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Abstract

The Swedish Nuclear Fuel and Waste Management Co (SKB) carries out extensive investigations on factors that can affect long-term storage of nuclear waste. Earthworms consume organic soil materials and when doing so they transport and mix mineral soil particles as well as litter and humus materials. Ants do not consume soil materials, but they collect and mix mineral soil particles and litter materials to construct their nests. This process of material displacement by earthworms and ants is called bioturbation and can be a mechanism for the redistribution (vertical and horizontal) of radionuclides within the soil profile.

The aim of the present study was to determine the quantitative impact of earthworms and ants on bioturbation of soil in different ecosystems at Forsmark and Oskarshamn. Earthworms were sampled at four 20×20 cm^2 sub-plots at each site and were determined, dried and weighed in the laboratory. Gut passage time and faeces production were determined in a laboratory experiment at constant temperature. Temperature dependence of earthworm growth was studied at 3, 6, 10 and 20°C, and it was assumed that defecation mirrored growth as regards temperature dependence. Ant species composition, ant nest density and nest volume were investigated in the field by using pitfall traps and a transect method to enumerate ant nests. Dry weights of ant nests were determined after weighing in the laboratory.

Earthworm abundances and biomasses were high in moist/wet alder forests and deciduous woodlands and low in pine and pine/spruce forests at both Forsmark and Oskarshamn. In mesic spruce forests, high estimates of abundance/biomass of earthworms were found at Forsmark but low at Oskarshamn, whereas grazed pastures had high estimates at Oskarshamn and ungrazed abandoned fields had relatively low estimates at Forsmark. High pH at Forsmark and low pH at Oskarshamn as well as high groundwater tables at some of the Forsmark sites can explain the difference between earthworm abundances/biomasses at Forsmark and Oskarshamn. Presence of ants and numbers of ant nests did not seem to be dependent on pH.

Earthworm bioturbation (estimated as faeces production) was high where the earthworm biomasses were high. At Forsmark, earthworm bioturbation was estimated at 16, 12, 10, 3 and 0.2 kg dry weight m^{-2} $year^{-1}$ in mesic spruce forests, moist alder forests, deciduous woodlands, abandoned fields and mixed coniferous forest, respectively. At Oskarshamn, earthworm bioturbation was estimated at 25, 23, 7, 0.5 and 0.0003 kg dry weight m^{-2} $year^{-1}$ in deciduous (mainly oak) woodlands, grazed pasture, moist alder forests, pine forests and spruce forests (on drained peatland), respectively. Ant bioturbation was markedly lower than earthworm bioturbation. Ant bioturbation varied between 0.004 (mixed coniferous forest) and 0.5 (abandoned field) kg dry weight m^{-2} $year^{-1}$ at Forsmark, whereas at Oskarshamn it varied between 0.026 and 0.068 kg dry weight m^{-2} $year^{-1}$ in the five ecosystems studied. Thus, the ants generally contributed 0–2% of total bioturbation with the exception of the abandoned fields at Forsmark (12%) and the acid spruce forests at Oskarshamn (93%), which had low earthworm populations.

In conclusion, the bioturbation was remarkably high at certain sites. Stone-free soils often contain 300 kg dry weight m^{-2} in the top 30 cm. Earthworms and ants can, thus, turn over the whole topsoil during a period of 12–20 years in suitable habitats.

Sammanfattning

Svensk Kärnbränslehantering AB (SKB) undersöker vilka faktorer som kan påverka långtidslagring av kärnbränsleavfall. Daggmaskar konsumerar jord och organiskt material som de transporterar och blandar. Myror äter inte jord, men de samlar och blandar jord och förna när de bygger sina bon. Den biologiska jordomblandning som daggmaskar och myror åstadkommer kallas för bioturbation, och den kan vara en potentiellt viktig mekanism för att omfördela radionuklider inom markprofilen.

Målet med denna studie var att bestämma den kvantitativa omfattningen av maskars och myrors bioturbation av jord i olika ekosystem i Forsmark och Oskarshamn. Maskarna insamlades från 20×20 cm^2 provytor genom att ta markprover till 40 cm djup. Maskarna framsorterades både i fält och på laboratoriet, där de artbestämdes, räknades, torkades och vägdes. För att uppskatta daggmaskarnas vertikala jordomblandning i fält bestämdes den mängd maskexkrementer som producerades under en viss tid.

Mängden jord som maskarna äter, liksom den tid det tar för jorden att passera genom maskarnas tarm, bestämdes på laboratoriet. Temperaturberoendet hos maskarnas tillväxt studerades vid 3, 6, 10 och 20 °C, och det antogs att samma temperaturberoende gällde för tillväxt och exkrementproduktion. Myrornas artsammansättning, botäthet och bovolym undersöktes i fält med fallfällor och genom att räkna och mäta alla bon i utlagda 50 meterstransekter. Myrbonas torrvikt bestämdes efter vägning på laboratoriet.

Daggmaskarnas antal och biomassa var hög i lövskog och aldominerad sumpskog och låg i sur barrblandskog i både Forsmark och Oskarshamn. Höga tätheter och biomassor av daggmaskar konstaterades i vissa granskogar i Forsmark, medan motsvarande skattningar var mycket låga i Oskarshamn. Betad gräsmark hade höga maskpopulationer i Oskarshamn, medan nedlagd åkermark i Forsmark hade låga maskpopulationer. Skillnaderna mellan granskogarna i Forsmark och Oskarshamn kan förklaras med högt pH (6–7) i de förra och lågt pH (4) i de senare. Låga populationer i nedlagd åkermark i Forsmark kan troligen förklaras med högt grundvatten, som ger ökad vinterdödlighet.

Daggmaskarnas bioturbation, skattad som exkrementproduktion, var hög där maskpopulationerna var höga. I Forsmark skattades maskarnas bioturbation till 16, 12, 10, 3 och 0,2 kg torrvikt m^{-2} år^{-1} i respektive frisk granskog, sumpskog, lövskog, nedlagd åkermark och barrblandskog. I Oskarshamn skattades maskarnas bioturbation till 25, 23, 7, 0,5 och 0,0003 kg torrvikt m^{-2} år^{-1} i respektive ekskog, betesmark, alsumpskog, tallskog och granskog (på dikad torvmark). Myrornas bioturbation var markant lägre än maskarnas bioturbation. Den varierade mellan 0,004 (barrblandskog) och 0,5 (nedlagd åkermark) i Forsmark och mellan 0,026 and 0,068 i Oskarshamn, räknat som kg torrvikt m^{-2} år^{-1}. Myrorna bidrog således med bara 0–2 % till den totala bioturbationen med undantag för den nedlagda åkermarken i Forsmark (12 %) och den sura granskogen i Oskarshamn (93 %), som hade låga maskpopulationer.

Sammanfattningsvis var bioturbationen anmärkningsvärt hög på vissa lokaler. Stenfria jordar innehåller ofta 300 kg torrvikt m^{-2} i markens översta skikt på 30 cm. Daggmaskar och myror kan således blanda om och omsätta hela detta jordskikt under en period på 12–20 år om miljöerna är lämpliga.

Contents

1 Introduction

The Swedish Nuclear Fuel and Waste Management Co (SKB) carries out extensive investigations on factors that can affect long-term storage of nuclear waste. Two of the sites suggested to be host areas of nuclear waste are Forsmark and Oskarshamn. The waste will be encapsulated deep in the bedrock, but if nuclear waste, for some reason, will penetrate through the bedrock to the upper part of the soil, soil processes will affect the radionuclides.

Plants can assimilate radionuclides by their roots, and the substances can be translocated from various depths in the soil up into the aboveground plant parts. Dead plant parts will reach the soil as litter, which will be decomposed and mineralised by microorganisms and soil animals. During decomposition, when carbon is dissipated as CO_2, radionuclides will probably accumulate in the topsoil. Soil, however, is dynamic and undergoes continuous mixing, caused by soil erosion and deposition processes and by biological processes /Balek 2002/. Soil mixing due to biological processes is called bioturbation /Armour-Chelu and Andrews 1994, Lavelle et al. 1997, Meysman et al. 2006/. Bioturbation can be a relevant mechanism for the redistribution (vertical and horizontal) of radionuclides within the soil profile and has been accounted for in models aiming at describing the distribution patterns of radioactive soil contaminants /Mueller-Lemans and van Dorp 1996, Tyler et al. 2001, Bunzl 2002/.

In non-alpine agricultural areas of central Europe, ants and earthworms are considered as the most important bioturbation agents /Darwin 1881, Scheu 1987, Mueller-Lemans and van Dorp 1996, Lavelle et al. 1997/. Both groups are commonly called ‘ecosystem engineers’ due to their significant role in material displacement that may substantially modify the physical structure of their habitats /Jones et al. 1994, Lavelle et al. 1997/. Earthworms change the soil structure by ingestion of organic particles, cast production and building of structures like burrows and moulds /Lavelle et al. 1997/. Ants change physical and chemical properties of the soil through building belowground galleries, mounding and material mixing and by the accumulation of organic material /Petal 1978, Mandel and Sorenson 1982, Folgarait 1998, Dostal et al. 2005/.

Thus, in a scenario where radionuclides are present in the soil, the two animal groups will contribute, to an unknown extent, to upward, downward and horizontal transports of contaminated soil particles and litter components.

The present report aims at estimating the bioturbation activity of earthworms and ants at the suggested host areas of nuclear waste close to Forsmark and Oskarshamn. In order to understand the diversity in earthworm and ant bioturbation, it is also necessary to consider some characteristics of the ecology of these animals.

1.1 Earthworms

In most temperate soils, earthworms form the largest part of the animal biomass /Paoletti 1999, Lavelle and Spain 2001/. Under favourable conditions, biomass can be as large as 200 g m^{-2} /Curry 1998/ and field densities may range from less than ten to several hundred individuals m^{-2} /Eijsackers and Van der Drift 1976, Lee and Pankhurst 1992, Curry 1998/.

Earthworms consume different forms of organic matter in the soil. The bulk of food ingested is dead plant material like decaying roots and leaves as well as living organisms such as nematodes, protozoans, rotifers, bacteria and fungi /Lee 1985/. They also feed on dung, manure or decomposing remains of other animals. Soil and organic matter pass through the guts in large quantities. /Satchell 1967 and Crossley et al. 1971/ estimated gut passage to be of the order of 20–30% of their body weight per day, but more recent estimates suggest even greater consumption /Bolton and Phillipson 1976, Scheu 1987/.

Earthworms excrete faeces in the form of casts, usually at another location than where the food was consumed. In grasslands it has been calculated that earthworms can turn over the topsoil (15 cm) in five to twenty years via the translocation of material due to casting /Mueller-Lemans and van Dorp 1996/.

Earthworm species strongly vary in their feeding and burrowing behaviour and, therefore, have different effects on their soil environment. Based on these differences in behaviour and morphology, European earthworm species are usually divided into three relatively distinct ecological groups /Bouché 1972, 1977, Wallwork 1983/.

Epigeic species are surface-dwelling species that live in the topsoil above the mineral soil (uppermost 5 cm) and in the litter layer. They ingest large amounts of undecomposed litter and produce only short-lived burrows in the mineral soil for diapause periods. As they are relatively exposed to climatic fluctuations and predator pressure, they tend to be small (2–10 cm) with short generation times. Common epigeic worms are *Dendrobaena octaedra, Dendrodrilus rubidus* and *Lumbricus rubellus*.

