

**Below ground movements of invertebrates
across woodland edges**

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Abstract

Bioturbation is an important but long been neglected concept in a variety of disciplines. Though there were extensive studies on organism or community response to edge effects, there were few studies examine the edge effect on the bioturbation of below ground animals. Thus this study will try to quantify the bioturbation rates of invertebrates along gradients extending from within woodlands, across the edge and out into pasture, and try to quantifying how the presence of the above ground edge might affect below ground invertebrate bioturbation rate.

The invertebrate survey using below ground pitfall traps shows that there is no evidence that supporting bioturbation rate change with distance to habitat edges or between habitats. This is possibly because different communities response to the environmental change differently and the overall effect is averaged out. The homogeneities within the habitats and relatively stable abiotic factors below ground may also help to maintain a certain level of bioturbation rate. However, the catch rate of earthworms using below ground pitfall traps is too low to be representative. A separate earthworm survey was employed using different techniques. The bioturbation rate of earthworm shows that the bioturbation rate increases as the distance to habitat edge increases. The bioturbation rate also differs between habitats and sites, which was due to the differences of abiotic factors (i.e. soil moisture, soil texture, and soil porosity) and food quality.

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Introduction

Importance of bioturbation with special focus on earthworms

The definition and importance of bioturbation

It is Darwin, the author of first scientific publication on biology functioning of soils, introduced the concept of bioturbation (Feller et al, 2003). In a broad sense, bioturbation is the biological reworking of soils and sediments by all kinds of organisms, including microbes, rooting plants and burrowing animals. In a strict sense, it is the enhanced dispersal of particles resulting from sediment reworking by burrowing animals (Meysman et al, 2006). The whole idea of bioturbation was triggered by Darwin's father-in-law Josiah Wedgwood in 1837. He took Darwin to several sites which were covered by lime, burnt marble and cinders 15 years ago. These materials were now buried at considerable depth below surface. A few weeks after, Darwin present his findings in a speech "On the Formation of Mould" to the Royal Geological Society, but his enthusiasm was not shared by his colleagues. They expect something more grandiose than a speech on worms (Darwin, 1881; Feller et al, 2003). Darwin devoted his last ten years life on earthworms and published "the bioturbation book". Though he thought the book is of small importance, the book become immediate popular among the general public. Unfortunately, the subject was largely neglected by the science community until the late 20th century (Johnson, 2002). However this subject has regained scientists' interest party because of the easiness of obtaining information, but most importantly due to the important role of

bioturbation discovered in many disciplines.

The burrowing organisms affect most, if not all, of the surface of the Earth, hence a variety of disciplines including ecology, pedology, hydrology, geomorphology, and even archaeology cited Darwin's book as their original reference (Meysman et al, 2006). The influence of bioturbation on soil formation, erosion and hill-slope stability makes it an important factor in landscape evolution which was long been neglected by geologist and geographers (Deitrich and Perron, 2006). The biogenic disturbance is shown to be very important on the production of soil (Gabet et al, 2003). The biological reworking also counteracts consolidation which stimulates downslope creep (Heimsath, 2002) and lowers the infiltration rate of water, making the soil more susceptible to erosion (Gabet et al, 2003). This leads to a smoothing of the landscape over longer timescales and enhanced sediment transfer by river from land to the oceans (Yoo et al, 2005).

In marine and lacustrine environments, small-scale bioturbation (from micrometers to meters) is believed to be a key factor in sediment transport, influencing the large-scale geomorphology of ocean and lake sediments (Murray et al, 2002). It also affect the ecosystem function via ecosystem engineering, altering the physical, chemical and biological properties of the substratum and the interstitial water (Gilbert et al, 2003; Mermillod-Blondin & Rosenberg, 2006; Nogaro et al, 2009; Rosenberg, 2001) .

Another astonishing example of the importance of bioturbation is its connection to the evolution of modern animal form. It is believed that bioturbation had a crucial role during the Cambrian explosion, when large variety of animals appeared in the fossil record over a relatively short time. Bioturbation by primitive terrestrial vegetation

invoked the increase in oxygen which then triggered the expansion of metazoan life at the ocean floor (Kennedy et al, 2006).

Earthworms as a bioturbator

To most of people especially in Darwin's day, the earthworms were merely unpleasantly slimy, ugly, blind, deaf and senseless animals, of little use except for fish-bait. They can learn but little about the outside world only through their well developed sense of touch. They are very sensitive to the invisible ultraviolet rays of the sun. A few hours exposure will be enough to kill them. On rainy days, however, when water fills up their borrows, they are faced with drowning if choose to stay underground or with being burnt by ultraviolet light if they choose to surface for oxygen (Nardi, 2007). They are very skilful in lining their burrows with their castings and with leaves, and in the case of some species in piling up their castings into tower-like constructions. They even surprisingly show some degree of intelligence instead of a mere blind instinctive impulse when sealing the mouths of their burrows (Darwin, 1881). However all of those amazing skills or tricks are trivial comparing to their importance in terrestrial ecosystem as a bioturbator. In Darwin's (1881) "bioturbation book", he wrote that:

'The plough is one of the most ancient and most valuable of man's inventions; but long before he existed the land was in fact regularly ploughed, and still continues to be thus ploughed by earth-worms. It may be doubted whether there are many other animals which have played so important a part in the history of the world, as have these lowly organized creatures.' (p. 65)

It highlighted the role of earthworm on soil preparation and nutrient cycling. The burial, combined with the re-worked physical state of the soil due to their castings and burrows, promotes moisture retention, absorption of soluble substances, nitrification and decomposition, bringing nutrients to plant roots (Darwin, 1881). These little creatures, however, are far more than just the “friend of farmers”. They are important in both physical and chemical rock weathering processes. Physical weathering was achieved mainly by the grinding action of their gizzards (Darwin, 1881). Though the amount of soil particles is highly variable depending on the feeding habits and function group of the earthworm (Bernier, 1998; Judas, 1992), the structure was totally re-worked and re-organized by the grinding and mixing of the soil and organic materials in their gizzards and intestines (Barois et al, 1993). The role of earthworms on chemical weathering was demonstrated in an experiment in Darwin’s (1881) “bioturbation book”. The red-oxide sand lost its colouration after passage through earthworm intestines. Therefore he concluded that the process of ingestion, passing through, mixing, grinding and digestion in the earthworm intestines, continually exposed rock particles in the superficial layer of top soil to chemical alteration, and thus increased the amount of soil (Darwin, 1881).

The earthworms are also very important in the humification process, possibly through controlling carbon inputs into the soil through litter burial and enhancing its decomposition rate, in regulating microbial activities and protecting carbon in stable aggregates (Bernier, 1998; Brown et al, 2000). Earthworms can have a major impact on the differentiation of soil horizons via their repeated digging and surface casting action. Though the surface castings are only a small fraction of the total amount of soil moved by worms, they are important in soil profile differentiation, porosity and hydrological processes. The castings deposited beneath the surface, however, contribute largely to pedogenesis and soil structural properties (Feller et al, 2003;

Gobat et al, 2004). Despite the benefits of earthworms on various physical or chemical soil processes, some recent studies showed that they can contribute either positively or negatively to the fertility of soils as well as to the native plants and animals associated with the soils depending on particular circumstances (Nardi, 2007; Yeates et al, 1997).

Edge effect

The influence of habitat edge has often been a hot research area in conservation biology. It is an important feature caused by landscape fragmentation. The edge effect is the result of the interaction between two adjacent ecosystems, when the two are separated by an abrupt transition (edge) (Primack, 2006). In traditional, edges are thought to have deleterious consequences for the organisms living in fragmented habitats. Fragmentation reduced the total area of the pristine habitats dramatically which exposes the organisms to the conditions of a different surrounding ecosystem and may result in the extinction of some species. Moreover, if exposure to the edge modifies the features of the habitats beyond their range of natural intrinsic variation, then the fragment area will be unsuitable for the original ecosystem, and the conservation value will be greatly reduced for the fragmented area (Murcia, 1995).

However, there have been extensively studies on the edge effect which shows different stories. Some forests shows higher stem densities and basal areas within 20m of the edge (Williams-linera, 1990). In Chen and Franklin's (1992) study, the growth rate of Douglas-fir and western hemlock near the edge increased and decrease exponentially with distance from the edge. Higher species richness of carabids was recorded in the forest edge than in the forest interior (Halme and Niemelä, 1993;

Magura and Tóthmérész 1997; Magura, 2002). Kotze and Samways (2001), however, found no general edge effect for invertebrate at Afonmontane forest and grassland ecotones.

The possible reason for increasing species richness near forest edge was probably related to the heterogeneity of the habitat created by edges and the overlapping in species groups at the edge. The increased habitat heterogeneity produces favourable microclimatic conditions. This small-scale habitat diversity generally promotes higher “biological productivity” and thus may increase niche-specialisation, smaller resource-overlap and the numbers of invertebrate herbivores. These invertebrate herbivores may therefore indirectly affect carabids abundance as their food sources (Halme and Niemelä, 1993; Magura and Tóthmérész 1997). It is also true that new habitat created by edges may favour species with good colonization ability. The edge thriving species will invade from the vicinity habitats which result in a higher biodiversity at edges (Ås, 1999). So the mixing of distinct fragment and invasion of matrix species at habitat edges result in a zone of overlap with greater overall biodiversity (Ewers and Didham, 2006).

Edges can alter species interactions and hence modify ecological processes and dynamics at a wider range of scales. The interactions between species may also become more dynamic at edges (Ewers and Didham, 2006). The habitat fragments are more susceptible to environmental stochasticity and the penetration of external dynamics from the matrix into fragments than large areas of continuous habitat, which may result in the destabilisation of animal populations (Laurance, 2002). For example, in a study of parasitism risk study, the parasitism risk of planthopper (*Prokelisia crocea*) is 60% more heterogeneous at the edge than interior of a patch (Cronin, 2003). However, habitat edge effects can sometimes be negated due to the diverse and

structurally complex landscapes (Tscharntke and Brandl 2004).

Edge effects have been measured in a large variety of habitat types with different edge characteristics. Yet there are little consensus in the results of the patterns of the effect. The edge effects do not vary monotonically with distance from the edge. The strength of an edge effect can be greatly moderated by changes in matrix structure (Ewers and Didham, 2006). There is also no clear-cut on the distance of edge effect. It is likely that the variables interact with each other and affect the interpretation of the results. For example, the creation of an edge increases the light, promoting plant growth, creating a concentration of leaf biomass at the edge. That, in turn, casts a shadow behind it which inhibits the growth of shade intolerance plants (Murcia, 1995). Studies that investigating the densities of multiple species at the same site could show contrasting edge effect between species with different life history strategies and habitat requirements. In Pajunen's et al (1995) study, it showed that large hunting spiders were most abundant near forest edges. The warmer, opener environment with thick enough leaf litter layer will allow stratification of adults and juveniles, which reduced the probability of cannibalism. By contrast, in the same forest, small web-building spiders prefer to inhabit the forest interior. The herb and moss cover may provide suitable microhabitat structures for web constructions (Pajunen et al, 1995).

