that were originally present may have disappeared

from the small fragments already before the first sampling. On the other hand, even the largest fragments were not large enough to ensure continuing persistence of rare species.

To compare the responses of predatory (mesostigmatid mites) and non-predatory microarthropods (oribatid mites and collembolans) to fragment size, species richness-area curves were drawn separately for each of these two groups (see III, Fig. 3). According to the slopes of the curves, the negative effect of decreasing fragment size was more pronounced in predatory than in non-predatory species. This verified the hypothesis of the relative sensitivity of predatory species to reduced habitat size, which was in accordance with the results of previous aboveground studies dealing with the responses of species at high trophic levels to fragmentation (e.g. Holt 1996, Kruess & Tscharrntke 1994, 2000).

### **3.1.2 Responses of soil microbes**

In general, the growth of soil microbes was not affected by habitat fragmentation; in fact, their biomass (as indicated by the PLFAs) was even higher in fragmented environments (V). Furthermore, the effect of habitat size on biomass was reversed in microbes: small habitat fragments had the highest and large fragments had the lowest biomass (III). On the other hand, the community structure of microbes was different both between the fragmented and continuous habitat and between the different habitat size classes. In other words, even though the growth of microbes as small-sized organisms appears not to be restricted by reduced habitat size, the community composition can differ between habitats of differing size and quality. The higher microbial biomass in small fragments can result from a supposedly lower number of microbial species in the small fragments than in the larger ones, leading to a possibility of competitive release in the small fragments. Besides biotic interactions, the community structure of microbes is determined by abiotic conditions (MacLean & Huhta 2000, Wilkinson et al. 2002). Difference in abiotic conditions (e.g. moisture, temperature) between the fragmented and continuous habitat serves as a likely explanation for the difference between the microbial communities in those habitats.

## **3.2 Effects of habitat corridors on soil decomposers (I-IV)**

### **3.2.1 Responses of soil fauna**

Contrary to my expectations, the presence of habitat corridors had no effects on the species richness of the fauna in the non-sterilised habitat patches (II, III). This is in contrast to previous findings on the utility of habitat corridors in the maintenance of species richness of moss patch inhabiting arthropod communities (Gilbert et al. 1998, Gonzalez et al. 1998, Gonzalez & Chaneton

2002). The most probable explanation for the lack of effect of corridors in the present studies is related to the lack of effect of fragmentation: since virtually no extinctions of populations took place, there were little grounds for the rescue effect to operate. This was especially the case in the mesocosms, where the species richness of the fauna inhabiting the fragments appeared to even increase during the experiment (although this result was probably an artefact: see paper II). In the field experiment, on the other hand, the observed decrease in the abundance of collembolans, followed by the loss of rare species, could have been expected to give grounds for the corridor-mediated rescue effect. Since this was not the case, it appears that the corridors were unsuccessful in providing a dispersal pathway – or habitat - for the fauna. Moreover, corridors appeared to function as “sinks” (Henein & Merriam 1990) for the nematode populations, leading to lower abundance of nematodes in the connected fragments. This response indicates that the quality of corridors was indeed low, possibly due to their (seasonal) dryness. Further, the evidently similar conditions in the fragments of the same system may have led to a synchrony of extinctions, leaving no “rescuers” in the close neighbourhood. It is also noteworthy that as our knowledge of active dispersal capacities of soil animals is still scanty (Wardle 2002), it is difficult to predict what kind of corridors would actually be functional for this fauna (Hudgens & Haddad 2003). Finally, the possibility of successful dispersal of fauna through the mineral soil matrix in the absence of corridors cannot be ruled out, either.

The only faunal group responding positively to the corridors connecting originally populated patches was enchytraeid worms in the mesocosm experiment (II): their population growth was slightly promoted by the presence of corridors. However, it is possible that this response was not only a result of improved dispersal route for the worms, but also due to an unexplained improvement e.g. in resource availability for the typically resource-controlled enchytraeid populations (Wardle 2002). This conclusion gained further support from the field experiment in which the influence of corridors on the colonisation of unpopulated habitats was investigated (IV). Here, the abundance of enchytraeid worms was highest in the patches with the longest corridors in relation to patch size. This indicates that the corridors may, indeed, have some unknown “side effects” that are especially beneficial to enchytraeid populations.

Besides increasing the abundance of enchytraeid worms in the originally sterile habitat patches, the presence of corridors had also a positive influence on the number of microarthropod taxa in those patches (IV). These positive corridor effects were not, however, consistent, which can be related to the unfavourable conditions (e.g. low biomass of microbes, low pH and moisture) in the initially autoclaved humus soil (Sulkava et al. 1996) and to different seasons at the subsequent samplings. In any case, the results showed that habitat corridors have the potential to facilitate the colonisation of new, previously unpopulated habitats by two rather different soil faunal groups.

### 3.2.2 Responses of soil microbes

The presence of corridors led to higher biomass of fungi in the initially non-sterilised habitat fragments (III) and facilitated the colonisation of the originally unpopulated habitats by fungal species both in the microcosms (I) and in the field (IV). Consequently, it appears that vegetatively growing soil microbes were able to utilise habitat corridors as a dispersal pathway and/or as a habitat. This is not surprising, since the habitat corridors were likely to provide a more beneficial substrate for growth of fungi than the surrounding mineral soil matrix. Interestingly, in microcosms, the dispersal of fungi was even more dependent on the presence of enchytraeid worms (see also Hedlund & Augustsson 1995) than on the corridors. In the field experiments, there was no clear evidence that soil animals functioned as dispersal vectors for soil fungi, although this possibility cannot be totally excluded. However, as shown in the microcosm experiment, some fungal species can disperse rather efficiently by vegetative growth. This implies that the corridor effects in the field may well have resulted from vegetative growth of the fungi and that the role of soil fauna in transporting fungal propagules was less important. In addition, the proportion of actinomycetal bacteria (with a similar growth form to fungi) increased in the presence of corridors (III), giving further support to the importance of habitat corridors for vegetatively dispersing soil microbes.