Endogeic species forage below the surface and inhabit the mineral soil layers (down to 60 cm depth). They ingest large quantities of soil that is often enriched with organic material and build continuous horizontal burrows. Examples are *Aporrectodea caliginosa*, *Aporrectodea rosea* and *Octolasion cyaneum*.

Anecic species are species that build permanent, vertical burrows deep into the subsoil (1–3 m). They are detritivores and come to the surface (mainly at night-time) to feed on partially decomposed litter, manure, and other organic matter. During these occasions they will also leave their casts on the soil surface. Examples are *Aporrectodea longa* and *Lumbricus terrestris.*

In order to give quantitative information on the displacement of soil by earthworms it is important to know how much the earthworms consume/defecate and where in the soil profile they consume/defecate. It becomes explicit from the classification above how different these effects are for different earthworm groups or species.

The amount of food consumed strongly depends on the nutritional quality of the food ingested. The lower the content of organic matter in the soil, the more the earthworms have to consume to meet their nutrient requirements. The endogeic species, thus, consume more soil than the epigeic ones.

Earthworms deposit the casts both on the soil surface and within the soil itself. The vertical distribution of the three earthworm groups suggests where their food is mainly consumed and where their casts are deposited, indicating that particularly endogeic species are important for soil mixing /Lavelle and Spain 2001/. These species often use casts to line their vertical burrows /Wilcke 1953, Graff and Makeschin 1979/ and mainly deposit them in burrows and soil spaces /Lee 1985/. Anecic species are particularly responsible for vertical transports of materials /Bouché 1981, Anderson 1988/. Earthworms in this group drag down litter from the soil surface into the soil but also excrete mineral soil consumed in deeper soil layers on the soil surface. Thereby they produce characteristic surface casts, which consist of materials from the construction/maintenance of their burrows /Bouché 1981/.

1.2 Ants

Ants are social insects like bees, wasps and bumblebees. They live in groups and cooperate. They can build huge nests that can be maintained during many years. The nests of the red forest ants (*Formica rufa* group) can be active for more than 30 years. Other ant species, like *Myrmica* spp., build small nests that are inhabited for only one or two months during summertime.

Usually these ants divide into small colonies during the spring and fuse into a single nest before over-wintering /Backus et al. 2006/. Also, during summer they can relocate their nests several times /Backus et al. 2006, Jakubczyk et al. 1972/.

An ant colony contains one or several queens that lay eggs from which larvae are hatched. Larvae develop into pupae, and these develop into sterile workers or fertile queens or males. The workers take care of the queens and the brood. Depending on species, workers can stay alive for as much as three years. This means that ant nests are inhabited by overlapping generations. Development time from egg to adult varies for different ant species and is also dependent on temperature. Forest ants have developing times of 30–45 days, *Myrmica* ants about 80 days and carpenter ants (*Camponotus* spp.) two years /Schoeters and Vankerkhoven 2001/.

Ants can be found in almost every habitat, e.g. in forests, grasslands, grazed pastures, gardens, road verges and outcrops. About 8,800 ant species have been described /Hölldobler and Wilson 1990/, but in Sweden only about 70 ant species have been found. Ant abundance and species composition differ a lot between habitats. Usually, semi-natural grasslands are species rich, and occasionally as many as one third of the ant fauna in Sweden has been found in a single field. The nest density can sometimes be as high as 2–5 per m^2 /Seifert 1996/. Forests are usually poorer in ant diversity than semi-natural grasslands.

Different ant species build nests of different materials. Forest ants build nests made of conifer litter, twigs, resin and soil particles, while *Myrmica* spp. and *Lasius niger* build nests mainly of soil. Other species construct nests in tree trunks (e.g. *Lasius platythorax*) or in trees (*L. brunneus*). Some nests are very voluminous like those of forest ants, whereas others are very small or even completely belowground as for many *Myrmica* species. *L. niger* and *L. flavus* can build huge soil nests, but sometimes they build small belowground nests, often under stones or dead wood. Inside the nests the workers build galleries and chambers, where the queens and the brood are kept. Ants continuously mix and re-arrange the nest materials and in so doing, they affect the soil structure and soil chemical contents /Lobry de Bruyn and Conacher 1990, Nkem et al. 2000/. Because ants are present in almost all terrestrial environments, and because ant nest densities can be large, ants have a potential to transport and mix soil and, thereby, redistribute radionuclides within the soil profile.

Because earthworms and ants seldom seem to live together in large abundances, we hypothesised that the impact of earthworms is greater in soils with fine texture and high pH and the impact of ants is greater in soils with coarse texture and low pH.

1.3 General information

This document reports the results gained by the investigation on bioturbation in different ecosystems, which is one of the activities performed within the site investigation at Forsmark and Oskarshamn. The work was carried out in accordance with the activity plans AP PF 400-06-012 och AP PS 400-06-004. In Table 1-1 controlling documents for performing this activity are listed. Activity plans are SKB's internal controlling documents.

The original results achieved in this study are stored in the primary database (SICADA) and are traceable by the activity plan number.

Table 1-1. Controlling documents for performance of the activity.

Activity plan	Number	Version
Biologisk markomblandning – bioturbation i olika vegetationstyper	AP PS 400-06-004 AP PF 400-06-012	1.0 1.0

2 Objective and scope

The aims of the study were:

1. To determine the quantitative impact of soil fauna (earthworms and ants) on bioturbation of soil in different ecosystems at Forsmark and Oskarshamn.
2. To test the hypothesis that the impact of earthworms is greater in soils with fine texture and high pH and the impact of ants is greater in soils with coarse texture and low pH.

3 Materials and methods

3.1 Site description

3.1.1 Forsmark

The Forsmark area (lat. 60°22’ N, long. 18°13’ E) is located in eastern central Sweden, about 60 km NNV of the city of Uppsala. The sampling area was located 200–2,000 m from the coastline of the Bothnian Sea, SE of the Forsmark nuclear power plant. The dominant vegetation in the forested areas sampled consisted of Norway spruce, *Picea abies* (L) Karst., Scots pine, *Pinus sylvestris* (L), common oak, *Quercur robur* L, ash, *Fraxinus excelsior* L., Norway maple, *Acer platanoides* L, silver birch, *Betula pendula* Roth, downy birch, *B. pubescens* Ehrh., and European alder, *Alnus glutinosa* (L.) Gaertner. In addition, sampling was also made in two abandoned fields with a dominance of grasses and forbs. The sampling areas are listed in Table 3-1 and their geographical location is given in Figure 3-1. A more complete site description is given in /Lundin et al. 2004/.

3.1.2 Oskarshamn

The Oskarshamn (Simpevarp) area (lat. 57°25’ N, long. 16°33’ E) is located in eastern southern Sweden about 10 km N of the city of Oskarshamn. The sampling area was located 100–2,000 m from the coastline of the Bothnian Sea, NW of the Oskarshamn nuclear power plant. The dominant vegetation in the forested areas sampled consisted of Norway spruce, *Picea abies* (L) Karst., Scots pine, *Pinus sylvestris* (L), common oak, *Quercur robur* L, ash, *Fraxinus excelsior* L., silver birch, *Betula pendula* Roth, downy birch, *B. pubescens* Ehrh., and European alder, *Alnus glutinosa* (L.) Gaertner. In addition, sampling was also made in two parts of a sheep-grazed pasture with a dominance of grasses and forbs. The sampling areas are listed in Table 3-2 and their geographical location is given in Figure 3-2. A more complete site description is given in /Lundin et al. 2005/.

Table 3-1. Sampling sites and a brief site description of the Forsmark area. Plot codes according to /Lundin et al. 2004/. B=borrhål (drill hole), FG=frisk gran (mesic spruce), FL=frisk lövskog (mesic deciduous forest), SS=sumpskog (swampy forest), A=nedlagd åker (abandoned field).

ID code	Site/plot	Description
AFM001247	B2A	Mixed coniferous forest
AFM001068	FG1	Mesic spruce forest
AFM001069	FG2	Mesic spruce forest
AFM001070	FL1	Mesic deciduous forest (alder, ash and tall herbs)
AFM001071	FL2	Mesic deciduous forest (maple, ash and grazed field vegetation)
AFM001076	SS1	Moist/wet alder forest
AFM001077	SS2	Moist/wet alder forest
AFM001080	A1	Abandoned field (high ground-water table)
AFM001081	A2	Abandoned field (drier than A1)

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2006-12-28, 16:00

Figure 3-1. Map of the sampling plots/sites at Forsmark (see also Table 3-1).

Table 3-2. Sampling sites and a brief site description of the Oskarshamn area. The site abbreviations are based on main vegetation, i.e. *Alnus glutinosa* (AG), *Quercus robur* (QR), grazed pasture (GP), *Picea abies* (PA) and *Pinus sylvestris* (PS).

ID code	Site	Plot	Description
ASM001434	AG	1	Moist/wet alder forest
ASM000011	AG	2	Moist/wet alder forest
ASM001426	QR	1	Oak forest near the shoreline
ASM000008	QR	2	Oak stand in a gentle slope
ASM001430	GP	1	Sheep-grazed pasture
ASM000010	GP	2	Sheep-grazed pasture
ASM001440	PA	1	Spruce on drained peatland (ca 20 cm peat)
ASM000012	PA	2	Spruce on drained peatland (ca 20 cm peat)
ASM001429	PS	1	Open pine forest
ASM000009	PS	2	Open pine forest