Aims and Hypotheses

There have been extensively large numbers of literatures regarding the bioturbation of invertebrates on aquatic environment but relatively fewer studies on terrestrial environment. Among those studies on terrestrial invertebrates, they mainly focused on physical properties altered by bioturbation or chemical redistribution caused by bioturbation. There is little on the comparison of bioturbation rate between habitats and whether edge effect applied to underground world or not. This project will aim to:

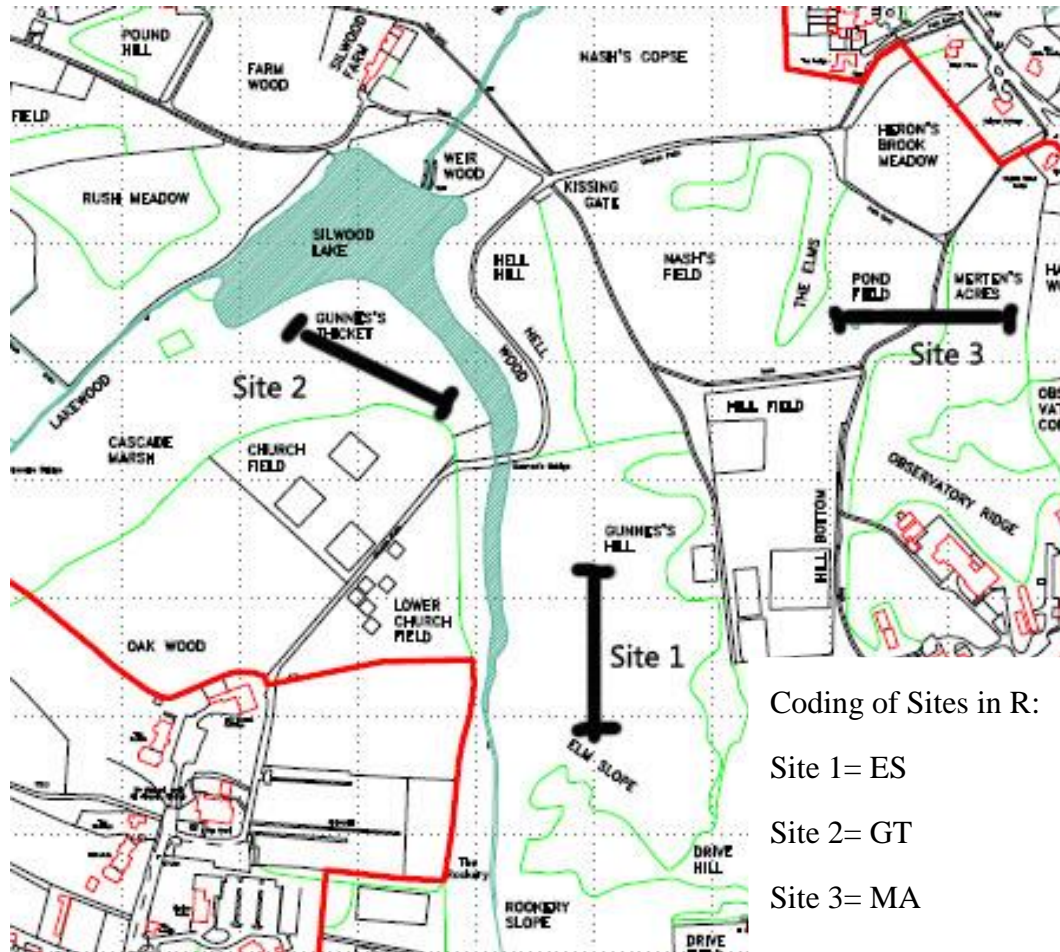
- Quantify bioturbation rates of invertebrates along gradients extending from within woodlands, across the edge and out into pasture.

- Quantifying how the presence of the above ground edge might affect below ground invertebrate bioturbation rates.

Methods and Material

Study sites

Plate 1. An ordinance survey map of Silwood Park, Berkshire, owned by Imperial College, London.



The study was carried out in Silwood Park Campus. Three transects with ten sampling stations of each have been set up. Each sampling station is 10 meters away from each other except the two close to edge. No sampling station was placed at the edge. So the distance between each of the first sampling station in woodland and grassland is 20 meters. The final sampling station was 50 meters from the edge.

Site 1: Elm Slope to Guinness's Hill

Site 1 was between Elm Slope and Guinness's Hill (Grid reference SU 94593 69079), with the sampling transect going south into the woodlands in Elm Slope and north into the grassland. Sampling stations were placed as straight as possible while avoiding trees and area with massive tree roots. There is no footpath in either habitats, but people occasionally check the bird nest in the woodland. The acid grassland is MG6 under National Vegetation Classification (NVC). The grassland is heavily grazed by rabbits. The woodland is broadleaved deciduous consisting mostly of oak trees with very dense leaf litter covering the ground. There is a canopy cap between sampling stations 10m to 30m, with high level of light penetration but there is not any vegetation at sampling station 20m. This woodland was formed from the acid grassland MG6 during 1956 to 1965 when the rabbits were absent, and the age structure was remarkably uniform (Crawley, 2005).

Site 2 Guinness's Thicket

This entire site is on a southwest facing hill with the grassland habitat on a greater gradient and the woodland habitat on a smaller gradient (Grid reference SU 94110 68966). The transect was placed as straight as possible but some sampling station has to be placed a few meters away from the original point to avoid trees and dense shrubs but keeping the same distance to edge. The woodland was also broadleaf deciduous

one, with oak, sycamore and a few birch trees, which is classified as W10 under NVC with various fringing vegetation associated with lakes. The 50m sampling station is about 20m to 30m away from the lake. Unlike the other two woodlands, its canopy is more open and its understory is covered with dense grass predominantly bracken at sampling station 40m and 50m. Sampling station 20m and 30m were covered by bluebells during the first phase sampling period (May to July). There is a foot path within the woodland closed the edge, but the foot path is only used by authorized people for checking bird nest. The disturbance is relatively low. The grassland is MG6 with heavy pressure of grazing by rabbits. There were quite a few rabbit burrows scatter around the grassland around which there was little vegetation (Crawley, 2005).

Site 3 Merten's Acres to Pond Field.

The grassland (Pond Field) is flat while the woodland is on a north facing uphill gradient. A grassy footpath runs at the edge between the 10m sampling station at both habitats. There were people occasionally checking the bird nest box, and the ground is subject to some experiments. Other than some quadrats, there was no other active experiment going on. So the disturbance in woodlands should be fairly low. This edge is more disturbed than the other two sites, but it is quite far from the nearest two sampling stations. The grassland vegetation is relatively species diverse with flowering plants nettle, thistle and ragwort. The rabbits were not observed within the grassland, but were often found at the edges of the field. The woodland is also deciduous broadleaf one, consisting of oak and sycamore. The ground is completely bare of vegetation and is covered only with leaf litter. Thistle and bramble dominate the ground at the edge. The woodland is as the same age of the one in site 1, formed because of the absence of rabbits during 1956 to 1965 (Crawley, 2005).

Invertebrate sampling techniques

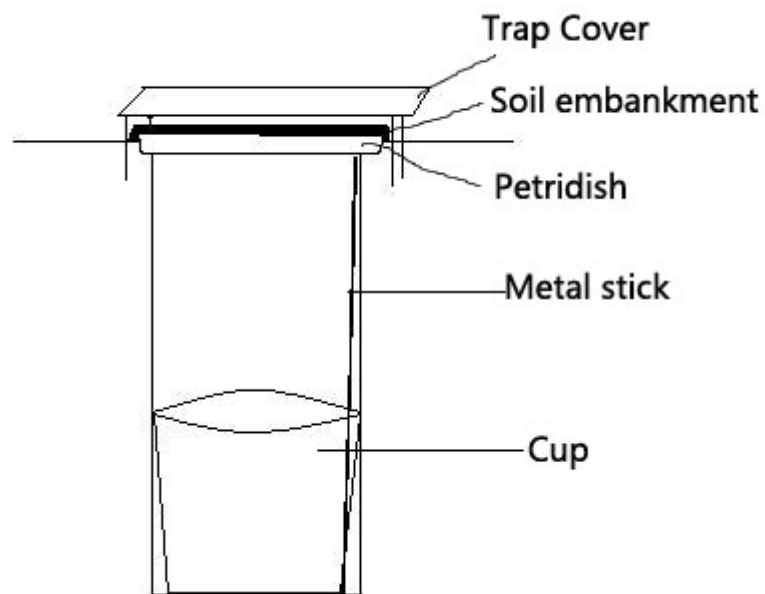
The whole study was divided into two phases: the first phase was from the end of May to the end of June, sampling invertebrates using special designed below ground pitfall traps. The second phase was from the middle of July to the middle of August sampling earthworms using standard methods suggested by Butt and Grigoropoulou (2010) and OPAL (2010). The study was divided into two phases because the catch rate of earthworm is too low (3 individuals were found out of 420 traps during 14 days) when the pilot study was carried out during late April to earth May.

Invertebrate sampling with special designed below ground pitfall traps

The below ground pitfall traps is made of three important parts. First is the ground cover which prevents the sunlight penetrating into the pitfalls to simulate the dark environment and prevent some above-ground invertebrates entering the trap. The second is a petridish immediately beneath the trap cover which is stuck into soil for about 1cm to absolutely prevent any non-burrowing or shallow-burrowing invertebrates (i.e. harvestman and some spiders) falling into the trap. Soil was put around and above the petridish to absolutely prevent sunlight penetrating into the holes and to repel some invertebrates due to the elevation of the soil embankment (Woodcock, 2005). The holes were dug using a petrol powered auger with a drill bit of 50mm. The hole was about 40cm to 50cm deep to allow an actual sampling depth of 30cm (deducting the height of the plastic cup). The third were the special made plastic cups which were cut and glued to fit the holes, and a metal stick was attached to each cup to help pulling them out of the holes. A stick was used to push the cups into the bottom of the hole as they were tightly fit to the hole (see plate 2 for more

detail). The date, time, site, sampling station was recorded at sites and samples were sent to entomology lab immediately for invertebrate identification. Each transect was sampled every other two days. Every individuals caught was identified to order level (with tadigrade to Phylum) using the key by Tilling (1987). The body size was measured using the scale provided by the dissecting microscope. Their body size was simplified by multiplying their length, width and height.

Plate 2 The design of below ground pitfall trap.



Earthworm survey and observing boxes

There are a lot of methods can be used to capture earthworms but not all of them are reliable and easy to apply. The mustard solution is one of the most environmental friendly yet effective way to collect deep burrowing earthworms (Butt and Grigoropoulou, 2010; OPAL, 2010). A standard 20cm by 20cm by 10cm (height) pit was dug at each sampling station and the soil removed were put on a plastic sheet. Musturd solution which was made of approximately 5g musturd dissolved into 750 ml water was poured into the pit. In the meanwhile, the removed soil was searched for any earthworms within it. The time for the mustard solution to totally infiltrate is recorded as drainage time. Any earthworms caught were collected in a bottle with the removed soil to prevent them from drying and burning by the sunlight. Soil moisture and bulk density of soil were obtained for each sampling station. Soil type and earthworms was indentified at sites using the key provide by OPAL (2010).

The earthworm were placed into observing box which was made of two glass sheet with a gap of approximately 5mm (to allow for the largest earthworm caught to fit in the box without squashing them) away from each other. The glass sheet was about 50cm high and 30cm wide. Three sides were sealed to prevent earthworm escaping. The box was erected vertically as earthworms tend to move vertically (Nardi, 2007). Bulk density of soil in observing box is measured by dividing the weight of soil used to fill the box by the volume of the soil occupied. The boxes were placed at CT room with a constant of 16 °C. This is the average temperature of soil about 20 cm below ground of all of the sampling station. Humidity was set at 50% and the room is completely dark 24 hours a day to simulate the dark environment below ground. Their patterns of burrow was drew by putting transparency film above the glass sheet and measured every 8 hours to minimize the bias as they may move backwards and

decrease the total length of their burrow measured.

Calculating the bioturbation rate

The bioturbation rate invertebrates caught using below ground pitfall traps was obtained by the following equation:

$$\text{Bioturbation rate} = N \cdot V / (\pi \cdot D \cdot H \cdot \text{Day})$$

Where N is the number of individuals caught; V is their body size; π is Pi which is 3.14; D is the diameter of the hole which is equivalent to the diameter of the cup; H is the distance from the top of cup to the top of the hole; Day is the time interval between sampling.