In contrast to soil fungi, the response of soil bacteria (other than actinomycetes) to the presence of corridors was variable, ranging from negative to positive. The non-existent effect of corridors in the microcosms (I) and in the field (III) is probably due to the predominantly passive dispersal mechanisms (e.g. with water or wind) of the bacteria (Richards 1987), rendering the habitat corridors useless. The negative effect of corridors in the colonisation of new habitats (IV) by bacteria was probably a consequence of the positive effect of corridors on the fungal species richness: stronger competition with fungi for resources (Møller et al. 1999) may have restricted the establishment of bacteria in the connected patches. At one sampling of the same experiment, bacterial species exhibited a contrasting positive response to the corridors. Since this coincided with the corridor-facilitated colonisation of enchytraeid worms, it is possible that the extra bacterial species were transported to the patches with the enchytraeids. This result, together with those of the microcosm experiment, give support to the role of the enchytraeid *Cognettia sphagnetorum* as a functionally important species in boreal coniferous forest soils (Laakso & Setälä 1999, Setälä et al. 2000), since carrying soil microbes to new resources is likely to enhance the rate of decomposition processes in soils.

Taken together, even though the functioning of corridors in the maintenance of species richness in the already established soil decomposer communities remained undetected, the results of my thesis suggest that corridors can facilitate both active and passive (soil fauna -mediated) colonisation of new habitats by soil organisms.

### 3.3 Effects of resources on soil decomposers (V)

#### 3.3.1 Responses of soil fauna

In concert with my hypothesis and previous studies focusing on the effects of resource enrichment on the abundance of soil organisms (Chen & Wise 1997, Chen & Wise 1999, Ponsard et al. 2000), improvement of resource quality led to higher abundances of nematodes, enchytraeid worms, dipteran larvae and microarthropods in the experimental patches. Thus, even a rather subtle qualitative change in the resource base was strong enough to cause clear effects on the populations of decomposer fauna. Furthermore, these effects propagated up to the predatory level in the communities of microarthropods and nematodes, underlining the importance of bottom-up control in soil food webs (Pimm 1982, Wardle 2002). However, the positive effects of resource quality improvement were not consistent, occurring mainly within the fragmented habitat and disappearing by the final sampling of the experiment. The fauna increasing in abundance were mainly species not originally present in the patches and numbers of juveniles were small, which indicates that the increases in abundance were mainly a result of enhanced colonisation of the patches by the fauna, rather than due to accelerated reproduction of the individuals. It was evident that the relatively mobile faunae occurring in the matrix environment (e.g. epigeic collembolans, egg-laying dipterans) were attracted to the litter-enriched patches over those with pure humus. Contrary to my expectations and previous results on the effects of resource enrichment on species richness of detrital communities (Hansen & Coleman 1998, Srivastava & Lawton 1998), resource quality did not affect the total species richness of microarthropods. The low number of rapid coloniser species in the surrounding matrix environment must have affected this result.

The predominant lack of resource quality effect on the fauna in the continuous habitat is probably related to the relatively low motility of fauna inhabiting favourable environments, such as humus soil (Bengtsson et al. 1994). On the other hand, also the low contrast between the experimental patches and the surrounding intact forest soil may have undermined the localisation of the patches by soil fauna. The disappearance of the resource quality effect over time was probably a result of physical and chemical modification of the litter material by the primarily colonising fauna (Hågvar & Kjøndal 1981), reducing its attractiveness to colonisers that follow.

#### 3.3.2 Responses of soil microbes

Resource quality improvement affected positively the biomass of soil fungi within both the fragmented and continuous habitat, while bacterial biomass was unaffected by resource quality. Apparently, fungi as primary colonisers of dead organic material (Ponge 1991) benefited from the presence of fresh litter

material, whereas bacteria were able to utilise also poorer resources of the pure humus patches (Berg et al. 2001). Also the community structure of microbes was affected by resource quality; in particular, the microbial communities in the pure humus patches differed from those in the resource-enriched patches. Thus, it is evident that different substrate quality selected for different microbial species (see also Wilkinson et al. 2002). Since a majority of soil animals are fungivorous, it can be assumed that the effect of resource enrichment on the soil fauna was mediated mainly by the response of soil fungi.

In conclusion, the results of this experiment, together with the results obtained from the other experiments described in this thesis, indicate that resource quality may be a far more important factor in determining the composition of the local soil decomposer community than are the various factors brought about by habitat fragmentation.

### **3.4 Relevance of the results at a wider perspective and future prospects**

One objective of this thesis was to use the soil decomposer community as a tool in studying the effects of habitat fragmentation. The benefit of this approach is that it enables studying an entire food web at the same time, which has not been done in previous studies focusing mainly on the responses of one or a few species only. The high diversity of organisms in soil decomposer communities was expected to offer plenty of material that would aid in the search for specific traits that might render a given organism vulnerable to fragmentation. The spatial and temporal scales of this study, albeit very restricted from the perspective of e.g. nature conservation, were selected solely with regard to the small size, short life span and limited dispersal capacities of the studied soil organisms. It was also presumed that the same traits that render a soil organism sensitive would also render any organism sensitive, irrespective of the ecosystem in which the organism lives.

Although one of the aims of my thesis was, at least implicitly, to use the results to predict the responses of aboveground communities and species operating at larger scales to habitat fragmentation and corridors, it is evident that making generalisations based on my results would be quite far-fetched. What the results suggest, however, is that it should not be taken for granted that all communities are unanimously negatively affected by habitat fragmentation. On the other hand, it was shown that even if the community in general does not suffer from fragmentation, it may nevertheless include individual species that do so. This underlines the importance of going down to species level when investigating the effects of habitat fragmentation (Robinson et al. 1992). Furthermore, it was evident that even the tightly interactive soil community (Setälä et al. 2004) does not respond to habitat change consistently, as a single operational unit, but that the collective response is a combination of

varying responses of its constituent members. The fact that many of the results obtained in micro- and mesocosms were verified in the field experiments renders support to the common, albeit controversial (e.g. Carpenter 1996, Drake et al. 1996, Lawton 1999), use of artificial miniecosystems in investigating ecological phenomena.