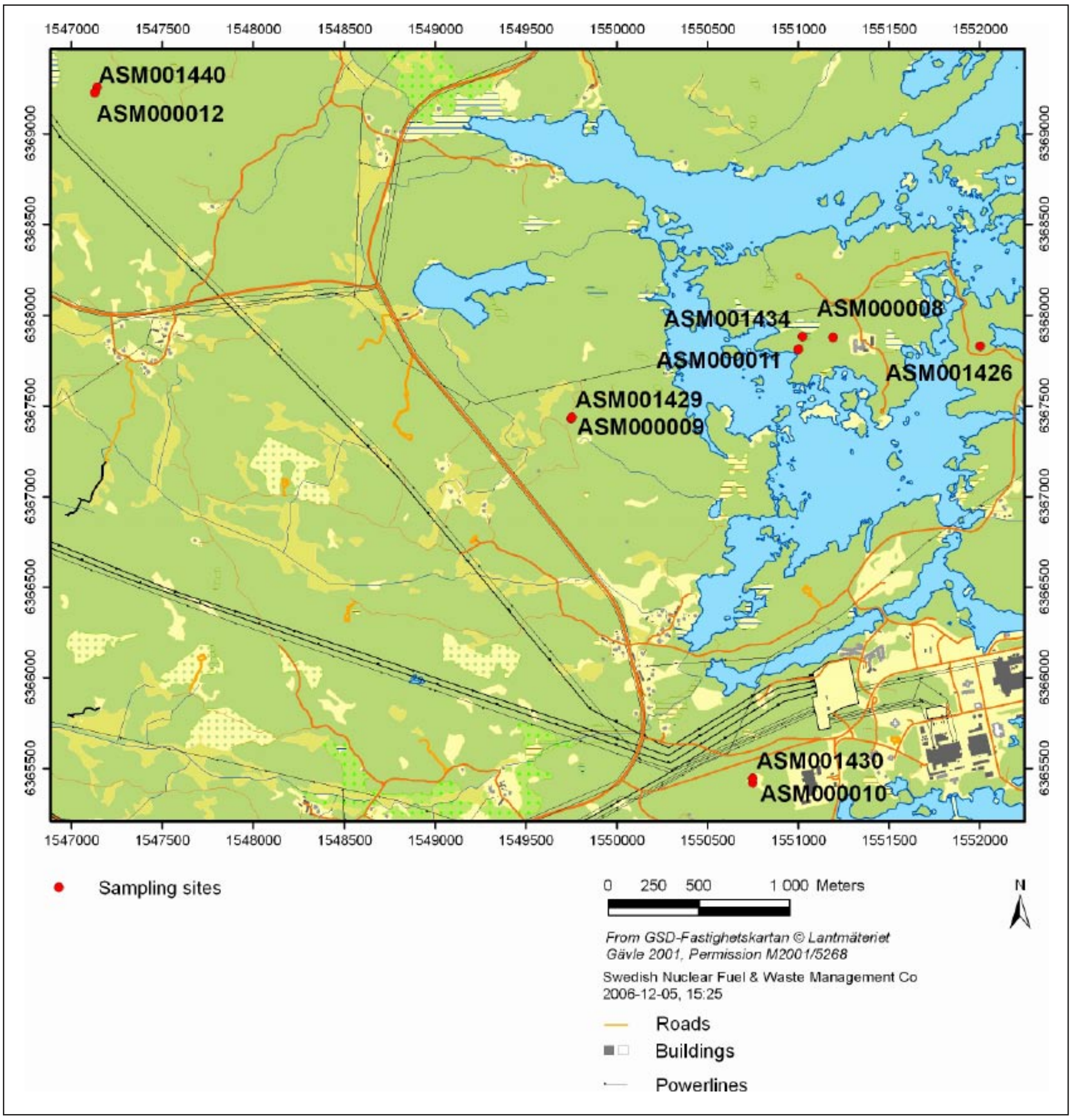

Figure 3-2. *Map of the sampling plots/sites at Oskarshamn (see also Table 3-2).*

3.2 Field sampling

3.2.1 Earthworms

Field sampling of earthworms was carried out in 2006 at both Forsmark and Oskarshamn. The sampling at Oskarshamn took place in mid-May 2006, whereas the sampling at Forsmark was partly performed in early May 2006 and partly in October 2006. This discrepancy was caused by an unexpected delay in receiving admission from the county administration to take samples within a nature reserve at Forsmark. The delay meant that the sampling in the deciduous woodland in the nature reserve (as well in a nearby woodland) had to be postponed until the soils had become equally moist as during the spring sampling.

To estimate the earthworm populations at Forsmark and Oskarshamn, four replicate soil samples per plot were taken with a 20×20 cm^2 frame to a depth of 40 cm. All soil from a depth of 20 to 40 cm was hand-sorted in the field, whereas the topsoil (0–20 cm) was transferred to the laboratory and after careful hand sorting extracted in Tullgren funnels. Earthworms were counted, determined to species, dried for 24 hours at 105°C and weighed individually to determine individual body dry weight as well as biomass.

To track in situ cast production over time, four observation squares were set up at each field plot. The squares were located 1 m from the spots where the soil sample had been removed. For each square, a surface area of 50×50 cm^2 was carefully cleared from vegetation, litter and old earthworm casts, to facilitate the detection of new casts. After a defined time interval (3 days at Oskarshamn in mid-May and 31/55 days at Forsmark in May-June (SS2, FG2), August–September (SS1, A2, FG1) and August–October (A1, FL1, FL2)), all casts produced after clearance of the squares were collected and dried for 24 hrs at 105°C to obtain the cast dry weight. Cast production was estimated as dry matter per unit area and time.

3.2.2 Ants

Ants were studied by two complementary methods, pitfall traps and transects.

Pitfall traps (plastic cups with a volume of 30 ml and a diameter of 3 cm) were filled to one third with a mixture of tap water and detergent. Traps were placed at each site at Forsmark (n=9) and Oskarshamn (n=10). The distance between individual traps was at least 7 m. The traps were inserted into the soil so that their openings were on the same level as the litter surface. They remained in the field for 96 hours during the periods of 15–19 May at Oskarshamn and 23–28 August at Forsmark.

At each site, two or three 50 m long and 3 m wide transects were established. Along these transects, every stone and piece of dead wood was, if possible, turned around. Tussocks were opened up with a knife and all other possible elements along the transects were investigated. Ants found along the transects were sampled and determined to species in the laboratory. Diameter, depth and height of the ant nests were measured. However, the exact boundaries of the nests below stones or in dead wood were often difficult to determine.

Volumes and dry weights of ant nests were determined at both Forsmark and Oskarshamn. In addition, ant nests in grasslands and coniferous forests at Marma and Lunsen (areas close to Uppsala) were sampled. At each site, diameter and height of the nests were measured, and one fourth of the nests of *Lasius niger*, *Formica exsecta* and *F. polyctena* was sampled to determine the volume above and below ground. The nest boundaries were defined as where no galleries, chambers or ants could be found. Sub-samples of the nest materials were taken to the laboratory for determination of volume, fresh weight and dry weight. Entire nests of *Myrmica scabrinodis* were sampled. Nest volume was estimated using the measurement-by-displacement-of-water-method. Each sample was tightly wrapped up in a plastic bag and volume was then estimated by submerging the bag in a water-filled graduated cylinder. The samples were dried at 105°C for 24 hrs to determine dry weight.

3.3 Laboratory experiments

A laboratory experiment was performed to investigate how much soil material passes through the gut of an earthworm per hour in relation to the body weight of the earthworms (g faeces g^{-1} body dry weight $hour^{-1}$). Approximately 20 earthworms (adults or subadults) of the genera *Aporrectodea* and *Lumbricus* were sampled in the field. Worms were placed in a mixture of soil materials (litter and fragmentation layer) and red ferric oxide (Fe_2O_3) for three hours. Earthworms were then transferred into individual 25 ml jars filled with natural soil, and the jars were regularly checked for red-coloured excrements. The time that elapsed from the transfer of worms to the natural soil until the stage when all ferric oxide had been defecated (only non-coloured faeces coming out) was considered as gut-passage time. After the red soil was excreted, each worm was placed in a moistened Petri dish to empty the gut. The Petri dishes were inspected daily, and the worms were removed to a new Petri dish if they had defecated to avoid ingestion of their own excrements. The total amount of faeces per worm was collected, dried for 24 hrs at 105°C and weighed. During the whole experiment, the earthworms were kept at 15°C.

A former laboratory experiment estimated the impact of temperature on earthworm growth and was evaluated to be included in this report. The earthworm species *Aporrectodea caliginosa* was placed in 2 dm^3 plastic bags filled with litter and topsoil material sampled at Andersby ängsbackar, a deciduous woodland with oak, birch and hazel as dominating tree species, about 30 km SSW of Forsmark. The bags were placed in rooms with constant temperature (3, 6, 10 and 20°C), and the worms were sorted by hand every tenth day for up to three years. On each occasion, the worms were weighed individually (after rinsing in tap water and drying on a filter paper) to obtain a growth curve for individual worms. The soil was replaced by fresh soil from the field every second month to prevent from food shortage. The number of replicate bags varied for different age-classes of the worms, and the replicates of 2–3 year-old worms were fewer than for young and medium-aged ones.

3.4 Statistical analyses

3.4.1 Earthworms

Mean (± one SE) abundance, biomass, cast production, defecation and bioturbation were estimated for each plot sampled (n=4). With one exception (B2A at Forsmark), two plots were chosen to represent the vegetation type (ecosystem). A comparison between ecosystems was made by means of one-way ANOVA.

3.4.2 Ants

Species frequencies were calculated as the percentage of pitfall traps within a site in which a particular species was found. Non-territorial species such as *Myrmica* spp. have smaller colony sizes and shorter foraging distances than territorial species. Frequency provides an indication of nest density of the smaller species and of the activity of the large species, e.g. *Formica* spp., with large territories. Data were arcsine-transformed and one-way ANOVA with habitat as factor was carried out.

Data on nest abundances based on transects were log (n+0.1)-transformed and one-way ANOVA with location as factor was carried out to investigate if the abundance of ant nests differed significantly between locations.

4 Results and discussion

4.1 Forsmark

4.1.1 Earthworms

Abundance and species richness

Total abundances of earthworms varied between about 25 and 300 ind. m^{-2} at Forsmark (Table 4-1, Figure 4-1). The mesic spruce site FG1 on a gleysol and silty till and the moist *Alnus* sites SS1 and SS2 on gleysol and peaty mor humus had high abundance of worms, whereas the other sites had lower abundances.

The epigeic *Dendrobaena octaedra*, the endogeic *Aporrectodea caliginosa* and the anecic/epigeic *Lumbricus* sp. had high abundances at most sites.

Soil pH in the mineral soil (0–10 cm depth and deeper) was always higher than 5.9 in the ecosystems studied /Lundin et al. 2004/. This indicates that deep-living earthworms were probably not limited by low pH. On the other hand, humus pH was as low as 4.4 at some sites (FG2), which indicates that epigeic worms might have suffered from suboptimal pH conditions at some of the coniferous sites. However, at most sites other factors than pH might be responsible for low abundances.

Earthworm biomass

Average earthworm biomass ranged from 0.3 to 23 g dry weight m^{-2} at Forsmark (Figure 4-2). At certain sites (FG2, FL2), the biomasses in the soil samples were unevenly distributed because of a few very large individuals resulting in large standard errors. The site B2A, which had a majority of small epigeic species, had the lowest biomass.

Table 4-1. Mean abundance m^{-2} and number of species at the different sites studied at Forsmark. Abundance is based on anterior worm parts (if cut), but species number is also based on posterior parts. Juvenile *Lumbricus* and *Octolasion* could often not be determined to species. *Based on both anterior and posterior parts.