We assumed that the amount of soil removed or disturbed is equal to their body size. The invertebrates cannot enter the trap via the top of the hole nor the bottom of the cup so the flank area of cylinder is used to determine the amount of invertebrates passing through per square meter.

The bioturbation rate by earthworm is calculated by:

$$\text{Bioturbation rate} = L \cdot \pi \cdot (D/2)^2 \cdot N/A$$

Where L is the total length of each earthworm burrowed per day; π is Pi which is 3.14; D is the diameter of each earthworm; N is the number of individuals caught in the pit.

We assume that the earthworms can burrow similar length at their respective habitats because high proportion (64%) of earthworms caught were juveniles which cannot be observed in the boxes (they are too small). So their respective body width was incorporated to account for their differences in bioturbation.

Statistical analysis

The Statistical package R (version 2.11.1 R Development Core Team 2010) was used for data analysis. The bioturbation rate for the first phase (invertebrates) is highly skewed but can be normalized by logarithm transformation. The linear mixed effect model (LME) was used to assess the differences of bioturbation rates between habitats, between sampling stations and any interactions between them. Analysis of variance (ANOVA) with error structure was also performed as references but not present in the results section. The bioturbation rate for the second phase (earthworms) cannot be normalized using simple transformation. Thus generalized linear mixed effect model (LMER) was used with quasipoisson errors.

Results

The result of invertebrate sampling using below ground pitfall traps

A total of 2235 individuals were caught, divided into 14 Orders (Phylum). The most abundant species sampled was the Springtails (Collembola) with 1680 individuals, contributing around 75% of the population caught. The second most abundant species was mites (Acari) with 255 individuals, contributing about 11% of the population caught. The other 12 Orders (Phylum) were less than 100 individuals respectively, contributing less than 5% of the whole population. However, the flat-backed millipede community has the highest bioturbation contribution (23.00%), followed by beetle community (17.55%), most of which are larvae. Both of their population is very low, both contributing less than 4% of the whole population (for other Orders/Phylum see Table 1).

Table 1 Numbers of individuals caught of each orders, their percentage contributing to whole population, the percentage contribution to total bioturbation of each orders

| Order/Phylum | Individuals | Percentage % | Percentage contribution of bioturbation% |
|-----------------------|--------------------|---------------------|---|
| Acari | 255 | 11.40939597 | 1.686946 |
| Coleoptera | 72 | 3.22147651 | 17.55123 |
| Collembola | 1680 | 75.16778523 | 15.32635 |
| Diplura | 35 | 1.565995526 | 0.754146 |
| Diptera | 24 | 1.073825503 | 10.60398 |
| Geophilomorpha | 9 | 0.402684564 | 4.81229 |
| Glomerida | 1 | 0.044742729 | 0.725134 |
| Hemenoptera | 68 | 3.042505593 | 3.933231 |
| Isopoda | 15 | 0.67114094 | 3.963198 |
| Julida | 3 | 0.134228188 | 3.073593 |
| Lithobiomorpha | 25 | 1.118568233 | 7.803433 |
| Haplotaxida | 4 | 0.178970917 | 6.695516 |
| Polydesmida | 43 | 1.92393736 | 23.00148 |
| Tadigrade | 1 | 0.044742729 | 0.069475 |

Table 2 Total number of individuals caught of each Order/Phylum at each sampling station across distance between habitats. The sum is the total number of each Order/Phylum within each habitat.

| Orders/Phylum | Habitat Type | Distance to edge | | | | | Sum |
|----------------|--------------|------------------|-----|-----|-----|-----|-----|
| | | 10 | 20 | 30 | 40 | 50 | |
| Acari | Woodland | 5 | 10 | 10 | 7 | 3 | 35 |
| | Grassland | 4 | 84 | 35 | 43 | 54 | 220 |
| Coleoptera | Woodland | 7 | 5 | 2 | 2 | 5 | 21 |
| | Grassland | 6 | 2 | 14 | 16 | 13 | 51 |
| Collembola | Woodland | 121 | 260 | 196 | 233 | 188 | 998 |
| | Grassland | 152 | 119 | 127 | 135 | 149 | 682 |
| Diplura | Woodland | 4 | 0 | 0 | 3 | 0 | 7 |
| | Grassland | 1 | 1 | 7 | 7 | 12 | 28 |
| Diptera | Woodland | 2 | 3 | 0 | 9 | 2 | 16 |
| | Grassland | 4 | 0 | 3 | 0 | 1 | 8 |
| Geophilomorpha | Woodland | 0 | 2 | 1 | 1 | 0 | 4 |
| | Grassland | 2 | 0 | 2 | 1 | 0 | 5 |
| Glomerida | Woodland | 0 | 0 | 1 | 0 | 0 | 1 |
| | Grassland | 0 | 0 | 0 | 0 | 0 | 0 |
| Hemiptera | Woodland | 6 | 7 | 1 | 0 | 1 | 15 |
| | Grassland | 0 | 10 | 12 | 21 | 10 | 53 |
| Isopoda | Woodland | 4 | 1 | 1 | 0 | 0 | 6 |
| | Grassland | 1 | 0 | 2 | 0 | 6 | 9 |
| Julida | Woodland | 0 | 1 | 2 | 0 | 0 | 3 |
| | Grassland | 0 | 0 | 0 | 0 | 0 | 0 |
| Lithobiomorpha | Woodland | 2 | 1 | 0 | 0 | 4 | 7 |
| | Grassland | 3 | 5 | 2 | 3 | 5 | 18 |
| Haplotaenidia | Woodland | 1 | 1 | 1 | 0 | 0 | 3 |
| | Grassland | 0 | 1 | 0 | 0 | 0 | 1 |
| Polydesmida | Woodland | 6 | 9 | 2 | 0 | 8 | 25 |
| | Grassland | 2 | 0 | 11 | 1 | 4 | 18 |
| Tadigrada | Woodland | 1 | 0 | 0 | 0 | 0 | 1 |
| | Grassland | 0 | 0 | 0 | 0 | 0 | 0 |

The linear mix effect model was employed to account for pseudoreplication. There is no evidence suggesting any interactions between distance to edge and habitat type ($p>0.1$), nor difference between habitats ($p>0.2$) or relationship between bioturbation rate (on a log scale) and distance to edge ($p>0.2$). After model simplification the bioturbation rate is significantly larger than 0 ($p=0$, $df = 158$), with an mean bioturbation rate of 21.26 ± 0.22 mm³/m²/day across all sampling stations (see Table 3).

Table 3 Influence of explanatory variables and their interactions on Bioturbation rate (on a log scale). Distance is continuous variable representing distance to habitat edge; type is categorical variable containing woodland and grassland factor levels.

| | Value | Std.Error | DF | t-value | p-value |
|---------------------------|----------|-----------|-----|----------|---------|
| (Intercept) | 3.695924 | 0.463507 | 158 | 7.973831 | 0 |
| Distance | -0.01421 | 0.013097 | 22 | -1.08477 | 0.2898 |
| TypeGrass | -1.11563 | 0.614166 | 2 | -1.8165 | 0.2109 |
| Distance:TypeGrass | 0.025766 | 0.01848 | 22 | 1.39428 | 0.1772 |

Though there is no difference between the bioturbation rate in woodland and in grassland nor across the distance to edges, there is significant site difference on mean bioturbation rate. The bioturbation rate (on a log scale) in Merten’s Acres is significantly different than that in Gunness’s Hill ($p<0.05$, $df=27$). The bioturbation rate (on a log scale) in Gunness’s Thicket is significantly different than that in Gunness’s Hill ($p<0.05$, $df=27$) but there is no evidences suggesting that the bioturbation rate is significantly different between Merten’s Acres and Gunness’s Thicket ($0.782531-0.696185= 0.086346$ which is less than 1 standard error 0.32) (see Table 4 for more details).

Table 4 Influence of explanatory variables obtained from minimal adequate model. SiteGT represents Guinness’s Thicket; SiteMA represents Merten’s Acres; SiteES represents Guinness’s Hills – Elm Slope.

| | Value | Std.Error | DF | t-value | p-value |
|--------------------|----------|-----------|-----|----------|---------|
| (Intercept) | 2.602093 | 0.231549 | 158 | 11.23775 | 0 |
| SiteGT | 0.782537 | 0.321205 | 27 | 2.436255 | 0.0217 |
| SiteMA | 0.696185 | 0.325025 | 27 | 2.14194 | 0.0414 |

The result of earthworm survey

A total of 86 individuals were caught during the sampling period, among which 29 were adult and viable to observe. Those 29 individuals were all Redhead worm *Lumbricus rubellus*, the rest (66.27% of the whole population) were immature individuals and cannot be identified using the key provided. No earthworm were captured at site 1 (Elm Slope to Guinness’s Hill) either in grassland or in woodland, so this site is excluded for the following analysis.

The generalized linear mix effect models were fit to account for pseudoreplication. Quasipoisson errors was employed to account for over-dispersion. The three-way interaction were significant ($t > 2$) obtained from minimal adequate model (see Table 5). There is a positive correlation between bioturbation rate and distance to edge on grassland at site Merten’s Acres (the slope is 0.115, $t > 2$). It suggests a negative relationship between bioturbation rate and distance to edge in woodland at site Merten’s Acres. However, there was only one data point which is not 0 out of 35 in woodland at this site (see Figure 1). The significant terms are arguable and it could be interpreted as no relationship between bioturbation and distance to edge. The intercept therefore is close to 0 despite the term is statistically significant. The intercept (2.80,

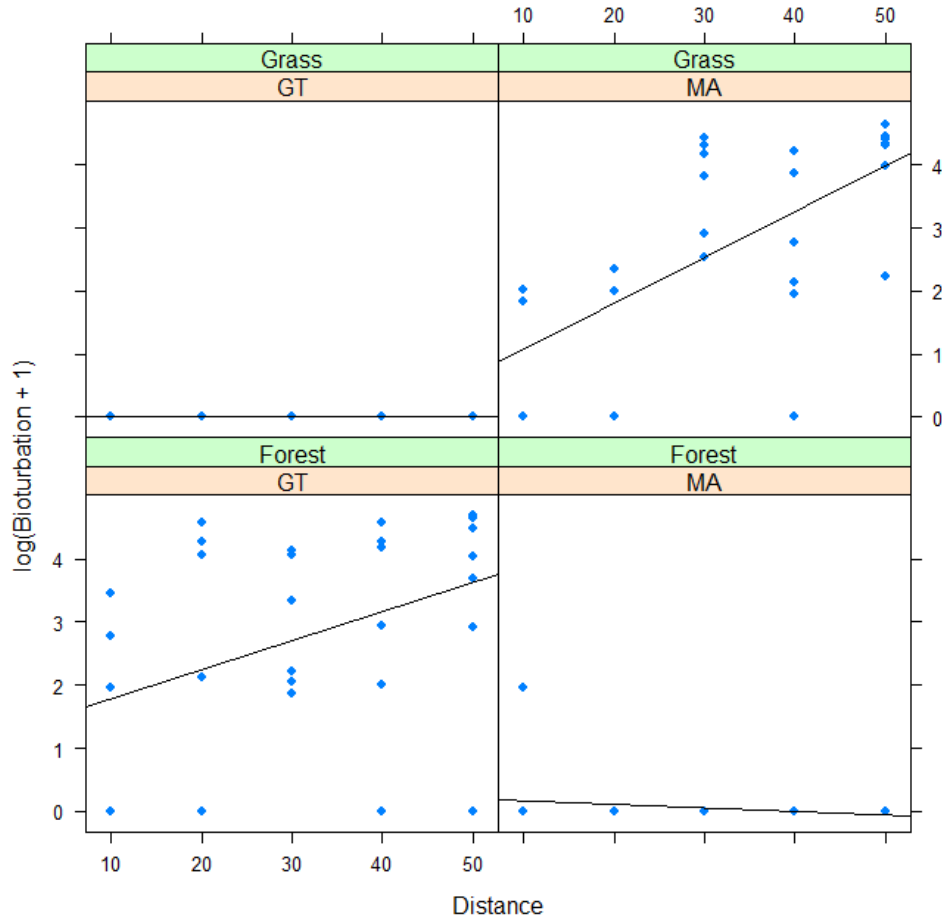
$t > 2$) on grassland is significantly different than that in woodland at site Merten's Acres. There is a positive correlation between bioturbation rate and distance to edge in woodland at site Gunness's Thicket (the slope is 0.039, $t > 2$). The mean bioturbation rate in woodland is significantly different than that on grassland at site Gunness's Thicket ($t > 2$). There is no relationship between bioturbation and distance to edge (slope is 0) on grassland at site Gunness's Thicket. The mean bioturbation rate is zero as no earthworm was found at this site. The bioturbation rate at the edge of grassland at site Merten's Acres is higher but not significantly higher than that of woodland at site Gunness's Thickets (the difference is 0.58747 which is less than 2 standard errors). The bioturbation rate increases faster from the edge into the interior on grassland of Merten's Acres than that in woodland of Gunness's Thickets (they are differ by 0.076 which is larger than 2 standard errors). In short, the relationship between bioturbation rate and distance to edge is significantly different between habitat type and sites.