Although the functioning of soil organism communities in soil processes was not measured in the field- or mesocosm experiments, the observed high resistance of soil communities to habitat fragmentation suggests that fragmentation may not induce substantial changes in the processes of soils either (but see Didham 1998). Furthermore, due to high functional redundancy of species in soils (Laakso & Setälä 1999, Liiri et al. 2002), it is unlikely that loss of some vulnerable species would lead to altered functioning of soils. It should be noted, however, that the fragmentation responses of some functionally important groups, such as mycorrhizal fungi or soil macroarthropods, were not studied in the present experiments. Thus, a possible direction for future studies would be investigating the interactions between the fragmentation responses of those groups and their functioning in the processes of soils.

Investigating the currently inadequately known active dispersal capacities of soil organisms could also form an important line of study in the future. Such knowledge would not only contribute to clarifying the processes that structure local soil decomposer communities, but could also promote markedly the applicability of soil organisms as models in studying the effects of fragmentation-induced habitat change. The information on dispersal ability of a given soil organism, combined with information on its other life-history traits, would provide grounds for using the responses of that organism to predict those of some other organism with a similar set of characteristics, albeit operating at a larger scale. For instance, it has been suggested that small mammals inhabiting woodland patches might be a suitable analogue for moss patch-inhabiting microarthropods (Gilbert et al. 1998). A self-evident prerequisite for such extrapolation is performing the experiments on scales that match the characteristics of the organisms studied, which again, cannot be accomplished without information on e.g. their dispersal capacity. As compared to the present experiments with a largely conjectural choice of scales, comparable experiments in the future should be designed on the grounds of specific knowledge on the life-history traits of soil organisms, which hopefully will be accumulated by that time. This could gradually lead to constructing a model of community dynamics of soil decomposers in fragmented habitats, and even to a functional guideline for applying the results obtained from experimental small-scale model systems of soil organisms to larger scales.

Even though the current experiments were relatively long-term, it is possible that due to the high resistance of soil organisms to habitat change, more severe effects of habitat fragmentation on e.g. species richness of soil faunae did not have time to surface. For instance, depletion of resources in the fragments could have caused extinctions in the communities in the long run. Therefore, forthcoming studies should focus on truly long-term effects, using

experiments lasting for several years, although I acknowledge the practical difficulties related to such studies. However, long lasting experiments, combined with extensive sampling effort, would also attenuate the inevitable obscuring of the results by different climatic conditions between the years and seasons. Comparing the decomposer community structure of experimentally fragmented habitats to that of natural, continuous soil habitats could also yield important information on the effects of habitat fragmentation in soils. Finally, due to the tightly interactive nature of soil decomposer communities, investigating the possible fragmentation-induced changes in e.g. competitive interactions or predator-prey relationships in the soil organism communities also represents an interesting direction for future studies.

## 4 CONCLUSIONS

The results of this thesis suggest that habitat fragmentation does not necessarily cause dramatic changes in the composition of biotic communities. Soil decomposer communities, which previously have been shown to be resistant to various environmental changes, appear to be particularly insensitive to habitat changes induced by fragmentation. However, it also was shown that soil decomposer communities involve species with life-history characteristics, such as rarity and high trophic position, which render them more sensitive to fragmentation effects than other taxa. These results give further support to findings suggesting that these two traits are good predictors of high vulnerability to habitat fragmentation. From another perspective, it is noteworthy that the responses of rare and predatory microarthropod species were similar to those previously observed with larger animals inhabiting aboveground environments. Thus, it appears that despite their unique environment, the soil decomposer fauna may not behave that differently from fauna in other terrestrial habitats, supporting the use of soil fauna as a practical tool in various ecological studies.

The usefulness of corridors in the colonisation of new, hitherto unpopulated habitats by various groups of soil biota indicates that entire communities, instead of only one or a few species, could benefit from the presence of corridors. On the other hand, the failure of corridors in improving the maintenance of decreasing populations of collembolans suggests that sheer structural connectivity is not a guarantee for functional connectivity. Further, my results imply that for organisms insensitive to fragmentation, the presence of corridors may be superfluous.

Although it may be premature to apply the results of this thesis to predict the responses of other communities to environmental change, the present thesis nevertheless offers further insights to the various responses of different communities to habitat fragmentation and habitat corridors. Furthermore, this thesis can offer a guideline for future studies in which the effects of habitat change on not only soil communities and their functioning but also on communities inhabiting other habitats are explored.

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## YHTEENVETO

### Metsämaaperän hajottajayhteisön vasteet elinympäristön pirstaloitumiseen

Elinympäristöjen pirstaloituminen esimerkiksi metsänhoitotoimenpiteiden seurauksena on johtanut maailmanlaajuiseen paikallisten populaatioiden ja lajin häviämisiin. Ilmiön yleisyyden vuoksi pirstaloitumisen vaikutuksia on tutkittu runsaasti erilaisissa elinympäristöissä ja useilla eliölajeilla. Pirstaloitumisen vaikutusten tutkiminen maaperän hajottajayhteisöissä on kuitenkin ollut yllättävän vähäistä ottaen huomioon hajottajien tärkeän merkityksen ekosysteemien perustoiminnoissa, kuten ravinnekierrossa. Tämän työn tarkoituksena oli tutkia kokeellisesti maaperän hajottajaravintoverkon vasteita elinympäristön pirstaloitumiseen. Lisäksi selvitin ekologisten käytävien merkitystä pirstaloitumisen haitallisten vaikutusten lieventäjinä. Tavoitteena oli myös selvittää, voiko maaperää ja sen eliöitä käyttää mallina ennustettaessa isommassa mittakaavassa elävien eliöyhteisöjen herkkyyttä pirstaloitumiselle. Tutkimuksissani uutta on se, että tutkimissani maaperän eliöyhteisöissä on laaja valikoima ominaisuuksiltaan erilaisia eliöitä, mikrobeista huippupetoihin, kun taas useimmat aikaisemmat tutkimukset ovat keskittyneet vain yhden tai muutaman lajin vastaisiin.