	B2A	FG1	FG2	SS1	SS2	A1	A2	FL1	FL2
Epigeic species									
Dendrobaena octaedra	19	69	0	63	81	0	0	0	6
Dendrodrilus rubidus	13	0	0	13	0	6	0	0	0
Eiseniella tetraedra	0	0	0	6	0	0	0	0	0
Epigeic/anecic species									
Lumbricus cf. rubellus	0	13	0	0	0	0	0	0	0
Lumbricus sp.	13	13	25	44	50	25	38	19	19
Anecic species									
Lumbricus terrestris	0	0	0	6	0	0	0	0	13
Endogeic species									
Aporrectodea cf. caliginosa	0	169	17	75	63	26	0	6	44
Aporrectodea rosea	0	44	25	0	0	13	0	0	19
Octolasion cyaneum	0	0	8	0	19	0	0	0	0
Octolasion lacteum	0	0	0	13	0	0	0	0	0
Octolasion sp.	0	13	8	38	13	0	0	0	6
Earthworms, total density	44	319	83	263	225	69	38	25	106
No. of species	3	6	5	6	4	4	2*	2	5

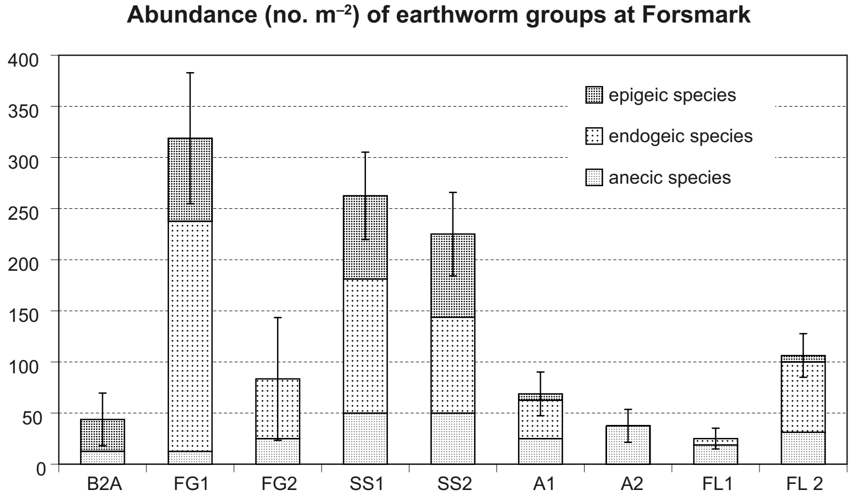

Figure 4-1. *Mean total abundance (± one SE) of earthworms in different ecosystems at Forsmark. The contribution of surface-living (epigeic), soil-living (endogeic) and vertical moving (anecic) earthworms to total abundance is also indicated.*

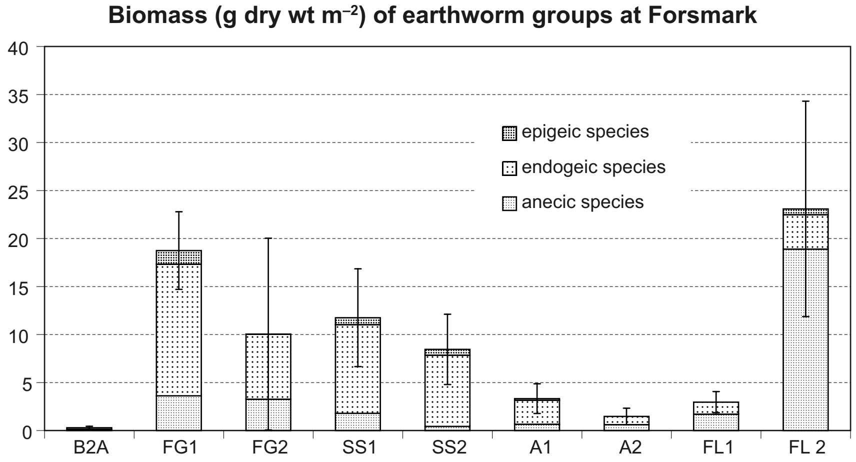

Figure 4-2. *Mean biomass (± one SE) of earthworms in different ecosystems at Forsmark. The contribution of surface-living (epigeic), soil-living (endogeic) and vertical moving (anecic) earthworms to total biomass is also indicated.*

Cast production

Cast production at Forsmark varied largely between sites (Figure 4-3). No casts were found in the mixed coniferous forest B2A and the mesic spruce forest FG2. This indicates that anecic earthworms, which are the main producers of excrement heaps on the soil surface, were lacking at these sites. This is partly supported by data from the earthworm samplings (Table 4-1). No *Lumbricus terrestris* (anecic species) was collected, and the juvenile *Lumbricus* found might have belonged to the epigeic *L. rubellus* at these sites. Cast production was fairly high in the mesic spruce site FG1 and the two deciduous sites (FL1 and FL2). This indicated that these sites would have had a fairly high population of *Lumbricus terrestris*.

Gut content and gut passage time

The gut content of earthworms seemed to be linearly dependent on the body size of the worms. However, *Lumbricus* and *Aporrectodea* worms had different relations between body mass (with empty gut) and gut content (Figure 4-4). The ratio of body mass to gut content was almost 1:1 for *Lumbricus* worms and 1:1.6 for *Aporrectodea* worms (Figure 4-4). One explanation of the

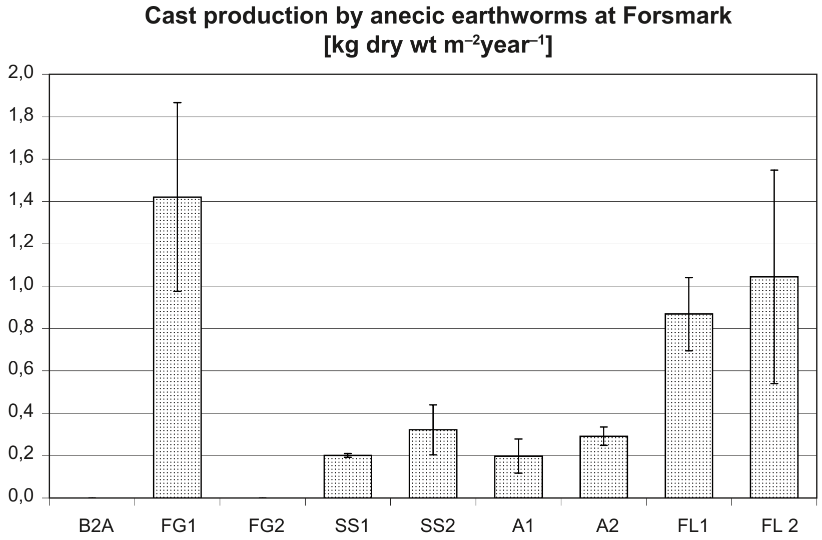

Figure 4-3. *Mean cast production (± one SE) on the soil surface by anecic earthworms in different ecosystems at Forsmark. Annual cast production was estimated as dry mass of casts produced per day times 200 days.*

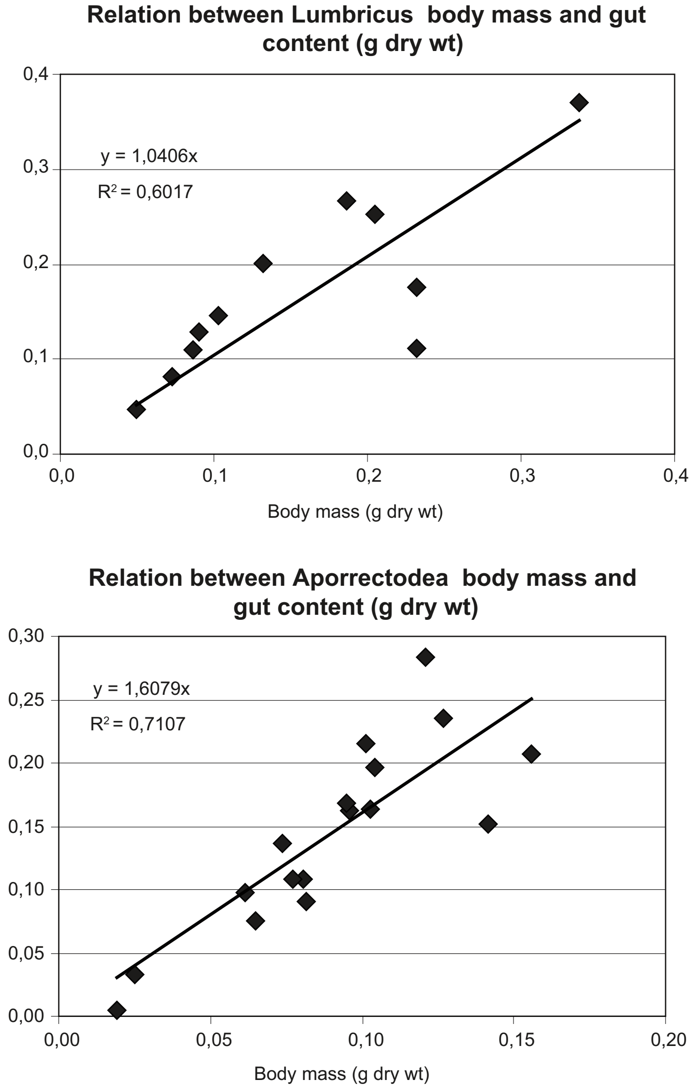

Figure 4-4. *Relation between Lumbricus (above) and Aporrectodea (below) body mass and gut content. The relations and R^2 values are given in the figure(s).*

differences is that *Lumbricus* species predominantly feed on organic matter and litter materials with low density whereas *Aporrectodea* species ingest mineral soil with high density.

Mean gut passage time as measured in the laboratory at 15°C was 6 hours for *Aporrectodea* and 7.75 hours for *Lumbricus*. This implies that *Aporrectodea* produces 0.268 and *Lumbricus* 0.134 g dry weight of faeces per g (dry weight) of worm per hour at the same temperature.

Temperature dependence

Earthworms, here illustrated by *Aporrectodea caliginosa,* in laboratory cultures had different growth rates at different temperatures (Figure 4-5). *A. caliginosa* reached maturity (indicated by the development of a clitellum, see Figure 4-5) at a body weight of about 350 mg fresh weight at 20°C. This weight was reached after 131, 400, 750 and 1,040 days (not shown in Figure 4-5) at 20, 10, 6 and 3°C, respectively. The corresponding growth rates were 7.6, 2.5, 1.3 and 0.96 mg d^{-1}, respectively. After the appearance of clitellum, the growth rate became lower, but the worms continued to gain weight.

The relation between temperature and growth rate was fitted by the polynomial equation given in Figure 4-6. According to this equation, the mean growth rate at 15°C, i.e. the temperature used for the study of gut passage, would be 4.6 mg d^{-1}.

When the equation in Figure 4-6 was combined with mean monthly soil data for 2002 (10 cm depth) obtained at Ultuna Meteorological Station, the dynamics of growth rates could be calculated (Figure 4-7). According to this calculation, the mean annual growth rate was 2.55 mg d^{-1}. This figure indicates that the annual growth rate (at field temperatures similar to those at Forsmark) would be 55.2% of that at 15°C. This percentage corresponds to a period of 202 days at 15°C.