Table5 Influence of significant explanatory variables and their interactions on bioturbation rate. The bioturbation rate is on a log scale (quasipoisson errors).

| | Estimate | Std. Error | t value |
|----------------------------------|-----------------|-------------------|----------------|
| (Intercept) | 2.21749 | 0.63312 | 3.502 |
| Distance | 0.03909 | 0.01897 | 2.060 |
| SiteMA | -1.93936 | 1.27329 | -1.523 |
| TypeGrass | -2.23852 | 0.952156 | -2.351 |
| Distance:SiteMA | -0.11082 | 0.05146 | -2.153 |
| Distance:TypeGrass | -0.03909 | 0.05900 | -0.663 |
| SiteMA:TypeGrass | 2.52680 | 1.22422 | 2.064 |
| Distance:SiteMA:TypeGrass | 0.18730 | 0.07846 | 2.387 |

Note: No p value is specified in this lmer model (see Bates 2006).

Figure 1 Correlation between bioturbation rate and distance to edge for each habitat and site. Bioturbation is on a log scale.



The generalized linear mix effect models were employed to account for pseudoreplication with quasipoisson errors to account for over-dispersion. Not all factor of drainage type appeared in all soil types, full factorial analysis is impossible. Therefore they were assessed separately to examine the possible reasons for the change of bioturbation rate across distance, habitat type and sites. The soil type sandy loam and loamy sand were grouped as “sandy”. The clay loam, sandy clay loam, and silty clay loam were grouped as “loam”. This does not cause significant lower explanatory power ($p > 0.1$ see Appendix). The two-way interaction soil moisture and drainage time, soil moisture and soil type were both significant ($t > 2$).

Bioturbation rate increases as the soil moisture increases for soil type sandy and loam, with the deeper slope (0.674) for soil type sandy and shallower slope (0.301) for soil type loam. It slightly decreases as the soil moisture increases for soil type silty clay (slope = -0.034). All slopes are significantly different from each other ($t > 2$). The intercept of soil type silty clay is significantly higher than that of soil type loam ($t > 2$). The intercept of soil type sandy is significantly lower than the other two (see Table 6 for more detail).

Table 6 Influence of significant explanatory variables and their interactions on bioturbation rate. The bioturbation rate is on a log scale (quasipoisson errors). Moisture is continuous variable, and newsoiltype is categorical variable containing sandy, loam and silty clay factor levels.

| | Estimate | Std. Error | t value |
|---------------------------------------|-----------------|-------------------|----------------|
| (Intercept) | 1.66436 | 0.38136 | 4.364 |
| Moisture | 0.30132 | 0.02064 | 14.599 |
| newsoiltypesandy | -6.25264 | 0.61786 | -10.120 |
| newsoiltypeSilty_Clay | 2.17439 | 0.68731 | 3.164 |
| Moisture:newsoiltypesandy | 0.37248 | 0.05122 | 7.273 |
| Moisture:newsoiltypeSilty_Clay | -0.33569 | 0.02437 | -13.773 |

Note: No p value is specified in this lmer model (see Bates 2006).

Bioturbation rate increases as the soil moisture increases when the drainage time is medium (slope=0.731) or long (slope=0.430). It decreases as the soil moisture increases when the drainage time is short (slope=-0.286). The increase rate is significantly higher when the drainage time is long than medium drainage time ($0.71566-0.44557=0.27009$ which is larger than 2 standard errors). The intercept is highest when the drainage time is short, followed by medium drainage time. The long drainage time has the lowest bioturbation rate and they are all significantly different than each other ($t > 2$, $-2.893+2.511=0.382$ which is larger than 2 standard errors).

Table 7 Influence of significant explanatory variables and their interactions on bioturbation rate. The bioturbation rate is on a log scale (quasipoisson errors). Moisture is continuous variable, and drainage time is categorical variable containing fast, medium and slow factor levels. Fast representing short drainage time, slow representing long drainage time.

| | Estimate | Std. Error | t value |
|------------------------------------|-----------------|-------------------|----------------|
| (Intercept) | 1.14665 | 0.62592 | 1.832 |
| Moisture | -0.28573 | 0.02379 | -12.012 |
| DrainageTimeMedium | -2.51085 | 0.14187 | -17.698 |
| DrainageTimeSlow | -2.89348 | 0.14657 | -19.741 |
| Moisture:DrainageTimeMedium | 0.44557 | 0.02916 | 15.278 |
| Moisture:DrainageTimeSlow | 0.71566 | 0.03302 | 21.670 |

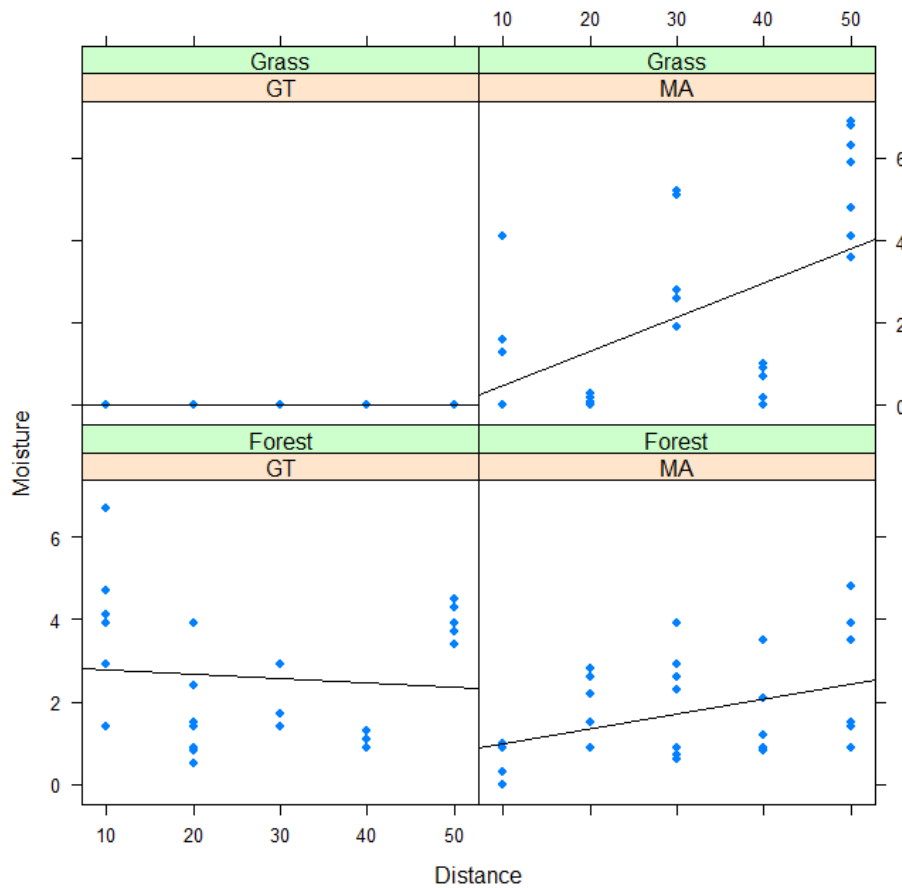
Note: No p value is specified in this lmer model (see Bates 2006).

Linear mix effect model was fit to assess the change of soil moisture across distance, habitat type and site. The minimal adequate model suggests that there is no relationship between soil moisture and distance to edge. The mean moisture, however, is different between habitats and sites. Then mean moisture on grassland is significantly higher than that in woodland at site Merten's Acres ($p < 0.05$). The mean moisture in woodland is significantly lower than that on grassland at site Guinness's Thickets ($p < 0.01$). The mean moisture of woodland at site Merten's Acres is smaller but close to that of woodland at site Guinness's Thickets ($p > 0.2$). The grassland of Merten's Acres has the highest mean moisture, followed by the woodland of Guinness's Thickets and the woodland of Merten's Acres. The soil moisture of grassland of Guinness's Thicket is close zero (see Table 8 and Figure 2 for more details).

Table 8 Influence of significant explanatory variables and their interactions on soil moisture obtained from minimal adequate model.

| | Estimate | Std. Error | DF | t value | p-value |
|------------------|-----------|------------|-----|-----------|---------|
| (Intercept) | 2.57428 | 0.5663001 | 120 | 4.545798 | 0.0000 |
| SiteMA | -0.880000 | 0.8008693 | 16 | -1.098806 | 0.2881 |
| TypeGrass | -2.574286 | 0.8008693 | 16 | -3.214364 | -0.0054 |
| SiteMA:TypeGrass | 3.028571 | 1.1326002 | 16 | 2.673999 | 0.0166 |

Figure 2 The correlation between soil moisture and distance for each habitat type and site.



Discussion and conclusion

Mean bioturbation rate for invertebrates

Springtails (Collembola) are clearly the most abundant below ground animals as they consist about three quarters of the invertebrates being caught by the below ground pitfall traps. The other orders, except mites (Acari), all consists less than 4% of the total population. However, some communities with very low population have unproportionally large influence on total bioturbation rate, such as Polydesmida, Coleoptera, and Diptera. This suggests that large invertebrates are more important as a bioturbator than small ones. The abundance is not as important as body size on determining bioturbation rate. It is also important to note that all but five individuals of Coleoptera are beetle larvae, and all individuals of Diptera are at larvae stage. It is likely to underestimate the abundance of non-predator species. Since the trap was left untouched for about three days, those individuals such as Collembola were vulnerable to the attack of predatory invertebrates such as beetle larvae and centipedes.

The mean bioturbation rate for invertebrates remains unchanged across distance to edge and between habitats, which suggests that Bioturbation rate is not significantly affected by the change of above ground environment. Physical-chemical factors are important in limiting the distribution and affecting demographic characteristics of animals. The burrows provide temporary or permanent habitats and refuges for the pedofauna. The internal microclimate is buffered compared to that of exposed earth surface. Many abiotic factors below ground are not as dynamic as that of above-ground (Gobat et al, 2004). For example, soil temperature and its variations strongly influence the life in the soil such as Bacteria. They are usually very sensitive and have well-defined ranges of physiological tolerance and optimum activity. The

soil temperature is linked to the general climate by heat flows depending on the seasons and by precipitation. However, the large thermal buffering capacity of a light-coloured, water-saturated fibrous peat may retain a constant temperature below 5-10 cm depth throughout the year greatly reducing the temperature variation below ground. In other cases, the survival of soil dwelling organisms is ameliorated by good snow cover, which insulates them against very low air temperatures above ground (Gobat et al, 2004). Therefore relatively stable below ground environment may help to maintain a constant bioturbation rate and most likely through keeping the activity of the bioturbators at a certain level.