Metsämaaperän hajottajaeliöstön vasteita tutkittiin sekä keinoekosysteemeissä, metsämaaperää simuloivissa pienekosysteemeissä laboratoriossa että luonnossa. Lähtökohtana kaikissa tutkimuksissa oli luoda maaperäeliöiden kannalta pirstaloitunut elinympäristö. Tämä saavutettiin rakentamalla koesysteemejä, joissa elinympäristöinä tutkituille maaperäeliöille toimivia maaperäsaarekkeita ympäröi mineraalimaa, joka on sopimatonta tai ainakin huonolaatuinen elinympäristö maaperäeliöille. Ekologiset käytävät koostuivat humuksesta ja yhdistivät maaperäsaarekkeet joko toisiinsa tai koskemattomaan metsämaaperään. Kokeissa selvitettiin 1) elinympäristön pirstaloitumisen ja maaperäsaarekkeen koon vaikutusta eliöiden lajimäärään ja populaatioiden kokoon, 2) saarekkeita yhdistävien käytävien merkitystä lajimäärän ja populaatioiden ylläpitäjinä, 3) maaperäeliöiden kykyä kolonisoida alunperin steriilejä maaperäsaarekkeita ja ekologisten käytävien merkitystä kolonisoinnissa ja 4) maaperäsaarekkeiden resurssien laadun (lehtikarikkeen määrän) vaikutusta maaperäyhteisön koostumukseen. Kokeiden kesto vaihteli yhdestä kahteen ja puoleen vuoteen.

Tuloksieni mukaan maaperän eliöyhteisöt – sekä mikrobit että eläimet – sietävät yleisesti ottaen melko hyvin elinympäristönsä pirstaloitumista: maaperäsaarekkeiden lajihäviöt olivat vähäisiä pitkäkestoisemmissakin kokeissa. Tämä tulos tukee aikaisempien tutkimuksien tuloksia, joiden mukaan maaperäyhteisöt ovat vastustuskykyisiä muutoksille elinympäristössään. Tämä voi olla seurausta muun muassa maaperäeliöiden kyvystä käyttää hyväkseen hyvin monenlaisia ravinnonlähteitä mahdollistaen niiden selviytymisen muuttuneisakin elinympäristöissä. Poikkeuksena tähän yleiseen sääntöön maaperäeliöiden korkeasta sietokyvystä elinympäristön koon muutoksille olivat eräät harvi-

naiset hyppyhäntäislajit, jotka hävisivät maaperäsaarekkeista. Lisäksi petopunkkilajit osoittautuivat olevan herkempiä habitaatin pienelle koolle kuin muut mikroniveljalkaislajit. Koska maan päällä elävien harvinaisten lajien ja petojen on todettu olevan erityisen herkkiä elinympäristön pirstaloitumiselle, näyttää siltä, että ainakin maaperän mikroniveljalkaisten vasteet pirstaloitumiseen olisivat samankaltaisia kuin isompia elinalueita hyödyntävien eliöiden. Maaperäsaarekkeen koko vaikutti myös siinä esiintyvien lajien määrään: mitä suurempi saareke, sitä enemmän lajeja siinä oli. Positiivinen korrelaatio habitaatin pinta-alan ja lajimäärän välillä on yksi ekologian perusilmiöistä ja tämä tutkimus osoitti sen pätevän myöskin maaperäyhteisöissä.

Koska pirstaloituminen ei juurikaan aiheuttanut lajien tai populaatioiden häviämisiä habitaattisaarekkeissa, myöskään käytävillä ei ollut odotettua merkitystä niiden ylläpitäjinä. Ekologiset käytävät osoittautuivat kuitenkin erityisen käyttökelpoisiksi kasvullisesti leviävälle mikrobeille, hajottajasienille ja rihmamaisille bakteereille. Lisäksi käytävät edistivät änkyrimatojen ja mikroniveljalkaisten levittäytymistä alunperin steriileihin saarekkeisiin. Nämä tulokset viittaavat siihen, että käytävien merkitys ei ole niin lajikohtainen kuin aikaisemmin on arveltu, vaan samoja käytäviä voivat hyödyntää elintavoiltaan ja leviämiskyvyltään hyvinkin erilaiset eliöt ja jopa kokonaiset yhteisöt.

Koska maaperäeliöiden populaatioiden uskotaan pääosin olevan resurssien saatavuuden ja laadun säätelemiä, ei ollut yllätys, että habitaattisaarekkeen resurssien laatu vaikutti tutkittujen maaperän eliöyhteisöjen koostumukseen: karikkeen lisääminen maaperäsaarekkeisiin johti suurempaan maaperäeläinpopulaatioihin ja sienten korkeampaan biomassaan. Resurssien laatu ei kuitenkaan vaikuttanut lajien määrään. Tulosten pohjalta on perusteltua olettaa, että maaperäeliöyhteisöjen koostumuksen kannalta saatavilla olevien resurssien laatu on tärkeämpi tekijä kuin pirstaloitumisen aiheuttama elinympäristön muutos.