Earthworm bioturbation

The temperature dependence of the rates estimated in Figure 4-6 was assumed to be valid for also (1) consumption/defecation rate and (2) other earthworm species than *A. caliginosa.* Thus, the faeces production of *Aporrectodea* (0.268 g g^{-1} h^{-1}) and *Lumbricus* (0.134 g g^{-1} h^{-1}) at 15°C was upscaled by combining the earthworm biomasses for each site and by using the scaling

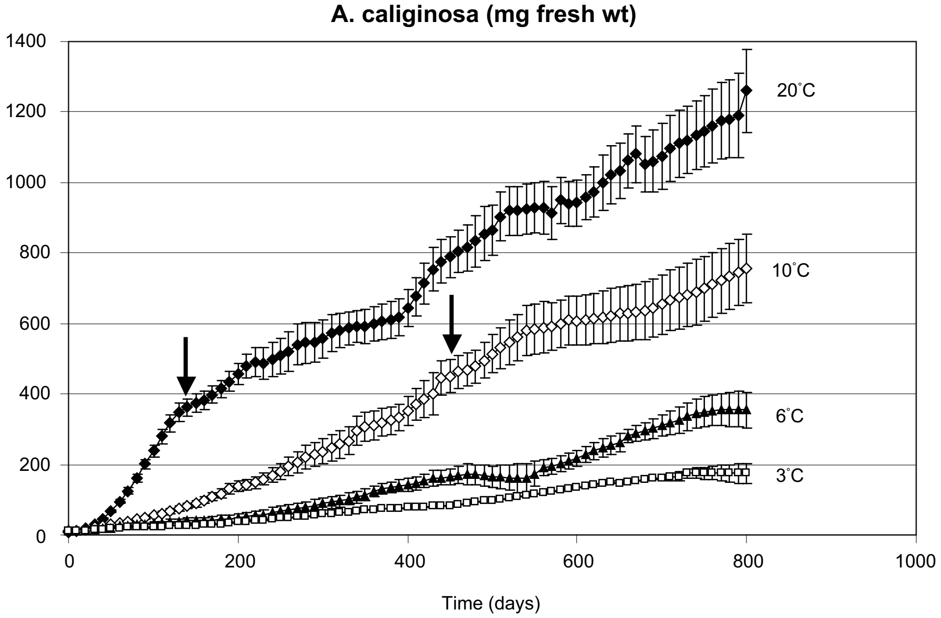

Figure 4-5. *Development of mean fresh body weights (± one SE) of Aporrectodea caliginosa at different temperatures. Arrows indicate appearance of clitellum, a glandular area typical for sexually mature earthworms.*

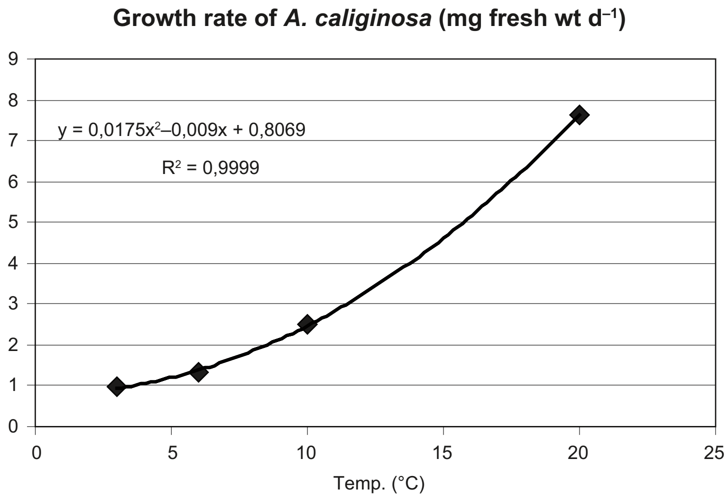

Figure 4-6. *Relation between soil temperature and growth rate from hatching to maturity (350 mg fresh body weight) for Aporrectodea caliginosa.*

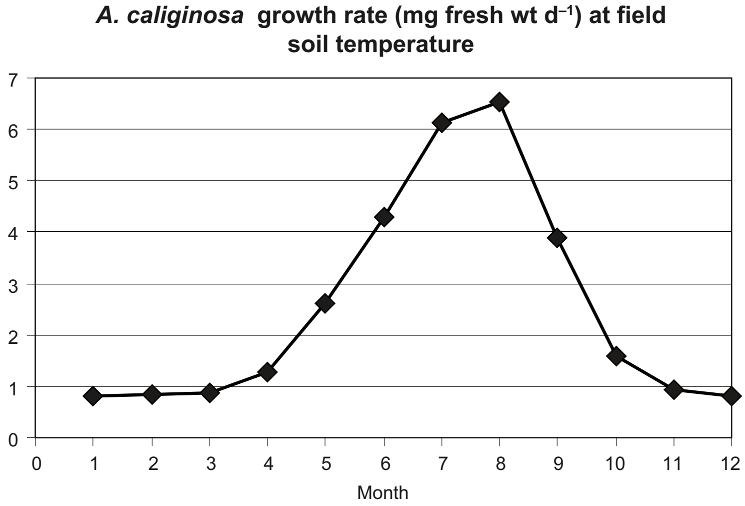

Figure 4-7. *Growth rate of Aporrectodea caliginosa at soil temperatures (10 cm depth) recorded during 2002 at Ultuna, Uppsala.*

factor of 55% (in relation to processes at 15°C) to estimate annual faeces production. Epigeic species were treated similarly as *Lumbricus*. Earthworm activity is also dependent on soil moisture, but in the following estimates, the moisture factor was neglected, assuming a rainy growing season.

The estimates of earthworm faeces production (bioturbation) were high at sites where the earthworm biomass was high (Figure 4-8). Endogeic earthworms, which produced twice as much faeces as anecic and epigeic worms per unit of body weight, had the highest faeces production at most sites, but anecic worms contributed more to faeces production than endogeic worms at FL2.

According to /Bouche 1981/, epigeic earthworms consume about 100 times their biomass of dry matter per year, anecic species 200 times and endogeic species 400 times. For an active period of 200 days per year (as at Forsmark), this gives daily values of 0.5, 1.0 and 2.0 times their own mass, respectively. Our estimates of defecation, which is slightly lower (1–5%) than consumption, indicate 1.75 and 3.5 times the body weights for anecic and endogeic earthworms, respectively. These rates agree fairly well with values given by other authors /Lee 1985, Scheu 1987/. The anecic species

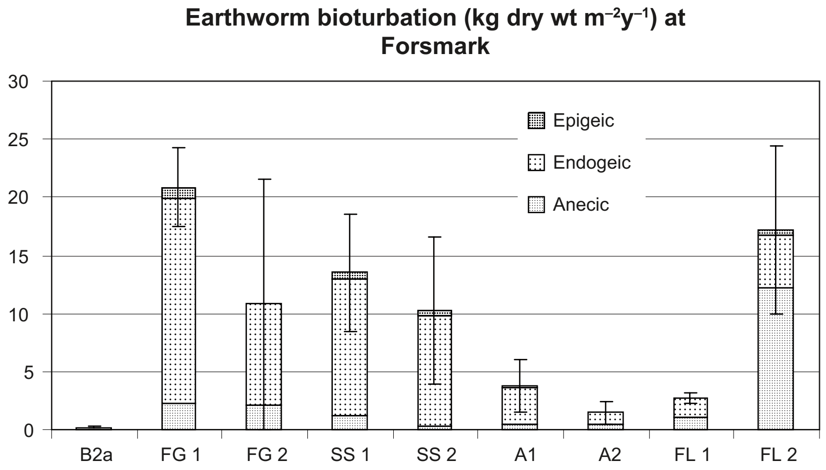

***Figure 4-8.** Estimated mean defecation/bioturbation (± one SE) of surface-living (epigeic), soil-living (endogeic) and vertical moving (anecic) earthworms in different ecosystems at Forsmark. SE bars indicate total bioturbation.*

sometimes pull leaves from the surface into the soil without consuming them immediately /Lee 1985/. Information on removal of organic material from the surface should, therefore, not be considered identical to ingestion rates.

In conclusion, earthworm bioturbation (movement and defecation of soil) was fairly high (100–200 tonnes dry matter per ha and year) at the mesic spruce sites, the wet alder sites and one of the deciduous woodland sites at Forsmark (Figure 4-8). Other sites had lower estimates of (total) bioturbation. Vertically moving (anecic) earthworms contributed 0–20 tonnes ha^{-1} $year^{-1}$ to these estimates at all sites except FL2, where the anecic bioturbation was estimated at about 100 tonnes ha^{-1} $year^{-1}$ (Figure 4-8). The estimates for the anecic species can be compared with the estimates of casts, which varied between 8 and 14 tonnes ha^{-1} $year^{-1}$ for the three sites/plots with the highest cast production (Figure 4-3). The two methods used in estimating defecation by anecic worms partly support each other and partly indicate discrepancies. One conclusion based on the comparison of methods is that the soil sampling to a depth of 40 cm is probably too shallow also during moist periods. Another conclusion is that cast production is probably only a fraction of total bioturbation, also among anecic worms, because excrements are also used to line the burrows.

4.1.2 Ants

Pitfall trapping

At Forsmark, nine different ant species were found by using pitfall traps, namely *Myrmica rubra*, *M. ruginodis*, *M. scabrinodis*, *M. lobicornis*, *Formica exsecta*, *F. fusca*, *F. polyctena*, *F. pratensis* and *Camponotus herculeanus*. The abandoned field A1 had more species than the other sites, but statistical analyses showed that this was not significant (Figure 4-9). In SS2 no ant species was found, neither by pitfall trapping nor by the transect method (see below).

Transects

Nests of two different *Myrmica* species, *Lasius niger*, *L. flavus* and *Formica fusca, F. polyctena* and *F. exsecta* were found by the transect method. A nest of *F. polyctena* was found in FL1. *L. niger* and *F. exsecta* were only found in A1 (Figure 4-10). The total density of *Myrmica* nests could not be shown to differ (p=0.9) between habitats. Neither pitfall trapping nor the transect method could detect any ants at SS2. Ants were not found at FG2 by the transect method. However, pitfall trapping indicated that the density of *M. ruginodis* nests was similar to that at FG1.

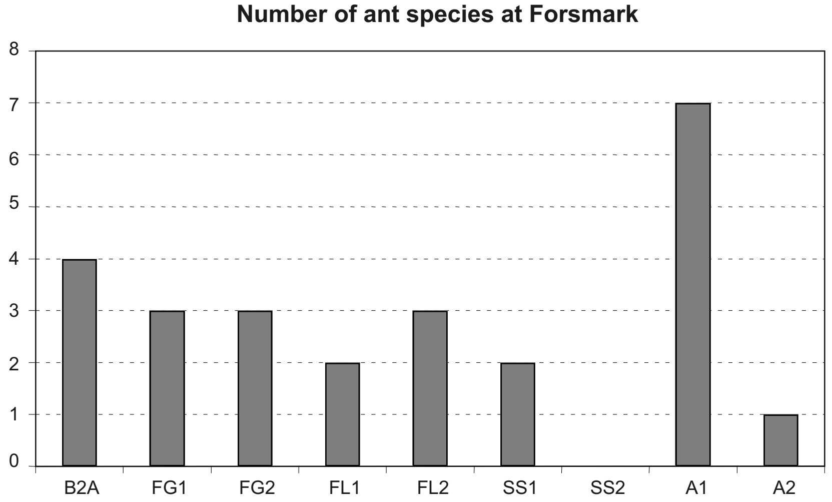

Figure 4-9. *Number of ant species caught by pitfall trapping on 23–28 August 2006 at Forsmark.*

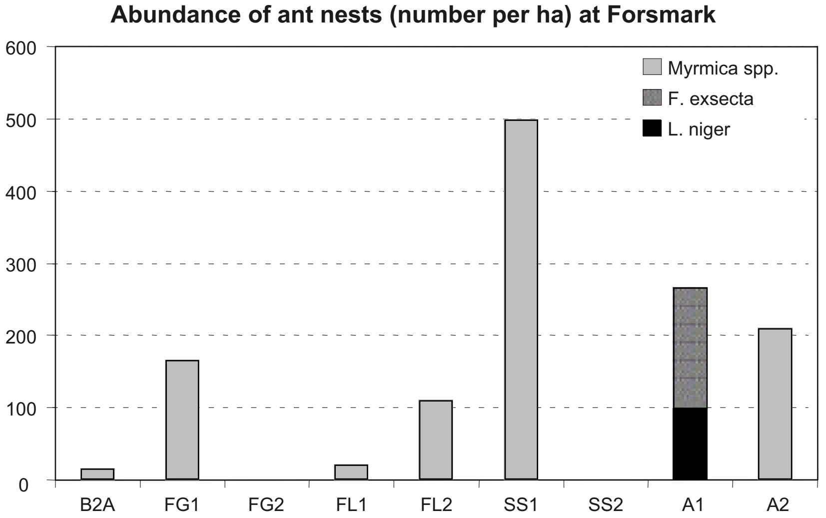

Figure 4-10. *Mean density of nest of L. niger, F. exsecta and Myrmica spp. at Forsmark according to the transect method.*

Size of ant nests

Myrmica species make quite small nests, while the nests of *F. polyctena, F. exsecta* and *Lasius niger* are often large. We did not include nests of *L. gredleri*, *L. brunneus*, *F. fusca* and *C. herculeanus* in our estimates of ant bioturbation, because these ants have either very small nests (*L. gredleri*) or build nests in dead wood or tree trunks. The knowledge of these ant species is poor with regard to how much soil material they collect. In addition, these species were only found in low numbers at Oskarshamn and Forsmark.