Another possible explanation is that below ground fauna community depends on the composition rather than the diversity in other domain. Effects of resource quality or quantity may outweigh effects of resource heterogeneity. In Wader et al.'s (1999) study, different functional groups of the flora were removed and the taxonomic composition of five functional groups of below ground organisms was monitored. They found no consistent evidence that below ground functional groups were positively related to the plant diversity above ground. They concluded that below ground community structure is more likely to be related to the traits of the dominant plant species present rather than to the plant diversity itself. In Chen and Wise's (1999) study, they found that plants may affect the densities of some below ground groups through amounts of production rather than diversity. More resources may sustain a larger and possibly more diverse soil and litter community. Thus the heterogeneity of primary productivity at habitat edge has little effect on the bioturbation rate at habitat edge compared to the interior. The homogeneities within habitats may result in a similar quantity or quality of resource input hence eliminating the variance across distance.

Despite the fact that some of the abiotic factors are fairly stable below ground, the soil microclimate and microstructure are very dynamic (Gobat et al, 2004). It is unlikely that the below ground community and the composition would remain the same between habitats (as shown in Table 2). However, it is possible that groups of animal could respond differently to the abiotic factors i.e. on different temporal or spatial scales. For example the total number of flat-backed millipedes caught in woodland is almost twice as many as that on grassland, but the total number of beetle larvae caught in woodland is less than half of the number on grassland. Though the bioturbation rate for certain groups of invertebrates may change along environmental gradients, the overall effects may be averaged out.

The mean bioturbation rate is statically significant differences between habitats, with site 1 (Elm Slope to Guinness's Hill) having the lowest value and the other two roughly the same. However, the largest variation between Guinness's Thickets and site 1 is about $1.19 \text{ mm}^3/\text{m}^2/\text{day}$, which is roughly equal to one more common soil dwelling collembola fallen into the trap per three days. It is biologically negligible as it is possible that the collembola fall into the trap from nearby leaf litter when pulling up the cup.

Mean bioturbation rate variations for earthworms

The mean bioturbation rate of *Lumbricus rubellus* in woodland of Guinness's Thicket is 34.88 cm³/m²/day which is roughly 0.012 m³/m²/year. The mean bioturbation rate of on grassland is 29.80 cm³/m²/day which is about 0.011 m³/m²/year. It is slightly higher than the estimate of 0.01 m³/m²/year by Gabet et al (2003). It is possibly because we assumed that the immature earthworms can burrow as long as an adult per day. This may cause overestimation of bioturbation rate since two thirds of the earthworms were immature one, and their burrowing ability cannot be observed directly. The bioturbation rate varies significantly across distance to habitat edge and between habitats. There were no earthworms on the grassland of Guinness's Thickets and only one individual was found near the woodland edge of Merten's Acres but nowhere else in the interior. The increase of bioturbation rate from the edge to the interior suggests that the edge may have deleterious effect on earthworms.

Soil moisture is very important to earthworms as they lack a mechanism to maintain constant internal water content (Edward & Lofty, 1977). *Lumbricus rubellus* seems to prefer wetter soil where possible as it is not desiccation tolerant (Edward & Bohlen, 1996). This could explain that the number of earthworm caught was low at the first three weeks as it hardly has any precipitation during that period (from 12th of July to 9th of August). The absence of earthworm on grassland at Guinness's Thicket is possibly due to the low water content of soil which was nearly zero. Prolonged

droughts decrease the number of earthworms dramatically, and it may take about 2 years for populations to recover even if the conditions become favorable again (Edward & Bohlen, 1996). So there is no change of catch rate at those sampling station where the soil moisture is nearly zero even after the raining events at the last week of sampling period. The higher bioturbation rate at the edge of grassland at Merten's Acres is probably due to higher soil moisture. The bioturbation rate at habitat edge of each site is closely related to soil moisture difference between habitats and sites. Soil moisture is the main reason of habitat and site differences.

Soil texture and the drainage time may partially explain the pattern of bioturbation change across distance to habitat edge. Drainage time directly depends on the soil texture, structure and porosity. Shorter drainage time reflecting looser soil may potentially prove the rework of soil by bioturbators. The bioturbation rate increases when the soil has more clay content. In the woodland of Guinness's Thickets, the soil texture is sandy loam at 10m sampling station, sandy clay loam at 20m and 30m sampling station, and clay loam at 40m and 50m sampling station. The clay content increases from the edge of woodland to the interior and so does the bioturbation rate. The soil type on grassland of Merten's Acres is silty clay loam at sampling station 10m and 20m and the soil type at the other sampling station is silt clay. The bioturbation rate change pattern shown at this habitat can be partially explained by the increase of clay content from habitat edge. The 30m and 40m sampling station, for most of the time, have a medium drainage time, and 50m always has a short drainage time. The increasing bioturbation rate from 30m to 50m is due to the looser soil at 50m. The above findings about bioturbation change due to soil texture is the same as in Edward & Lofty's (1977) book which states that there is positive correlation between earthworm densities and soil clay content. However it is likely that the soil texture affect earthworm population via other important abiotic factors such as soil

moisture, nutrient status and cation exchange capacity (Edward & Bohlen, 1996). The deleterious effect of edge may be caused by the unfavorable environment for earthworms in the other domain. The abiotic factors (i.e. soil moisture and soil texture) are more strongly affected by the other domain near the edge, which results in a less favorable environment comparing to habitat interior. It is interesting to note that looser soil have higher bioturbation rate or in other words higher earthworm densities. Whether the presence of the earthworm loosens the soil or the loose soil attracts earthworms due to its easy burrowing properties is unknown. It is likely to be the latter case as *Lumbricus rubellus* prefers loose soil to burrow (Edward & Lofty's, 1977).

The absence of earthworm from the woodland at Merten's acres cannot be explained by either soil texture or soil moisture effect. It is possible that the absence is possibly due to the organic matter source. Leaves of oak and beech contain condensed tannins, which are unpalatable to earthworms. Other study shows that earthworm biomass diminished under oak stands due to poor quality of the oak litter and acidification of the soil by oak leaves (Muys et al, 1992). *Lumbricus rubellus* also consumes material rich in relatively undecomposed plant remains. Therefore the cover of decomposed oak leaves with little ground flora may result in the absence of *Lumbricus rubellus* for that habitat. Though the oak trees are present in the woodland of Gunness's Thicket, there are considerable amount of birch and sycamore leaves together with oak leaves. The ground floor is covered by various flora such as bluebells and brackens. Therefore it may provide enough undecomposed plant remains to support the population of *Lumbricus rubellus*. The ungrazed grassland of Merten's Acres is no doubt the heaven for *Lumbricus rubellus* as it provides enough food for them.

It is not hard to explain the absence of earthworms at site 1 (Elm Slope to

Gunness's Hill). The soil moisture on grassland is 0.04 which is very close to zero. It is too dry to support any earthworms. The woodland is covered by dense oak leaves despite the fact that the soil moisture is high (see Appendix). Therefore it is not surprising that no *Lumbricus rubellus* was found at this site.

Conclusion

The invertebrate survey using below ground pitfall traps shows that there is no evidence that supporting bioturbation rate change with distance to habitat edges or between habitats. It is possibly because different communities response to the environmental change differently and the overall effect is averaged out. The homogeneities within the habitats and relatively stable abiotic factors below ground may also help to maintain a certain level of bioturbation rate. However, the earthworm survey shows that the bioturbation rate increases as the distance to habitat edge increases. There are significantly differences of bioturbation rate between habitats and sites. Bioturbation rate of *Lumbricus rubellus* increases with soil moisture, content of clay in soil, and looseness of soil. Oak leaves have adverse effect on *Lumbricus rubellus* and hence *Lumbricus rubellus* was absent from woodland with mainly oak trees. The deleterious edge effect is possibly due to the transit from favourable conditions in habitat interior to unsuitable environments in the other domain.

Limitations and future work

It is almost certain that the bioturbation rate is overestimated due to the ways of estimating the body size. The body size was calculated by multiplying the length, width and height of each individual together. No animal is a cuboids and it occupy less space than a cuboids with same parameter. Thus all body sizes of the invertebrates are overestimated and it is difficult to get a common inflation rate to correct the body size due to the irregular shape of many species.

The earthworms should be observed *in situ* as the bulk density of soil and soil structure are changed in the observing boxes and it is almost impossible to prepare the soil exactly as where it was. Therefore the bioturbation rate and burrowing behavior may not be as same as it was in the field. The bioturbation rate obtained in this way can only be used as a reference but not actual value in the field.

The drainage time is a rather arbitrary variable and it would be much better to find a way of describing the looseness of soil caused by the bioturbation of earthworms. It would be more fruitful if other abiotic factors were measured such as temperature, pH, and porosity. More work should be done to investigate the possible causes of abiotic shifts (i.e. soil texture, soil moisture) across distance, between habitats and sites. Higher resolution of taxa or functional groups could be incorporated into this study to examine the community changes along each of the environmental gradients. An above ground flora and fauna survey may provide a lot more information on their interactions with below ground communities. It is also very interesting to note that the below ground pitfall traps works well for most of the soil-dwelling invertebrates but not for earthworms. It would be interesting to know how “smart” they could be in terms of avoiding traps.

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Wardle, D.A., Bonner, K.I., Barker, G.M., Yeates, G.W., Nicholson, K.S., Bardgett, R.D., Watson, R.N. and Ghani, A. (1999) Plant removals in perennial grassland:

Vegetation dynamics, decomposers, soil biodiversity and ecosystem properties. *Ecological Monographs*. 69: 535–568.

Williams-Linera, G. (1990) Vegetation structure and environmental conditions of forest edges in Panama. *Biotropica*. 22: 235–241.

Woodcock, B.A. (2005) Pitfall trapping in ecological studies. In: Leather, S. (eds.) *Insect sampling forest ecosystems*. Blackwell Publishing. Oxford. pp. 37-57

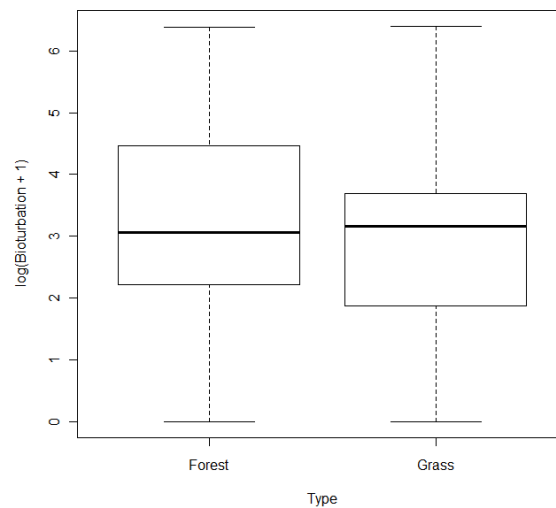
Yeates, G.W., Bardgett, R.D., Cook, R., Hobbs, P.J., Bowling, P.J. and Potter, J.F. (1997) Faunal and microbial diversity in three Welsh grassland soils under conventional and organic management regimes. *Journal of Applied Ecology*. 34: 453–470.

Yoo, K. Amundson, R., Heimsath, A.M. and Dietrich, W.E.(2005) Process-based model linking pocket gopher (*Thomomys bottae*) activity to sediment transport and soil thickness. *Geology*. 33: 917–920.