Väitöskirjani tulokset viittaavat siihen, etteivät kaikki yhteisöt ole herkkiä elinympäristön pirstaloitumiselle. Toisaalta, stabiilitkin yhteisöt voivat sisältää yksittäisiä lajeja, joiden vaste pirstaloitumiseen eroaa yleisestä yhteisötason vasteesta. Tämä korostaa lajitason vasteiden tutkimisen tärkeyttä. On huomionarvoista, että tämä näyttää pätevän myös tiukkojen eliöiden välisten vuorovaikutussuhteiden sekä resurssien saatavuuden säätelemässä maaperän hajottajayhteisöissä. Vaikka väitöskirjassa esittämäni tulokset eivät suoraan soveltuisikaan muihin, isommassa mittakaavassa toimiviin yhteisöihin tai eliöihin, mikroniveljalkaisten vasteet viittaavat siihen, että niiden käyttö mallieliöinä ekologisten ilmiöiden ja teorioiden tutkimisessa on mahdollista ja jopa perusteltua. Maaperän eliöyhteisöjen tutkimiseen voi suhteellisen helposti liittää myös niiden toiminnallisen vasteen tutkimisen, minkä sisällyttäminen vastaaviin tutkimuksiin tulevaisuudessa voisi tuoda tärkeää uutta tietoa elinympäristön pirstaloitumisen vaikutuksista paitsi maaperäyhteisön, myös koko ekosysteemin toimintaan.

## REFERENCES

- Anderson, G.S. & Danielson, B.J. 1997. The effects of landscape composition and physiognomy on metapopulation size: the role of corridors. *Landscape Ecol.* 12: 261–271.
- Andreassen, H.P., Halle, S. & Ims, R.A. 1996. Optimal width of movement corridors for root voles: not too narrow and not too wide. *J. Appl. Ecol.* 33: 63–70.
- Andreassen, H.P., Hertzberg, K. & Ims, R.A. 1998. Space-use responses to habitat fragmentation and connectivity in the root vole *Microtus oeconomus*. *Ecology* 79: 1223–1235.
- Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71: 355–366.
- Andrén, H. 1996. Population responses to habitat fragmentation: statistical power and the random sample hypothesis. *Oikos* 76: 235–242.
- Beier, P. & Noss, R.F. 1998. Do habitat corridors provide connectivity? *Conserv. Biol.* 28: 1241–1252.
- Bengtsson, G., Hedlund, K. & Rundgren, S. 1994. Food- and density-dependent dispersal: evidence from a soil collembolan. *J. Anim. Ecol.* 63: 513–520.
- Berg, M., De Ruiter, P., Didden, W., Janssen, M., Schouten, T. & Verhoef, H. 2001. Community food web, decomposition and nitrogen mineralisation in a stratified Scots pine forest soil. *Oikos* 94: 130–142.
- Brown, J.H. & Kodric-Brown, A. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58: 445–449.
- Burkey, T.V. 1989. Extinction in nature reserves: the effect of fragmentation and the importance of migration between reserve fragments. *Oikos* 55: 75–81.
- Burkey, T.V. 1995. Extinction rates in archipelagos: implications for populations in fragmented habitats. *Conserv. Biol.* 9: 527–541.
- Burkey, T.V. 1997. Metapopulation extinction in fragmented landscapes: using bacteria and protozoa communities as model ecosystems. *Am. Nat.* 150: 568–591.
- Cabeza, M. & Moilanen, A. 2001. Design of reserve networks and the persistence of biodiversity. *Science* 292: 242–248.
- Carpenter, S.R. 1996. Microcosm experiments have limited relevance for community and ecosystem ecology. *Ecology* 77: 677–680.
- Chen, B. & Wise, D.H. 1997. Responses of forest-floor fungivores to experimental food enhancement. *Pedobiologia* 41: 316–326.
- Chen, B. & Wise, D.H. 1999. Bottom-up limitation of predaceous arthropods in a detritus-based terrestrial food web. *Ecology* 80: 761–772.
- Clinchy, M. 1997. Does immigration “rescue” populations from extinction? Implications regarding movement corridors and the conservation bargain. *Oikos* 80: 618–622.

- Coffman, C.J., Nichols, J.D. & Pollock, K.H. 2001. Population dynamics of *Microtus pennsylvanicus* in corridor-linked patches. *Oikos* 93: 3–21.
- Collinge, S.K. 1996. Ecological consequences of habitat fragmentation: implications for landscape architecture and planning. *Landscape Urban Plann.* 36: 59-77.
- Collinge, S.K. 1998. Spatial arrangement of habitat patches and corridors: clues from ecological field experiments. *Landscape Urban Plann.* 42: 157-168.
- Connor, E.F. & McCoy, E.D. 1979. The statistics and biology of the species-area relationship. *Am. Nat.* 113: 791-833.
- Copley, J. 2000. Ecology goes underground. *Nature* 406: 452-454.
- Davies, K.F. & Margules, C.R. 1998. Effects of habitat fragmentation on carabid beetles: experimental evidence. *J. Anim. Ecol.* 67: 460-471.
- Davies, K.F., Margules, C.R. & Lawrence, J.F. 2000. Which traits of species predict population declines in experimental forest fragments? *Ecology* 81:1450-1461.
- Davies, K.F., Melbourne, B.A. & Margules, C.R. 2001. Effects of within- and between-patch processes on community dynamics in a fragmentation experiment. *Ecology* 82: 1830-1846.
- Debinski, D.M. & Holt, R.D. 2000. A survey and overview of habitat fragmentation experiments. *Conserv. Biol.* 14: 342–355.
- De Vries, H.H., Den Boer, P.J. & Van Dijk, T.S. 1996. Ground beetle dispersal in heathland fragments in relation to survival, dispersal, and habitat preferences. *Oecologia* 107: 332–342.
- Diamond, J.M. 1972. Biogeographic kinetics: estimation of relaxation times for avifaunas of Southwest Pacific Islands. *Proc. Natl. Acad. Sci. USA* 69: 3199-3203.
- Didham, R.K. 1998. Altered leaf-litter decomposition rates in tropical forest fragments. *Oecologia* 116: 397-406.
- Didham, R.K., Ghazoul, J., Stork, N.E. & Davis, A.J. 1996. Insects in fragmented forests: a functional approach. *Trends Ecol. Evol.* 11: 255-260.
- Dighton, J., Jones, H.E., Robinson, C.H. & Beckett, J. 1997. The role of abiotic factors, cultivation practices and soil fauna in the dispersal of genetically modified microorganisms in soils. *Appl. Soil Ecol.* 5: 109-131.
- Drake, D.R., Mulder, C.P.H., Towns, D.R. & Daugherty, C.H. 2002. The biology of insularity: an introduction. *J. Biogeogr.* 29: 563-569.
- Drake, J.A., Huxel, G.R. & Hewitt, C.L. 1996. Microcosms as models for generating and testing community theory. *Ecology* 77: 670-677.
- Ekschmitt, K. & Griffiths, B.S. 1998. Soil biodiversity and its implications for ecosystem functioning in a heterogeneous and variable environment. *Appl. Soil Ecol.* 10: 201-215.
- Fagan, W.F., Cantrell, R.S. & Cosner, C. 1999. How habitat edges change species interactions. *Am. Nat.* 153: 165-182.
- Fahrig, L. 2001. How much habitat is enough? *Biol. Conserv.* 100: 65-74.
- Forman, R.T.T. & Godron, M. 1986. *Landscape ecology*. 619 p., John Wiley & Sons, New York.