Ten nests of *Myrmica scabrinodis* were sampled at Marma to determine the relation between above- and belowground volume and weight. There was no clear relation between above- and belowground volumes (Figure 4-11), and belowground parts were 1–14 times larger than the corresponding aboveground parts.

There was a linear relationship between volume and dry weight of *M. scabrinodis* nests (Figure 4-12) indicating that nest size did not change the composition of the nests.

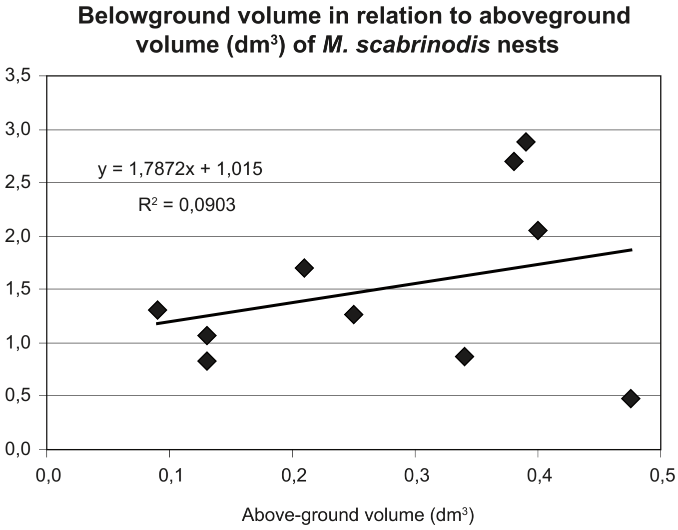

Figure 4-11. *Relation between above- and belowground parts of ten Myrmica scabrinodis nests sampled at Marma.*

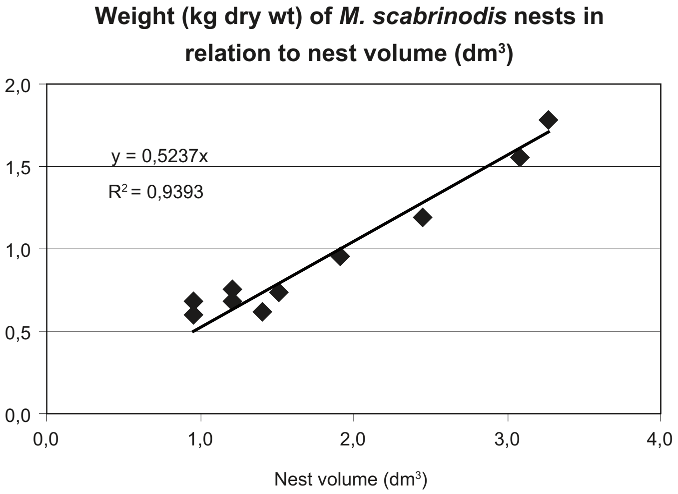

Figure 4-12. *Relation between volume and dry wt of ten Myrmica scabrinodis nests sampled at Marma.*

Nest volume and soil transformation is dependent on the number of workers present in the nests. Most *Myrmica* species build small colonies with a few hundred up to one thousand workers /Elmes et al. 1998/. The mean number of workers in a *M. scabrinodis* nest is about 2,500 /Seifert 1996/ and between 300–3,000 workers in *M. ruginodis* nests /Hölldobler and Wilson 1990/. Nests of *M. rubra* may be larger and may have more than 20 000 workers /Seifert 1996/. However, most *M. rubra* nests contain 1,000–2,000 workers /Wardlaw and Elmes 1996/ cit. in /Elmes et al. 1998/.

Ten nests of *L. niger* were sampled to determine the relation between volume and weight, three at Forsmark, two at Oskarshamn and five at Lunsen. The nests at Forsmark were much larger than those at Oskarhamn (Figure 4-13), while those at Lunsen had medium sizes. In contrast to M. *scabrinodis* (Figure 4-12), *L. niger* had much larger nests (up to 530 kg dry weight), and the relation between volume and weight was lower indicating that *L. niger* nests had higher density and more mineral soil.

Depth varied a lot between ant nests, even within the same site. In general, *Myrmica* spp. made nests of 10 and 25 cm depth. This is in agreement with /Czerwinski et al. 1971/, who found nest depths of *Myrmica* spp. between 10 and 20 cm. Nest depths for *L. niger* varied between 15–30 cm,

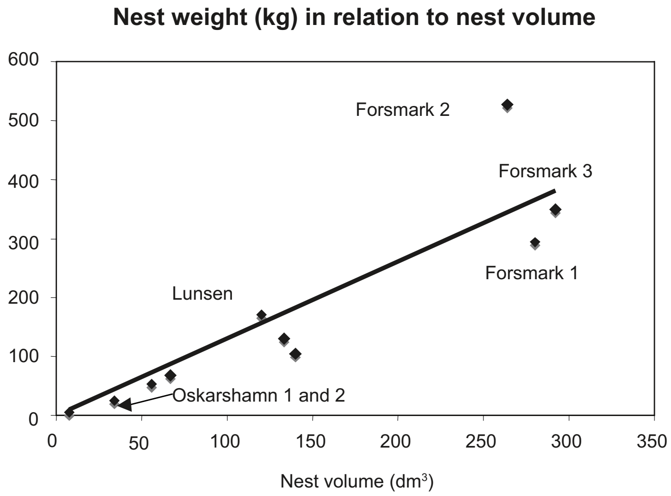

***Figure 4-13.** Relation between volume and dry weight of ten nests of Lasius niger at three locations (Oskarshamn, Lunsen and Forsmark).*

for *F. exsecta* between 20–30 cm and for *F. polyctena* between 20–55 cm. /Czerwinski et al. 1971/ found that the nests of *L. niger* and *L. flavus* were 20 cm deep and /Coenen-Stass et al. 1980/ reported the nest depth of *F. polyctena* to be 50 cm.

Nest residence time

The residence time of ant nests could not be studied in the present one-year project. Thus, we had to rely on literature data. According to /Hölldobler and Wilson 1990/ residence time is reported from only 30 out of 8,800 ant species. There are also some reports on longevity of queens of individual ant species. For ant species that do not migrate too often, e.g. *Lasius* spp. and *Formica* spp., this may be an indication of residence time. *Formica polyctena* nests may be active for more than 30 years /Hölldobler and Wilson 1990/ Pokarzhevskii pers. comm. /Wilson 1971/ reported that some *Formica* colonies persist for 20–65 years. *Lasius niger* nests may persist for more than 20 years /Hölldobler and Wilson 1990/. However, the latter figure is based on the longevity of one *L. niger* queen reared in the laboratory. Ants may migrate after disturbance, e.g. trampling by grazing animals, flooding, clear-cutting or after natural succession of the vegetation. *F. exsecta*, for instance, needs open fields without trees, shrubs or high grass vegetation but have difficulties to persist in grazed fields. Their residence time may be 5–10 years depending on the productivity of the site. For the same reasons we assumed that *L. niger* and *L. flavus* nest have a residence time of 5 years. Most *Myrmica* species have a very short residence time and they relocate their mounds 2–3 times per season /Jakubczyk et al. 1972, Backus et al. 2006/. In conclusion, the residence times used in this study was 0.4 years for *Myrmica* and 5 years for *Lasius* and *Formica*.

Ant bioturbation

At Forsmark, bioturbation was highest in A1, where we found large nests of *L. niger* and *F. exsecta* (Figure 4-14). The three *L. niger* nests found at Forsmark had a mean dry weight of 390 kg (Figure 4-13). The weight of the *F. exsecta* nest was 49 kg. We did not find any ant nest in FG2 with the transect method, but pitfall trapping indicated an ant density corresponding to a bioturbation in GF2 to be approximately 300–400 kg ha^{-1} year^{-1} (not shown in Figure 4-14).

Formica polyctena was only found once (FL1 at Forsmark). The height of these nests can be more than 2 m /Hölldobler 1960/, and the density at suitable forest sites can be 11 nests per hectare. The nests are made of different materials that are mixed. The aboveground part mainly consists of conifer resin (up to 40%, Heikki Setälä, pers. comm.), needles and small twigs. The

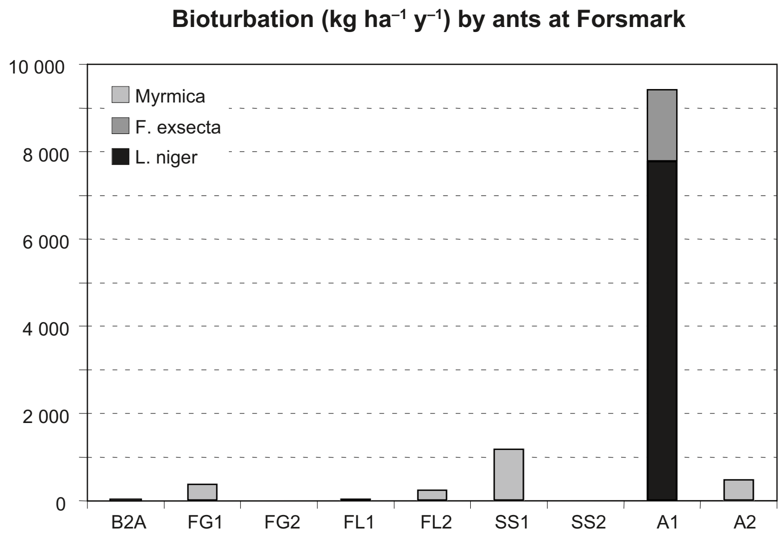

***Figure 4-14.** Estimated bioturbation by ants in different ecosystems at Forsmark.*

belowground part consists of twigs, dead wood and soil particles. For five nests at Lunsen, we estimated the mean dry weight of the aboveground parts to be 370 kg, the belowground core of twigs and dead wood to be 63 kg and belowground soil particles 522 kg, i.e. a total weight of 955 kg. For 11 nests per ha and a mean residence time of 10 years, this weight indicates a soil/litter turnover of (955×11)/10 = 1,050 kg ha^{-1} $year^{-1}$. However, the activity of *F. polyctena* is very dependent on local conditions (e.g. sunlight and suitable tree species). Therefore, the impact of *F. polyctena* and other wood ant species on bioturbation can only be evaluated in a landscape context, and no attempt was made to upscale the single nest at Forsmark.

4.2 Oskarshamn

4.2.1 Earthworms

Abundance and species richness

Total abundances of earthworms varied between 0 and 425 ind. m^{-2} at the Oskarshamn sites (Table 4-2, Figure 4-15), and species numbers ranged from one species at the PA2 site to six species at the AG1 site (Table 4-2).