Appendix

Graphs for invertebrate sampling using below ground pitfall traps.

Figure 1 Bioturbation rate between habitats. Bioturbation is on a log scale.



Command lines in R and outputs

Model fitting for invertebrates without site (linear mix effect model)

```
> repeats<-Site:Type:factor(Distance)
>
model<-lme(log(Bioturbation+1)~Distance*Type,random=~1|repeats,method
="ML")
> modell<-lme(log(Bioturbation+1)~1,random=~1|repeats,method="ML")
> anova(model,model1)
      Model df    AIC    BIC  logLik  Test  L.Ratio p-value
model    1  8 688.7003 714.5919 -336.3502
modell    2  5 685.9668 702.1490 -337.9834 1 vs 2 3.266515 0.3523
> summary(model1)
```

Linear mixed-effects model fit by maximum likelihood

Data: NULL

| | AIC | BIC | logLik |
|--|----------|---------|-----------|
| | 685.9668 | 702.149 | -337.9834 |

Random effects:

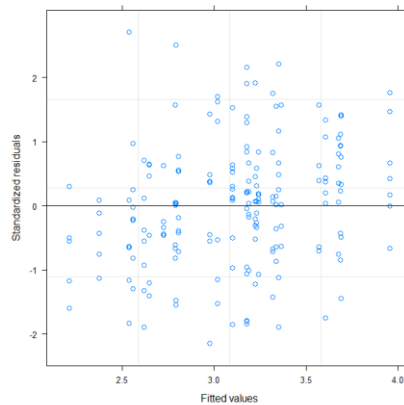
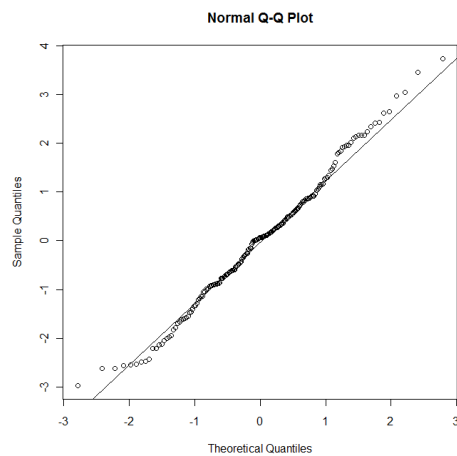
Formula: ~1 | repeats

(Intercept) Residual

StdDev: 0.6402581 1.782894

Fixed effects: log(Bioturbation + 1) ~ 1

| | Value | Std.Error | DF | t-value | p-value |
|-------------|----------|-----------|-----|----------|---------|
| (Intercept) | 3.102741 | 0.2017962 | 158 | 15.37561 | 0 |



Model fitting for invertebrates with site (linear mix effect model)

>

```
model<-lme(log(Bioturbation+1)~Distance*Type*Site,random=~1|repeats)
```

```
> summary(model)
```

Linear mixed-effects model fit by REML

Data: NULL

| | AIC | BIC | logLik |
|--|---------|----------|----------|
| | 726.608 | 770.9947 | -349.304 |

Random effects:

Formula: ~1 | repeats

(Intercept) Residual

StdDev: 0.5402481 1.382904

Fixed effects: log(Bioturbation + 1) ~ Distance * Type * Site

| | Value | Std.Error | DF | t-value | p-value |
|---------------------------|------------|-----------|-----|-----------|---------------|
| (Intercept) | 3.0089996 | 0.7942040 | 158 | 3.788699 | 0.0002 |
| Distance | -0.0173854 | 0.0242404 | 18 | -0.717209 | 0.4824 |
| TypeGrass | -0.8862585 | 1.1700640 | 18 | -0.757444 | 0.4586 |
| SiteGT | 1.5891512 | 1.1316229 | 18 | 1.404312 | 0.1772 |
| SiteMA | 0.4439572 | 1.1628347 | 18 | 0.381789 | 0.7071 |
| Distance:TypeGrass | 0.0372119 | 0.0354277 | 18 | 1.050362 | 0.3075 |
| Distance:SiteGT | -0.0165632 | 0.0342098 | 18 | -0.484164 | 0.6341 |
| Distance:SiteMA | 0.0280287 | 0.0353293 | 18 | 0.793357 | 0.4379 |
| TypeGrass:SiteGT | -0.7256645 | 1.6276065 | 18 | -0.445848 | 0.6610 |
| TypeGrass:SiteMA | 0.0170221 | 1.6500996 | 18 | 0.010316 | 0.9919 |
| Distance:TypeGrass:SiteGT | 0.0038890 | 0.0491992 | 18 | 0.079047 | 0.9379 |
| Distance:TypeGrass:SiteMA | -0.0383039 | 0.0498504 | 18 | -0.768378 | 0.4522 |

>

```
model<-lme(log(Bioturbation+1)~Distance*Type*Site,random=~1|repeats,method="ML")
```

```
> model1<-update(model,~.-Distance:Site:Type)
```

```
> anova(model,model1)
```

| | Model | df | AIC | BIC | logLik | Test | L.Ratio | p-value |
|--------|-------|----|----------|----------|-----------|--------|----------|---------------|
| model | 1 | 14 | 688.3637 | 733.6739 | -330.1818 | | | |
| model1 | 2 | 12 | 685.8037 | 724.6410 | -330.9019 | 1 vs 2 | 1.440050 | 0.4867 |

```
> model2<-update(model1,~.-Distance:Type)
```

```
> anova(model1,model2)
```

| | Model | df | AIC | BIC | logLik | Test | L.Ratio | p-value |
|--------|-------|----|----------|---------|-----------|--------|---------|---------------|
| model1 | 1 | 12 | 685.8037 | 724.641 | -330.9019 | | | |
| model2 | 2 | 11 | 686.2411 | 721.842 | -332.1206 | 1 vs 2 | 2.43739 | 0.1185 |

```
> model3<-update(model2,~.-Site:Type)
```

```
> anova(model2,model3)
```

| | Model | df | AIC | BIC | logLik | Test | L.Ratio | p-value |
|--------|-------|----|----------|----------|-----------|--------|----------|---------------|
| model2 | 1 | 11 | 686.2411 | 721.8420 | -332.1206 | | | |
| model3 | 2 | 9 | 685.6981 | 714.8261 | -333.8491 | 1 vs 2 | 3.457015 | 0.1775 |

```
> model4<-update(model3,~.-Site:Distance)
```

```
> anova(model3,model4)
```

| | Model | df | AIC | BIC | logLik | Test | L.Ratio | p-value |
|--|--------|----|-----|----------|----------|-----------|---------|------------------------|
| | model3 | 1 | 9 | 685.6981 | 714.8261 | -333.8491 | | |
| | model4 | 2 | 7 | 682.8569 | 705.5120 | -334.4285 | 1 vs 2 | 1.158765 0.5602 |

```
> model5<-update(model4,~.-Type)
```

```
> anova(model4,model5)
```

| | Model | df | AIC | BIC | logLik | Test | L.Ratio | p-value |
|--|--------|----|-----|----------|----------|-----------|---------|------------------------|
| | model4 | 1 | 7 | 682.8569 | 705.5120 | -334.4285 | | |
| | model5 | 2 | 6 | 682.7525 | 702.1711 | -335.3762 | 1 vs 2 | 1.895584 0.1686 |

```
> model6<-update(model5,~.-Distance)
```

```
> anova(model5,model6)
```

| | Model | df | AIC | BIC | logLik | Test | L.Ratio | p-value |
|--|--------|----|-----|----------|----------|-----------|---------|--------------------------|
| | model5 | 1 | 6 | 682.7525 | 702.1711 | -335.3762 | | |
| | model6 | 2 | 5 | 680.7733 | 696.9555 | -335.3867 | 1 vs 2 | 0.02084284 0.8852 |

```
> summary(model6)
```

Linear mixed-effects model fit by maximum likelihood

Data: NULL

| | AIC | BIC | logLik |
|--|----------|----------|-----------|
| | 680.7733 | 696.9555 | -335.3867 |

Random effects:

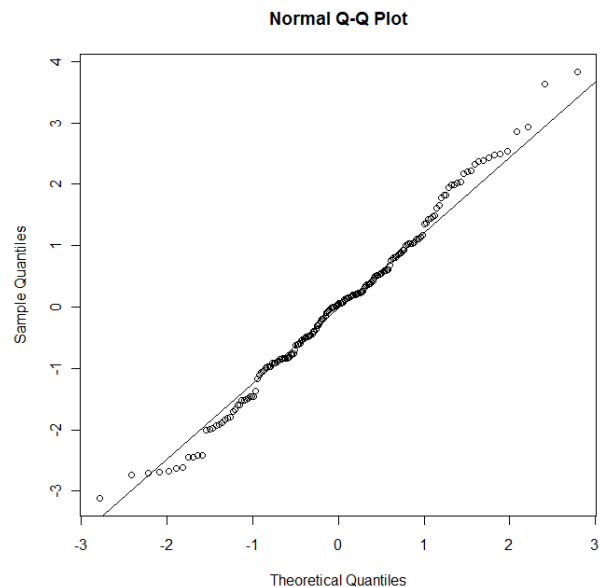
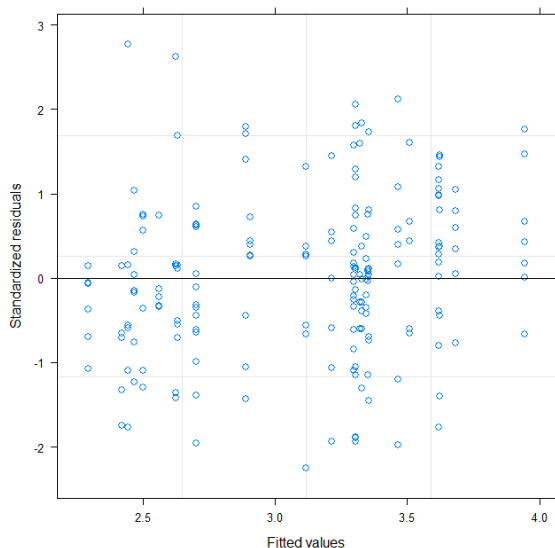
Formula: ~1 | repeats

(Intercept) Residual

StdDev: 0.4487257 1.383651

Fixed effects: log(Bioturbation + 1) ~ Site

| | Value | Std.Error | DF | t-value | p-value |
|-------------|-----------|-----------|-----|-----------|---------------|
| (Intercept) | 2.6020931 | 0.2315494 | 158 | 11.237748 | 0.0000 |
| SiteGT | 0.7825372 | 0.3212050 | 27 | 2.436255 | 0.0217 |
| SiteMA | 0.6961849 | 0.3250254 | 27 | 2.141940 | 0.0414 |



Graphs for earthworm survey.