- Frostegård, Å., Tunlid, A. & Bååth, E. 1993. Phospholipid fatty acid composition, biomass, and activity of microbial communities from two soil types experimentally exposed to different heavy metals. *Appl. Environ. Microbiol.* 59: 3605-3617.
- Gilbert, F., Gonzalez, A. & Evans-Freke, I. 1998. Corridors maintain species richness in the fragmented landscapes of a microecosystem. *Proc. R. Soc. Lond.* 265: 577-582.
- Giller, P.S., 1996. The diversity of soil communities, the 'poor man's tropical rainforest'. *Biodiv. Conserv.* 5: 135-168.
- Golden, D.M. & Crist, T.O. 1999. Experimental effects of habitat fragmentation on old - field canopy insects: community, guild and species responses. *Oecologia* 118: 371 - 380.
- Gonzalez, A. 2000. Community relaxation in fragmented landscapes: the relation between species richness, area and edge. *Ecol. Letters* 3: 441-448.
- Gonzalez, A. & Chaneton, E.J. 2002. Heterotroph species extinction, abundance and biomass dynamics in an experimentally fragmented microecosystem. *J. Anim. Ecol.* 71: 594-602.
- Gonzalez, A., Lawton, J.H., Gilbert, F.S., Blackburn, T.M. & Evans-Freke, I. 1998. Metapopulation dynamics, abundance and distribution in a microecosystem. *Science* 281: 2045-2047.
- Gustafson, E.J. & Gardner, R.H. 1996. The effect of landscape heterogeneity on the probability of patch colonization. *Ecology* 77: 94-107.
- Haddad, N.M., Rosenberg, D.K. & Noon, B.R. 2000. On experimentation and the study of corridors: response to Beier and Noss. *Conserv. Biol.* 14: 1543-1545.
- Haddad, N.M., Bowne, D.R., Cunningham, A., Danielson, B.J., Levey, D.J., Sargent, S. & Spira, T. 2003. Corridor use by diverse taxa. *Ecology* 84: 609-615.
- Hågvar, S. & Kjøndal, B.R. 1981. Succession, diversity and feeding habits of microarthropods in decomposing birch leaves. *Pedobiologia* 22: 385-408.
- Haimi, J. 1993. Effects of earthworms on soil processes in coniferous forest soil. *Biological Research Reports from the University of Jyväskylä* 32.
- Hansen, R.A. & Coleman, D.C. 1998. Litter complexity and composition are determinants of the diversity and species composition of oribatid mites (Acari: Oribatida) in litterbags. *Appl. Soil Ecol.* 9: 17-23.
- Hanski, I. 1994. Patch-occupancy dynamics in fragmented landscapes. *Trends Ecol. Evol.* 9: 131-135.
- Hanski, I., 1999. *Metapopulation Ecology*. 313 p., Oxford University Press, New York.
- Harrison, S. & Bruna, E. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography* 22: 225-232.
- Hedlund, K. & Augustsson, A. 1995. Effects of enchytraeid grazing on fungal growth and respiration. *Soil Biol. Biochem.* 27: 905-909
- Henein, K. & Merriam, G. 1990. The elements of connectivity where corridor quality is variable. *Landsc. Ecol.* 4: 157-170.