Earthworm abundance was highest at the QR2 site, at least twice as high as at all the other sites, which was mostly caused by very high numbers of the endogeic species *Aporrectodea caliginosa* (Figure 4-15).

At the sites with high earthworm abundance, endogeic species accounted for the main part (> 50%) of the earthworm community. At the GP2 site, the abundance of the anecic *Lumbricus* species was high (100 ind m^{-2}) constituting 46% of the earthworm community.

Almost no earthworms were found at the PA sites, and average densities were also low at the pine sites (PS). Epigeic earthworm species were more abundant at the PS sites than at any other sites, on average 81 ind. m^{-2}, while no other species were found.

Table 4-2. Mean abundance m^{-2} and number of species at the different sites studied at Oskarshamn. Abundance is based on anterior worm parts (if cut), but species number is also based on posterior parts. Juvenile *Lumbricus* and *Octolasion* could often not be determined to species. *Based on posterior parts.

	AG1	AG2	QR1	QR2	GP1	GP2	PA1	PA2	PS1	PS2
Epigeic species										
Dendrobaena octaedra	6	19	19	19	0	0	0	0	56	56
Dendrodrilus rubidus	19	0	0	0	0	0	0	0	13	6
Epigeic/anecic species										
Lumbricus cf. rubellus	0	6	0	0	0	6	0	0	6	25
Lumbricus sp.	6	13	50	44	31	100	0	0	0	0
Anecic species										
Lumbricus terrestris	0	0	0	0	6	0	0	0	0	0
Endogeic species										
Aporrectodea tuberculata	6	0	0	13	0	0	0	0	0	0
Aporrectodea caliginosa	0	6	0	6	13	0	0	0	0	0
Aporrectodea cf. caliginosa	63	0	31	344	0	19	0	0	0	0
Aporrectodea cf. rosea	19	0	38	0	6	13	0	0	0	0
Octolasion cyaneum	0	0	0	0	25	25	0	0	0	0
Octolasion lacteum	25	6	0	0	0	0	0	0	0	0
Octolasion sp.	25	6	0	0	106	56	0	0	0	0
Unidentified worms	0	0	0	0	0	6	0	0	0	0
Earthworms, total density	169	56	138	425	188	225	0	0	75	88
No. of species	6	4	4	5	4	4	1*	0	3	3

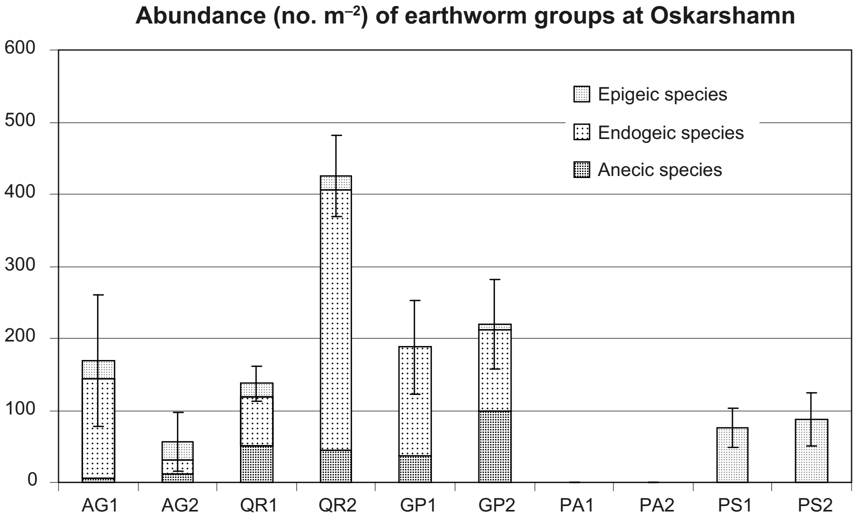

Figure 4-15. *Mean total abundance (± one SE) of earthworms in different ecosystems at Oskarshamn. The contribution of surface-living (epigeic), soil-living (endogeic) and vertical moving (anecic) earthworms to total abundance is also indicated.*

The differences between sites in earthworm abundances could largely be explained by pH, and there was a positive relation between pH (at sites recorded by /Lundin et al. 2005/) and earthworm abundance at Oskarshamn (R^2=0.92, p=0.004, Figure 4-16). No significant relation was found between pH and abundance of ant nests.

Earthworm biomass

Average earthworm biomasses ranged from 0 to 35 g dry weight m^{-2} at the different plots at Oskarshamn (Figure 4-17). Very high biomasses, mainly of endogeic species, were found at one of the oak plots (QR2) and one of the pasture plots (GP1). At the PS sites, where only small epigeic species were found, biomass was low.

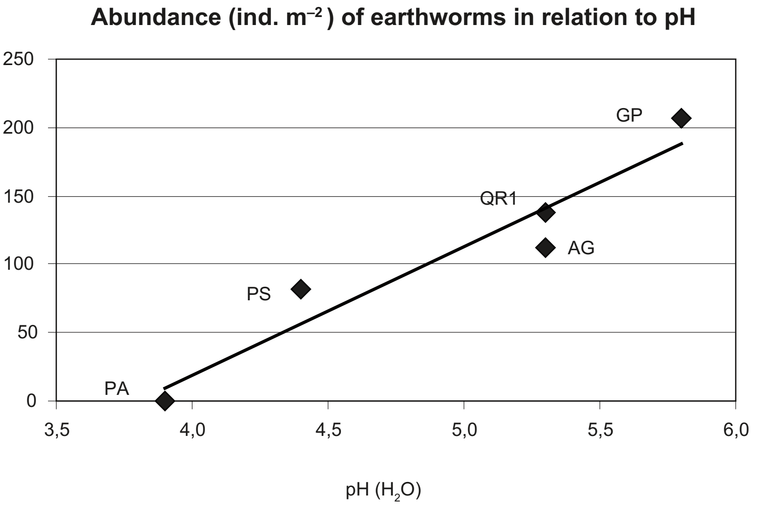

Figure 4-16. Relation between soil pH at 0–10 cm depth /Lundin et al. 2005/ and earthworm abundances at Oskarshamn. Site/plot abbreviations are explained in Table 3-2.

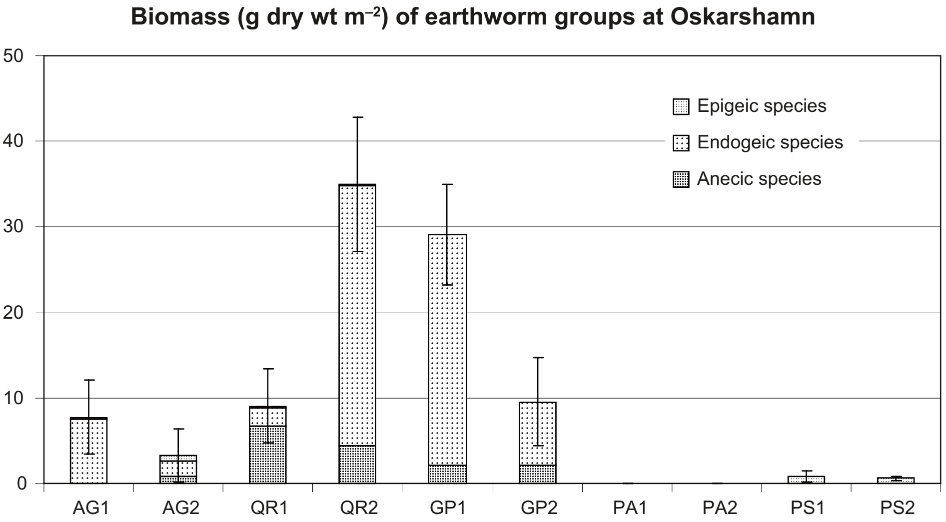

Figure 4-17. Mean biomass (± one SE) of earthworms in different ecosystems at Oskarshamn. The contribution of surface-living (epigeic), soil-living (endogeic) and vertical moving (anecic) earthworms to total biomass is also indicated.

Cast production

Cast production at Oskarshamn was high at the oak (QR) and pasture (GP) sites (Figure 4-18). No casts were found at the spruce (PA), pine (PS) and one of the moist alder (AG) sites. These observations, although made during only a period of three days, largely fit with the biomass estimates for anecic earthworms, which were relatively high at the oak and pasture sites (Figure 4-17).

Earthworm bioturbation

The same scaling factor in calculating annual defecation/bioturbation at field temperatures at Forsmark (55% of the rates obtained at 15°C) was also used for Oskarshamn. The result is indicated in Figure 4-19. Bioturbation was estimated to be very high at one of the oak and one of the pasture plots, in which 35–40 kg dry weight of soil m^{-2} $year^{-1}$ was processed. On average, 25, 23, 6.5, 0.5 and 0.003 kg dry weight m^{-2} $year^{-1}$ was defecated at the oak, pasture, alder, pine and spruce sites, respectively. Endogeic species, such as *Aporrectodea* and *Octolasion* species, had the highest defecation/bioturbation and contributed 38–99% to total bioturbation at the non-coniferous sites. Only at one site (QR1), the anecic *Lumbricus* species contributed more than the endogeic species to total bioturbation (Figure 4-19).

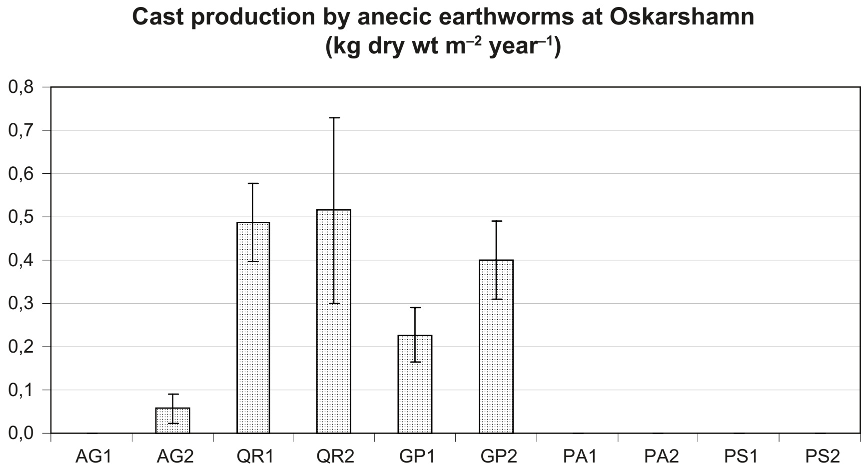

***Figure 4-18.** Mean cast production at soil surface (± one SE) of earthworms in different ecosystems at Oskarshamn.*

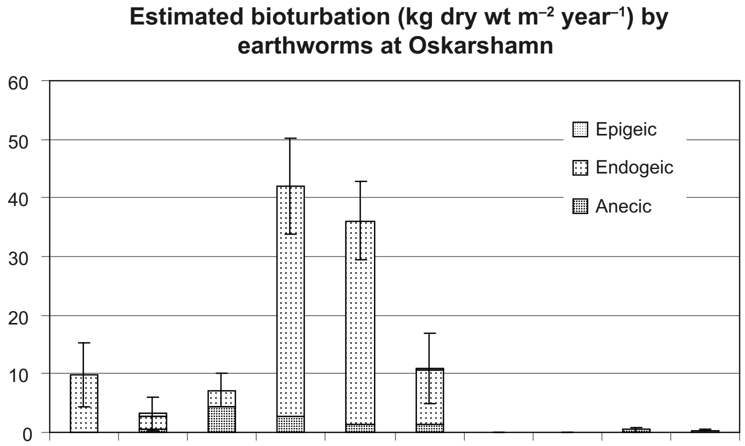

***Figure 4-19.** Estimated mean bioturbation (± one SE) of earthworms in different ecosystems at Oskarshamn.*

4.2.2 Ants

Pitfall trapping

Eleven ant species were detected at Oskarshamn: *M. rubra*, *M. ruginodis*, *M. scabrinodis*, *M. lobicornis*, *M. schencki*, *Leptothorax gredleri*, *Lasius niger*, *L. brunneus*, *F. fusca*, *F. sanguinea* and *F. polyctena*. Ant species richness was highest in the grazed pasture (Figure 4-20). Nest frequency of most *Myrmica* species and *L. niger* differed significantly between the sites. Low species richness and few nests were found in the pine (PS) and alder (AG) forests (Figure 4-20).