Figure 2 Correlation between bioturbation rate and soil moisture. It is on a log-log scale

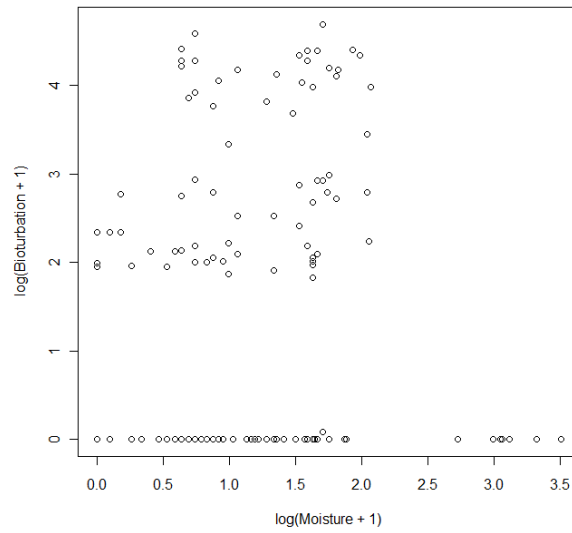


Figure 3 Bioturbation rate between different soil types. Bioturbation rate is on a log scale

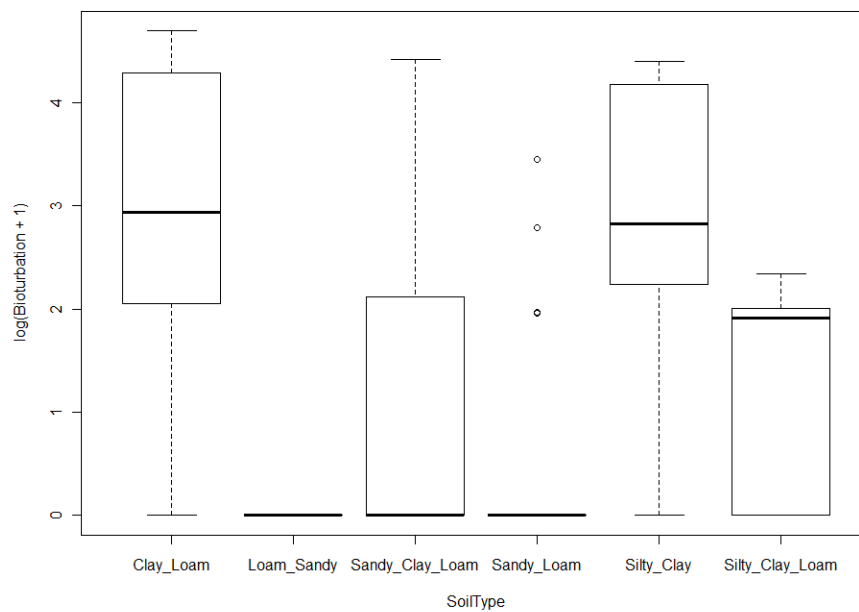
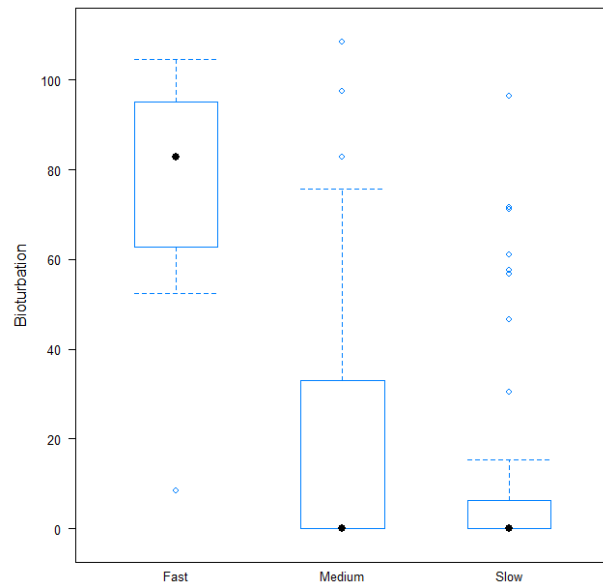


Figure 4 Bioturbation rate between different drainage time categories.



Command lines in R and outputs

The mean bioturbation rate of each habitats for the three sites

```
> tapply(Bioturbation, list(Site, Type), mean)
      Forest  Grass
ES 0.0000000 0.00000
GT 34.8782144 0.00000
MA 0.1749755 29.80411
```

The mean soil moisture of each habitats for the three sites

```
> tapply(Moisture, list(Site, Type), mean)
      Forest  Grass
ES 6.502857 0.04857143
GT 2.434286 0.00000000
MA 1.694286 2.57857143
```

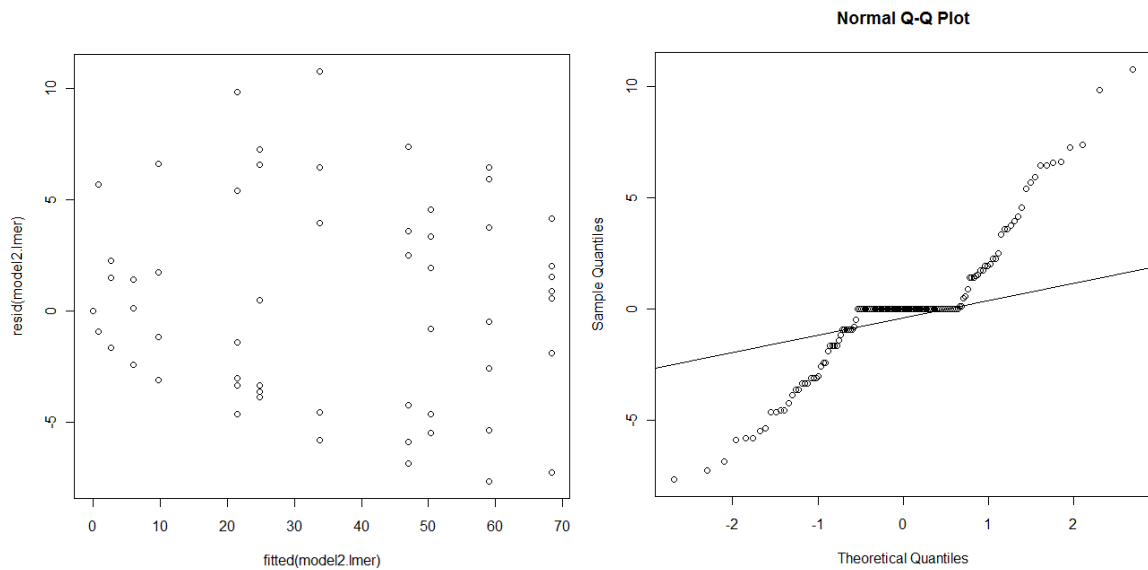
Model fitting for earthworms. Bioturbation is response variable , sites, habitat types and distance to edges as explanatory variable (generalized linear mix effect model)

```

>
model.lmer<-lmer(Bioturbation~Distance*Site*Type+(1|repeats),family=q
uasipoisson,REML=FALSE)
> summary(model.lmer)
Generalized linear mixed model fit by the Laplace approximation
Formula: Bioturbation ~ Distance * Site * Type + (1 | repeats)
  AIC   BIC logLik deviance
1559 1588 -769.3   1539
Random effects:
Groups   Name          Variance Std.Dev.
repeats (Intercept) 0.34672  0.58883
Residual                1.80487  1.34346
Number of obs: 140, groups: repeats, 20

Fixed effects:
              Estimate Std. Error t value
(Intercept)      2.21749    0.63312   3.502
Distance          0.03909    0.01897   2.060
SiteMA           -1.93936    1.27329  -1.523
TypeGrass        -2.23852    0.952156 -2.351
Distance:SiteMA  -0.11082    0.05146  -2.153
Distance:TypeGrass -0.03909    0.05900  -0.663
SiteMA:TypeGrass  2.52680    1.22422   2.064
Distance:SiteMA:TypeGrass 0.18730    0.07846   2.387
> m2<-update(model.lmer,~.-Distance:Type:Site)
> anova(model.lmer,m2)
Data:
Models:
m2: Bioturbation ~ Distance + Site + Type + (1 | repeats) +
m2:   Distance:Site + Distance:Type + Site:Type
model.lmer: Bioturbation ~ Distance * Site * Type + (1 | repeats)
              Df    AIC    BIC logLik Chisq Chi Df Pr(>Chisq)
m2              9 1566.7 1593.2 -774.34
model.lmer     10 1558.6 1588.0 -769.28 10.106      1 0.001478 **
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

```



Model fitting for earthworms. Bioturbation is response variable , with soil moisture and soil type as explanatory variables (generalized linear mix effect model)

```
> newsoiltype<-SoilType
> levels(newsoiltype)
[1] "Clay_Loam"      "Loam_Sandy"      "Sandy_Clay_Loam" "Sandy_Loam"
[5] "Silty_Clay"     "Silty_Clay_Loam"
> levels(newsoiltype) [c(2,4)]<-"Sandy"
>
l1<-lmer(Bioturbation~Moisture*newsoiltype+(1|repeats),family=quasipoisson,REML=FALSE)
> summary(l1)
Generalized linear mixed model fit by the Laplace approximation
Formula: Bioturbation ~ Moisture * newsoiltype + (1 | repeats)
  AIC   BIC logLik deviance
 1503 1538 -739.3   1479
Random effects:
Groups   Name          Variance Std.Dev.
repeats (Intercept) 0.99858 0.99929
Residual                0.28548 0.53431
Number of obs: 140, groups: repeats, 20
```

Fixed effects:

| | Estimate | Std. Error | t value |
|-------------------------------------|----------|------------|---------|
| (Intercept) | 3.71238 | 0.72606 | 5.113 |
| Moisture | 0.09667 | 0.06408 | 1.509 |
| newsoiltypeSandy | -8.10221 | 0.87789 | -9.229 |
| newsoiltypeSandy_Clay_Loam | -2.63016 | 0.94386 | -2.787 |
| newsoiltypeSilty_Clay | 0.12614 | 0.92855 | 0.136 |
| newsoiltypeSilty_Clay_Loam | -3.00248 | 1.02366 | -2.933 |
| Moisture:newsoiltypeSandy | 0.57857 | 0.08222 | 7.037 |
| Moisture:newsoiltypeSandy_Clay_Loam | 0.20921 | 0.06910 | 3.028 |
| Moisture:newsoiltypeSilty_Clay | -0.13091 | 0.06565 | -1.994 |
| Moisture:newsoiltypeSilty_Clay_Loam | 0.41786 | 0.10158 | 4.114 |

>

```
l2<-lmer(Bioturbation~Moisture*SoilType+(1|repeats),family=quasipoisson,REML=FALSE)
```

Warning message:

In mer_finalize(ans) : gr cannot be computed at initial par (65)

```
> anova(l1,l2)
```

Data:

Models:

```
l1: Bioturbation ~ Moisture * newsoiltype + (1 | repeats)
```

```
l2: Bioturbation ~ Moisture * SoilType + (1 | repeats)
```

| | Df | AIC | BIC | logLik | Chisq | Chi | Df | Pr(>Chisq) |
|--|----|-----|-----|--------|-------|-----|----|------------|
|--|----|-----|-----|--------|-------|-----|----|------------|

| | | | | | | | | |
|----|----|--------|--------|---------|--|--|--|--|
| l1 | 12 | 1502.6 | 1537.9 | -739.31 | | | | |
|----|----|--------|--------|---------|--|--|--|--|

| | | | | | | | | |
|----|----|--|--|--|--|--|---|--|
| l2 | 14 | | | | | | 2 | |
|----|----|--|--|--|--|--|---|--|

```
> levels(newsoiltype)
```

```
[1] "Clay_Loam" "Sandy" "Sandy_Clay_Loam" "Silty_Clay"
```

```
[5] "Silty_Clay_Loam"
```

```
> levels(newsoiltype)[c(1,3,5)]<-"Loam"
```

>

```
l2<-lmer(Bioturbation~Moisture*newsoiltype+(1|repeats),family=quasipoisson,REML=FALSE)
```

```
> anova(l1,l2)
```

Data:

Models:

```
l2: Bioturbation ~ Moisture * newsoiltype + (1 | repeats)
```

```
l1: Bioturbation ~ Moisture * newsoiltype + (1 | repeats)
```

```

      Df   AIC   BIC logLik Chisq Chi Df Pr(>Chisq)
12  8 1501.5 1525.0 -742.75
11 12 1502.6 1537.9 -739.31 6.8779    4    0.1425
> l3<-update(l2,~.-Moisture:newsoiltype)
> anova(l2,l3)
Data:
Models:
l3: Bioturbation ~ Moisture + newsoiltype + (1 | repeats)
l2: Bioturbation ~ Moisture * newsoiltype + (1 | repeats)
      Df   AIC   BIC logLik Chisq Chi Df Pr(>Chisq)
13  6 1592.2 1609.9 -790.12
12  8 1501.5 1525.0 -742.75 94.748    2 < 2.2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
> summary(l2)
Generalized linear mixed model fit by the Laplace approximation
Formula: Bioturbation ~ Moisture * newsoiltype + (1 | repeats)
      AIC   BIC logLik deviance
1501 1525 -742.7    1485
Random effects:
Groups   Name          Variance Std.Dev.
repeats (Intercept) 0.97545  0.98765
Residual                0.23472  0.48448
Number of obs: 140, groups: repeats, 20

Fixed effects:
              Estimate Std. Error t value
(Intercept)    1.66436    0.38136   4.364
Moisture        0.30132    0.02064  14.599
newsoiltypeSandy -6.25264    0.61786 -10.120
newsoiltypeSilty_Clay 2.17439    0.68731   3.164
Moisture:newsoiltypeSandy 0.37248    0.05122   7.273
Moisture:newsoiltypeSilty_Clay -0.33569    0.02437 -13.773

Model fitting for earthworms. Bioturbation is response variable, with soil moisture and drainage time as explanatory variables (generalized linear mix effect model)
>
d1<-lmer(Bioturbation~Moisture*DrainageTime+(1|repeats),family=quasip

```

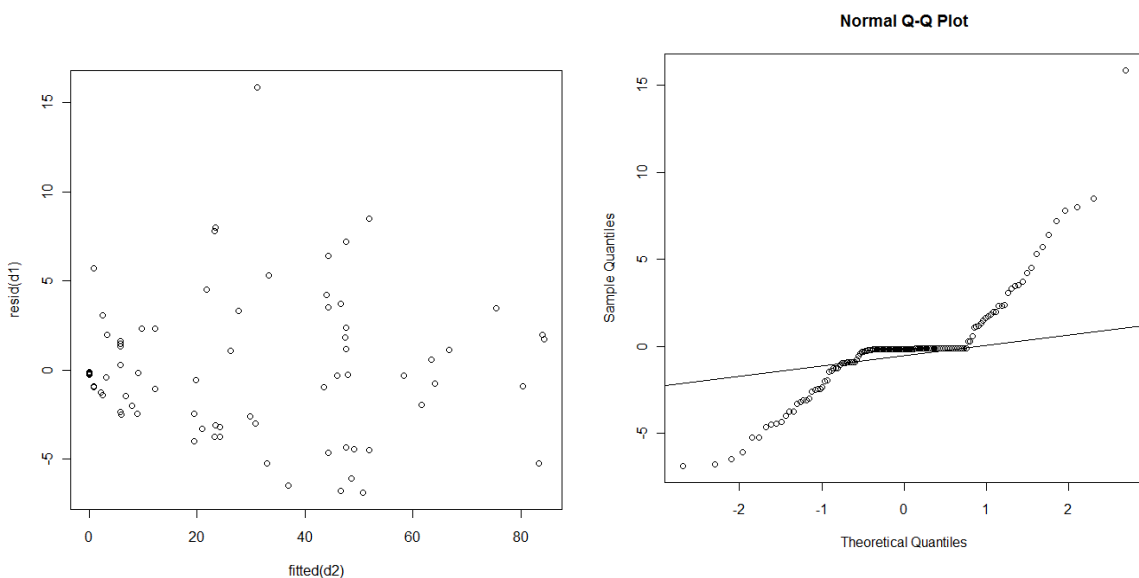


```

oisson,REML=FALSE)
>
d2<-lmer(Bioturbation~Moisture+DrainageTime+(1|repeats),family=quasipo
oisson,REML=FALSE)
> anova(d1,d2)
Data:
Models:
d2: Bioturbation ~ Moisture + DrainageTime + (1 | repeats)
d1: Bioturbation ~ Moisture * DrainageTime + (1 | repeats)
  Df   AIC   BIC logLik Chisq Chi Df Pr(>Chisq)
d2  6 1574.5 1592.2 -781.27
d1  8 1394.6 1418.2 -689.32 183.91    2 < 2.2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
> summary(d1)
Generalized linear mixed model fit by the Laplace approximation
Formula: Bioturbation ~ Moisture * DrainageTime + (1 | repeats)
  AIC   BIC logLik deviance
1395 1418 -689.3    1379
Random effects:
Groups   Name      Variance Std.Dev.
repeats (Intercept) 6.56166  2.56157
Residual              0.36142  0.60118
Number of obs: 140, groups: repeats, 20

Fixed effects:
              Estimate Std. Error t value
(Intercept)      1.14665    0.62592   1.832
Moisture          -0.28573    0.02379  -12.012
DrainageTimeMedium -2.51085    0.14187  -17.698
DrainageTimeSlow  -2.89348    0.14657  -19.741
Moisture:DrainageTimeMedium 0.44557    0.02916  15.278
Moisture:DrainageTimeSlow  0.71566    0.03302  21.670

```



Model fitting for earthworms. Moisture is response variable, with distance to edges sites and habitat type as explanatory variables (generalized linear mix effect model)

```

>
lme1<-lme(Moisture~Distance*Site*Type,random=~1|repeats,method="ML")
> lme2<-update(lme1,~-Distance:Site:Type)
> anova(lme1,lme2)
      Model df      AIC      BIC    logLik  Test  L.Ratio p-value
lme1     1 10 451.2601 480.6765 -215.6300
lme2     2  9 449.5340 476.0088 -215.7670 1 vs 2 0.2739331  0.6007
> lme3<-update(lme2,~-Distance:Site)
> anova(lme2,lme3)
      Model df      AIC      BIC    logLik  Test  L.Ratio p-value
lme2     1  9 449.5340 476.0088 -215.7670
lme3     2  8 450.8391 474.3723 -217.4196 1 vs 2 3.305162  0.0691
> lme4<-update(lme3,~-Distance:Type)
> anova(lme3,lme4)
      Model df      AIC      BIC    logLik  Test  L.Ratio p-value
lme3     1  8 450.8391 474.3723 -217.4196
lme4     2  7 449.4227 470.0142 -217.7114 1 vs 2 0.5835776  0.4449
> lme5<-update(lme4,~-Site:Type)
> anova(lme4,lme5)
      Model df      AIC      BIC    logLik  Test  L.Ratio p-value
lme4     1  7 449.4227 470.0142 -217.7114
lme5     2  6 454.2366 471.8865 -221.1183 1 vs 2 6.813883  0.009
> summary(lme4)
Linear mixed-effects model fit by maximum likelihood
Data: NULL
      AIC      BIC    logLik
449.4227 470.0142 -217.7114

Random effects:
Formula: ~1 | repeats
      (Intercept) Residual
StdDev:  1.130608 0.968418

Fixed effects: Moisture ~ Distance + Site + Type + Site:Type
      Value Std.Error DF  t-value p-value
(Intercept) 1.7653571 0.7889464 120  2.237613  0.0271

```

```

Distance      0.0269643 0.0191348 15  1.409178  0.1792
SiteMA        -0.8800000 0.7653904 15 -1.149740  0.2683
TypeGrass     -2.5742857 0.7653904 15 -3.363363  0.0043
SiteMA:TypeGrass 3.0285714 1.0824256 15  2.797949  0.0135

```

```
> lme5<-update(lme4,~.-Distance)
```

```
> anova(lme4,lme5)
```

| Model | df | AIC | BIC | logLik | Test | L.Ratio | p-value |
|-------|----|-----|----------|----------|-----------|---------|------------------------|
| lme4 | 1 | 7 | 449.4227 | 470.0142 | -217.7114 | | |
| lme5 | 2 | 6 | 449.3828 | 467.0326 | -218.6914 | 1 vs 2 | 1.960068 0.1615 |

```
> summary(lme5)
```

Linear mixed-effects model fit by maximum likelihood

Data: NULL

| | AIC | BIC | logLik |
|--|----------|----------|-----------|
| | 449.3828 | 467.0326 | -218.6914 |

Random effects:

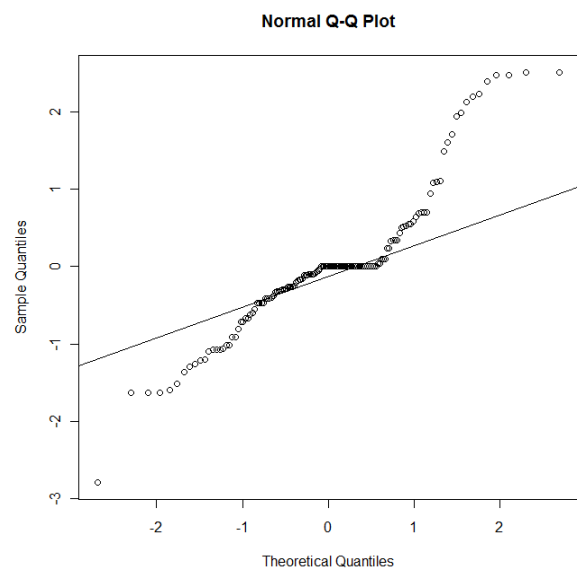
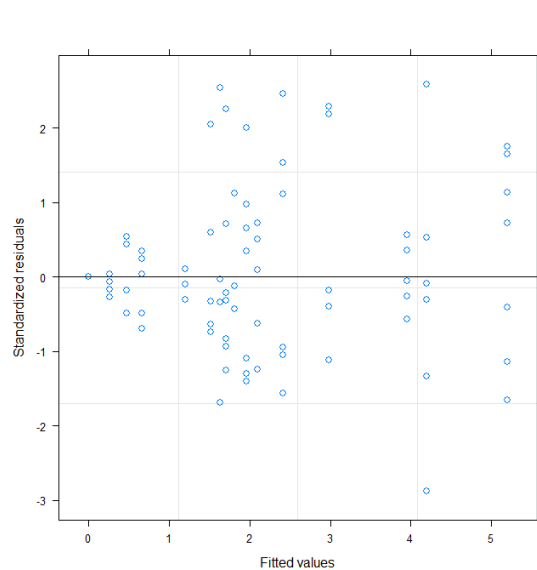
Formula: ~1 | repeats

(Intercept) Residual

StdDev: 1.193184 0.968418

Fixed effects: Moisture ~ Site + Type + Site:Type

| | Value | Std.Error | DF | t-value | p-value |
|------------------|-----------|-----------|-----|-----------|---------------|
| (Intercept) | 2.574286 | 0.5663001 | 120 | 4.545798 | 0.0000 |
| SiteMA | -0.880000 | 0.8008693 | 16 | -1.098806 | 0.2881 |
| TypeGrass | -2.574286 | 0.8008693 | 16 | -3.214364 | 0.0054 |
| SiteMA:TypeGrass | 3.028571 | 1.1326002 | 16 | 2.673999 | 0.0166 |



Model fitting for earthworms. Moisture is response variable, with distance to edges sites and habitat type as explanatory variables including site 1(ES) (generalized linear mix effect model)

```
> lme1<-lme(Moisture~Site,random=~1|repeats)
> summary(lme1)
Linear mixed-effects model fit by REML
Data: NULL
      AIC      BIC    logLik
948.987 965.6505 -469.4935

Random effects:
Formula: ~1 | repeats
      (Intercept) Residual
StdDev:   4.173204 1.784136

Fixed effects: Moisture ~ Site
              Value Std.Error  DF   t-value p-value
(Intercept)  3.275714  1.336801 180  2.4504130  0.0152
SiteGT       -1.988571  1.890522  27 -1.0518637  0.3022
SiteMA       -1.354286  1.890522  27 -0.7163554  0.4799
```