- Hess, G.R. 1994. Conservation corridors and contagious disease: a cautionary note. *Conserv. Biol.* 8: 256–262.
- Hess, G.R. & Fischer, R.A. 2001. Communicating clearly about conservation corridors. *Landscape Urban Plann.* 55: 195–208.
- Hobbs, R.J. 1992. The role of corridors in conservation: solution or bandwagon? *Trends Ecol. Evol.* 7: 389–392.
- Holt, R.D. 1996. Food webs in space: An island biogeographic perspective. In: Polis, G.A. & Winemiller, K.O. (eds), *Food webs*: 313–323. Chapman Hall, New York.
- Hudgens, B.R. & Haddad, N.M. 2003. Predicting which species will benefit from corridors in fragmented landscapes from population growth models. *Am. Nat.* 161: 808–820.
- Huhta, V., Hyvönen, R., Koskenniemi, A., Vilkkamaa, P., Kaasalainen, P. & Sulander, M. 1986. Response of soil fauna to fertilization and manipulation of pH in coniferous forest soil. *Acta Forestalia Fennica* 195, Society of Forestry in Finland, Helsinki.
- Jordán, F. 2000. A reliability-theory approach to corridor design. *Ecol. Modell.* 128: 211–220.
- Kotze, D.J. & O'Hara, R.B. 2003. Species decline – but why? Explanations of barabid beetle (Coleoptera, Carabidae) declines in Europe. *Oecologia* 135: 138–148.
- Kruess, A. & Tscharntke, T. 1994. Habitat fragmentation, species loss and biological control. *Science* 264: 1581–1584.
- Kruess, A. & Tscharntke, T. 2000. Species richness and parasitism in a fragmented landscape: experiments and field studies with insects on *Vicia sepium*. *Oecologia* 122: 129–137.
- Laakso, J. 1998. Sensitivity of ecosystem functioning to changes in the structure of soil food webs. *Biological Research Reports from the University of Jyväskylä* 66, Jyväskylä.
- Laakso, J. & Setälä, H. 1999. Sensitivity of primary production to changes in the architecture of belowground food webs. *Oikos* 87: 57–64
- Lavelle, P. & Spain, A.V. 2001. *Soil Ecology*. 654 p., Kluwer Academic Publishers, Dordrecht.
- Lawton, J. 1999. Size matters. *Oikos* 85: 19–21.
- Levin, S. 1992. The problem of pattern and scale in ecology. *Ecology* 73: 1943–1967.
- Liiri, M. 2001. Complexity of soil faunal communities in relation to ecosystem functioning in coniferous forest soil – a disturbance oriented study. *Jyväskylä Studies in Biological and Environmental Science* 104.
- Liiri, M., Setälä, H., Haimi, J., Pennanen, T. & Fritze, H. 2002. Relationship between soil microarthropod species diversity and plant growth does not change when the system is disturbed. *Oikos* 96: 137–149.
- MacArthur, R.H. & Wilson, E.O. 1967. *The theory of island biogeography*. 203 p., Princeton University Press, Princeton.

- MacLean, M.A. & Huhta, V. 2000. Temporal and spatial fluctuations in moisture affect humus microfungus community structure in microcosms. *Biol. Fertil. Soils* 32: 114-119.
- Maraun, M., Martens, H., Migge, S., Theenhaus, A. & Scheu, S. 2003. Adding to 'the enigma of soil animal diversity': fungal feeders prefer similar food substrates. *Eur. J. Soil Biol.* 39: 85-95.
- Martikainen, E. 1998. Environmental factors influencing effects of chemicals on soil animals: Studies at population and community levels. *Biological Research Reports from the University of Jyväskylä* 71.
- Menge, B.A. & Olson, A.M. 1990. Role of scale and environmental factors in regulation of community structure. *Trends Ecol. Evol.* 5: 52-57.
- Mikola, J. 1997. Trophic-level dynamics in microbial-based soil food webs. *Biological Research Reports from the University of Jyväskylä* 61.
- Møller, J., Miller, M. & Kjølter, A. 1999. Fungal-bacterial interaction on beech leaves: influence on decomposition and dissolved organic carbon quality. *Soil Biol. Biochem.* 31: 367-374.
- Mönkkönen, M. & Reunanen, P. 1999. On critical thresholds in landscape connectivity: a management perspective. *Oikos* 84: 302-305.
- Moore, J.C. & De Ruiter, P.C. 1997. Compartmentalization of resource utilization within soil ecosystems. In: Gange, A.C. & Brown, V.K. (eds), *Multitrophic interactions in terrestrial systems*: 375-393. Blackwell Science, London.
- Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends Ecol. Evol.* 10: 58-62.
- Ney-Nifle, M. & Mangel, M. 1999. Habitat loss and changes in the species-area relationship. *Conserv. Biol.* 14: 893-898.
- Niemelä, J. 2001. The utility of movement corridors in forested landscapes. *Scand. J. For. Res. Suppl.* 3: 70-78.
- Nieminen, J. 2002. Modelling the functioning of experimental soil food webs. *Jyväskylä Studies in Biological and Environmental Science* 108.
- Nieminen, J. & Setälä, H. 1998. Enclosing decomposer food web: implications for community structure and function. *Biol. Fertil. Soils* 26: 50-57.
- Noss, R.F. & Beier, P. 2000. Arguing over little things: response to Haddad et al. *Conserv. Biol.* 14: 1546-1548.
- Ovaskainen, O. & Hanski, I. 2002. Transient dynamics in metapopulation response to perturbation. *Theor. Popul. Biol.* 61, 285-295.
- Pennanen, T., 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. *Microbiol. Ecol.* 38: 168-179.
- Pennanen, T., Paavolainen, L. & Hantula, J. 2001. Rapid PCR-based method for the direct analysis of fungal communities in complex environmental samples. *Soil Biol. Biochem.* 32: 697-699.
- Petersen, H. & Luxton, M. 1982. A comparative analysis of soil fauna populations and their role in decomposition process. *Oikos* 39: 287-376.