Transects

Nests of *Lasius niger*, *L. flavus, Formica fusca* and three different *Myrmica* species were found by the transect method. No nests of *Formica polyctena* or *F. rufa* were found at the plots, but these ant species are common inhabitants of coniferous forests. For example, one big nest was found about 100 m outside the PA1 plot. The total density of *Myrmica* nests was not significantly different between the habitats (p=0.2). The abundance of *L. niger* nests differed significantly between the habitats (p=0.001), but this was mainly due to their absence in the alder (AG) and spruce (PA) forests (Figure 4-21). *L. flavus* was found only once in one of the oak forests (QR1).

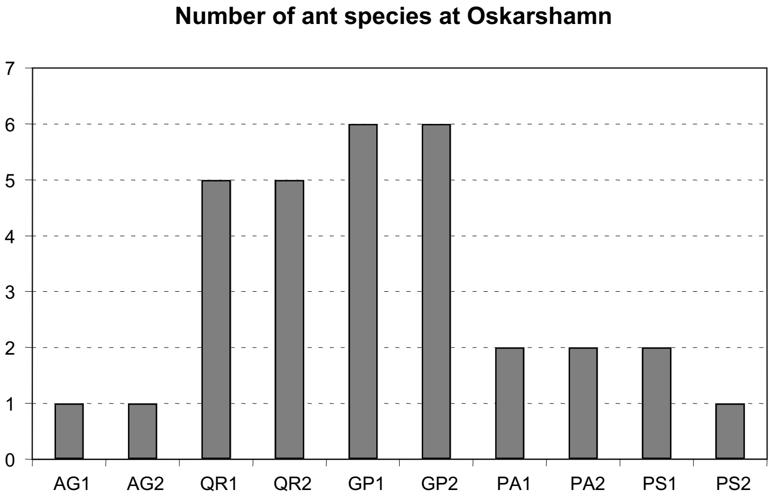

Figure 4-20. *Number of ant species caught by pitfall trapping in different ecosystems at Oskarshamn on 15–19 May 2006.*

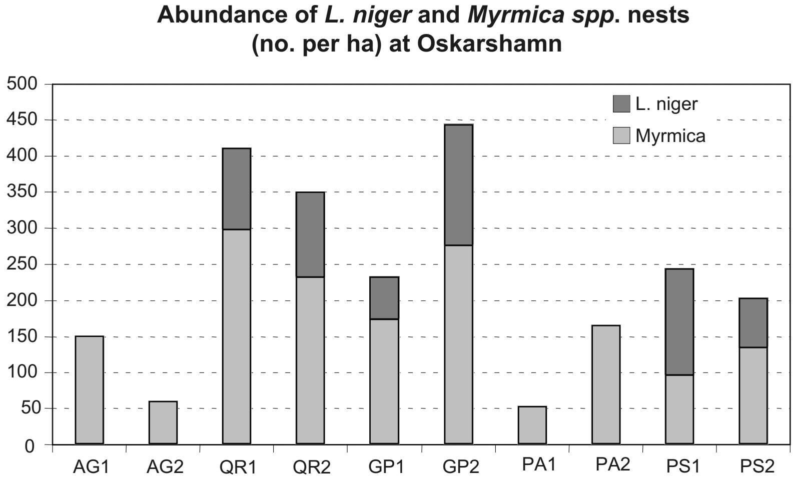

Figure 4-21. *Mean density of ant nests of L. niger and Myrmica spp. in different ecosystems at Oskarshamn according to the transect method.*

Ant bioturbation

The nests of *L. niger* were very small at Oskarshamn (see Figure 4-13). Therefore, most soil turnover, using the same residence times as at Forsmark, was made by *Myrmica* spp. (Figure 4-22). The oak forests (QR) and grazed pastures (GP) had the highest densities of nests and the highest bioturbation.

The estimates of bioturbation presented here might be overestimated. The transect method provides an estimation of the number of ant nests per hectare. However, little is known about the vitality and activity of the whole ant population. The effects of ant on soil turnover may be very local, and ant communities are characterized by large spatial and temporal variation /Herbers 1989/. Long-term population studies are needed to estimate more exact estimates on bioturbation by ants over a longer time period. /Lobry de Bruyn and Conacher 1994/ calculated the amount of soil deposited on the surface of ant nests from measurements of the nest dimensions every second month. Only long-term population dynamic studies can answer the question if and how much the ant hills will grow and if soil turnover will change over years. In our study this was not possible because of the short study period.

4.3 Comparison of bioturbation by ants and earthworms

The contribution by earthworms to bioturbation was almost always larger than that of the ants. The contribution by worms varied between 80% and 100% at Forsmark and, in four out of five ecosystems, between 93% and 99.9% at Oskarshamn. The only exception was the spruce forests (PA) at Oskarshamn, where the abundance of earthworms was extremely low and the contribution by ants to bioturbation was 84%. In ecosystems where earthworms are abundant, the pedological effects of ants may be negligible or very local /Lobry de Bruyn and Conacher 1990/. On the other hand it has been proposed that ants are as important as earthworms in soil transformation /Göttwald 1986/ cit. by /Folgarait 1998, Briese 1982/ estimated the annual soil turnover by ants to be 350–420 kg ha^{-1} year^{-1} in a shrub steppe in Australia. In Argentina, estimates of soil bioturbation by *Camponotus punctulatus* were 2,100 kg ha^{-1} year^{-1} (Folgarait, unpublished data). /Lobry de Bruyn and Conacher 1994/ estimated that bioturbation by *Aphaenogaster* sp. was 100–370 kg ha^{-1} year^{-1}. /Eldridge and Pickard 1994/ reported that bioturbation by *Aphaenogaster* spp. varied between 280 and 8,410 kg ha^{-1} year^{-1}. /Paton et al. 1995/ (cit. in /Folgarait 1998/) suggested from a comparison of global rates of bioturbation that earthworms normally contribute more to bioturbation (150,000 kg ha^{-1} year^{-1}) than ants.

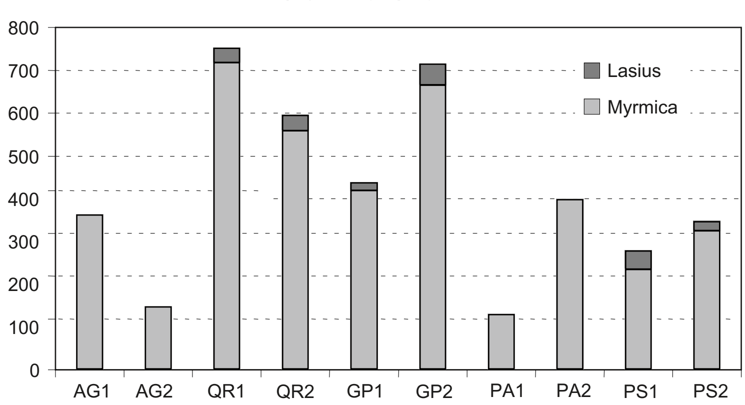

Figure 4-22. Estimated bioturbation by ants in different ecosystems at Oskarshamn.

4.4 Bioturbation at Forsmark and Oskarshamn

The estimates of total bioturbation by earthworms and ants indicated both similarities and dissimilarities between Forsmark and Oskarshamn. On average, 159, 119, 99, 31 and 1.9 tonnes dry weight ha^{-1} $year^{-1}$ were turned over at the mesic spruce, alder, deciduous woodland, abandoned field and mixed coniferous sites, respectively, at Forsmark. At Oskarshamn, 247, 235, 66, 4.9 and 0.3 tonnes dry weight ha^{-1} $year^{-1}$ were turned over at the deciduous (oak) woodland, grazed pasture, alder, pine and spruce sites, respectively.

Two main factors seemed to be responsible for the discrepancies, soil pH and groundwater table. The high bioturbation at the mesic spruce site at Forsmark (pH 7) and low bioturbation at the spruce site at Oskarshamn (pH 3.9) obviously reflected an earthworm response to high/low pH. The low bioturbation in at least one abandoned field at Forsmark (pH 7.1) and the high bioturbation in the grazed pastures at Oskarshamn (pH 5.8) cannot be explained by pH but possibly by high groundwater table at Forsmark. During the sampling at Forsmark in October, the deeper parts of the sample pits at A1 became water-filled. During wintertime, endogeic and anecic earthworms move vertically to avoid frost. High groundwater tables cause anoxic conditions under the frozen soil, and deep frost and high water table will cause high earthworm mortality. Moderate bioturbation in the deciduous woodland at Forsmark (pH 7) and high bioturbation in the oak woodland at Oskarshamn (pH 5.3) can probably also be explained by higher groundwater table at Forsmark.

5 Conclusions

Earthworm abundances, biomasses and turnover of soil were markedly dependent on site characteristics, both at Forsmark and Oskarshamn. There was a positive correlation between pH and abundance of earthworms at Oskarshamn. At Forsmark, where the soils are generally rich in $CaCO_3$, soil pH was often close to 7 except for the litter and humus layers in some coniferous forests. Some of the sites at Forsmark had high groundwater tables, and this fact can explain reduced figures of earthworm bioturbation. Earthworm bioturbation varied between 80% and 100% of total bioturbation at Forsmark and, in four out of five ecosystems, between 93% and 99.9% at Oskarshamn.

No significant correlation was found between pH and abundance of ant nests. Bioturbation by ants varied from around 130 to 750 kg dry weight ha^{-1} $year^{-1}$ at Oskarshamn and was mainly caused by *Myrmica* species. At Forsmark, ant bioturbation was generally lower than at Oskarshamn. However, one abandoned field (A1) was estimated to have a bioturbation estimate of almost 9,500 kg dry weight ha^{-1} $year^{-1}$ caused by two ant species that build huge nests.

Total bioturbation estimated for earthworms and ants was 159, 119, 99, 31 and 1.9 tonnes dry weight ha^{-1} $year^{-1}$ at the mesic spruce, alder, deciduous woodland, abandoned field and mixed coniferous sites, respectively, at Forsmark, and 247, 235, 66, 4.9 and 0.3 tonnes dry weight ha^{-1} $year^{-1}$ at the deciduous (oak) woodland, grazed pasture, alder, pine and spruce sites, respectively, at Oskarshamn. Consequently, the bioturbation by especially earthworms can be remarkably high. A normal stone-free mull soil contains about 300 kg dry weight m^{-2} (3,000 tonnes ha^{-1}) in the top 30 cm. Earthworms and ants can, thus, turn over the topsoil during 12–20 years in suitable habitats.

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