- Pimm, S.L. 1982. Food webs. 219 p., Chapman & Hall, London.
- Ponge, J.F. 1991. Succession of fungi and fauna during decomposition of needles in a small area of Scots pine litter. *Plant Soil* 138: 99-113.
- Ponsard, S., Arditì, R. & Jost, C. 2000. Assessing top-down and bottom-up control in a litter-based soil macroinvertebrate food chain. *Oikos* 89: 524-540.
- Quinn, J.F. & Harrison, S.P. 1988. Effects of habitat fragmentation and isolation on species richness: evidence from biogeographic patterns. *Oecologia* 75: 132-140.
- Richards, B.N. 1987. The microbiology of terrestrial ecosystems. 399 p., Longman Group UK, Singapore.
- Robinson, G.R., Holt, R.D., Gaines, M.S., Hamburg, S.P., Johnson, M.L., Fitch, H.S. & Martinko, E.A. 1992. Diverse and contrasting effects of habitat fragmentation. *Science* 257: 524-526.
- Rosenberg, D.K., Noon, B.R. & Meslow, E.C. 1997. Biological corridors: form, function and efficacy. *Bioscience* 47: 677-687.
- Rosenzweig, M.L. 1995. Species diversity in space and time. Cambridge University Press, New York.
- Saunders, D.A., Hobbs, R.J. & Margules, C.R. 1991. Biological consequences of ecosystem fragmentation: a review. *Conserv. Biol.* 5: 18-32.
- Setälä, H. 1990. Effects of soil fauna on decomposition and nutrient dynamics in coniferous forest soil. *Biological Research Reports from the University of Jyväskylä* 20.
- Setälä, H., Tyynismaa, M., Martikainen, E. & Huhta, V. 1991. Mineralization of C, N and P in relation to decomposer community structure in coniferous forest soil. *Pedobiologia* 35: 285-296.
- Setälä, H., Laakso, J., Mikola, J. & Huhta, V. 1998. Functional diversity of decomposer organisms in relation to primary production. *Appl. Soil Ecol.* 9: 25-31.
- Setälä, H., Haimi, J. & Siira-Pietikäinen, A. 2000. Sensitivity of soil processes in northern forest soils: are management practices a threat? *For. Ecol. Manage.* 133: 5-11.
- Setälä, H., Berg, M. & Jones, T.H. 2004. Trophic structure and functional redundancy in soil communities. Cambridge University Press, in press.
- Siepel, H. 1994. Life-history tactics of soil microarthropods. *Biol. Fertil. Soils* 18: 263-278.
- Sih, A., Jonsson, B.G. & Luikart, G. 2000. Habitat loss: ecological, evolutionary and genetic consequences. *Trends Ecol. Evol.* 15: 132-134.
- Siira-Pietikäinen, A. 2002. Decomposer community in boreal coniferous forest soil after forest harvesting: Mechanisms behind responses. *Jyväskylä Studies in Biological and Environmental Science* 117.
- Siira-Pietikäinen, A., Pietikäinen, J., Fritze, H. & Haimi, J. 2001. Short-term responses of soil decomposer communities to forest management: clear felling versus alternative methods. *Can. J. For. Res.* 31: 88-99.

- Siira-Pietikäinen, A., Haimi, J. & Fritze, H. 2003. Organisms, decomposition, and growth of pine seedlings in boreal forest soil affected by sod cutting and trenching. *Biol. Fertil. Soils* 37: 163-174.
- Simberloff, D., Farr, J.A., Cox, J. & Mehlman, D.W. 1992. Movement corridors: conservation bargains or poor investments? *Conserv. Biol.* 6: 493-504.
- Srivastava, D. & Lawton, H. 1998. Why more productive sites have more species: an experimental test of theory using tree-hole communities. *Am. Nat.* 152: 510-529.
- Steffan-Dewenter, I. & Tsharntke, T. 2002. Insect communities and biotic interactions on fragmented calcareous grasslands – a mini review. *Biol. Conserv.* 104: 275-284.
- Sulkava, P. 2001. Interactions between faunal community and decomposition processes in relation to microclimate and heterogeneity in boreal forest soil. *Jyväskylä Studies in Biological and Environmental Science* 100.
- Sulkava, P. & Huhta, V. 1998. Habitat patchiness affects decomposition and faunal diversity: a microcosm experiment on forest floor. *Oecologia* 116: 390-396.
- Sulkava, P., Huhta, V. & Laakso, J. 1996. Impact of soil faunal structure on decomposition and N-mineralisation in relation to temperature and moisture in forest soil. *Pedobiologia* 40: 505-513.
- Summerville, K.S. & Crist, T.O. 2001. Effects of experimental habitat fragmentation on patch use by butterflies and skippers (Lepidoptera). *Ecology* 82: 1360-1370.
- Tewksbury, J.J., Levey, D.J., Haddad, N.M., Sargent, S., Orrock, J.L., Weldon, A., Danielson, B.J., Brinkerhoff, J., Damschen, E.I. & Townsend, P. 2002. Corridors affect plants, animals, and their interactions in fragmented landscapes. *Proc. Natl. Acad. Sci. USA* 99: 12923-12926.
- Tiebout III, H.M. & Anderson, R.A. 1996. A comparison of corridors and intrinsic connectivity to promote dispersal in transient successional landscapes. *Conserv. Biol.* 11: 620-627.
- Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* 80: 1455-1474.
- Tischendorf, L. & Fahrig, L. 2000. On the usage and measurement of landscape connectivity. *Oikos* 90: 7-19.
- Tracy, C.R. & George, T.L. 1992. On the determinants of extinction. *Am. Nat.* 139: 102-122.
- Tsharntke, T. & Kruess, A. 1999: Habitat fragmentation and biological control. In: Hawkins, B.A. & Cornell, H.V. (eds), *Theoretical approaches to biological control*: 190-205. Cambridge University Press, Cambridge.
- Vainio, E.J. & Hantula, J. 2000. Direct analysis of wood-inhabiting fungi using denaturing gradient gel electrophoresis of amplified ribosomal DNA. *Mycol. Res.* 104: 927-936
- Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. 1997. Human domination of earth's ecosystems. *Science* 277: 494-499.

- Wardle, D.A. 2002. *Communities and ecosystems: Linking the aboveground and belowground components*. 392 p., Princeton University Press, New Jersey.
- Wardle, D.A., Yaetes, G.W., Barker, G.M., Bellingham, P.J., Bonner, K.I. & Williamson, W.M. 2003. Island biology and ecosystem functioning in epiphytic soil communities. *Science* 301: 1717-1720.
- Wilkinson, S.C., Anderson, J.M., Scardelis, S.P., Tisiafouli, M., Taylor, A. & Wolters, V. 2002. PLFA profiles of microbial communities in decomposing conifer litters subject to moisture stress. *Soil Biol. Biochem.* 34: 189-200.
- Wright, D.H. & Coleman, D.C. 1993. Patterns of survival and extinctions of nematodes in isolated soil. *Oikos* 67: 563-572.
- Zar, J.H. 1999. *Biostatistical Analysis*, 4th edn. 663 p., Prentice Hall, New Jersey.