Two aspects of earthworm bioturbation: Crop residue burial by foraging and surface casting in no-till management

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Abstract

In no-till agroecosystems, presence of the earthworm *Lumbricus terrestris* L. can be a key driver in the replenishment of soil organic matter stocks post-harvest, through surface residue foraging and incorporation. The impact on such systems under different climatic conditions is, however, still unquantified. A field experiment was designed to determine incorporation of cereal harvest residues at three no-till agricultural sites in boreal conditions (SW Finland) focusing on *L. terrestris* impacts over the period from autumn harvest to spring sowing. Either spring barley, wheat or oats were cultivated at the sites. Following the harvests, representative masses of residues were applied on small experimental plots (0.25 m^2) with cleaned soil surfaces in areas of inherently high (LT+: 10.6 ± 2.1 ind. 0.25 m^{-2}) and low (LT-: 1.8 ± 0.7 ind. 0.25 m^{-2}) *L. terrestris* density within the fields. Residues were covered with metal mesh caging and left until spring sowing, when changes in residue mass were recorded and plots sampled for earthworms. The reduction of straw residue mass varied between sites, from no difference between the LT+ and LT- treatments to 19% and 59% higher mass reduction in LT+. Amount of earthworm castings on the residues was also quantified and findings indicated a positive correlation with earthworm (also endogeic) density. For *L. terrestris*, earthworm species abundance relationships indicated competitive interaction with epigeics and positive interaction with endogeics. Results showed that *L. terrestris* foraging can enhance the incorporation of cereal surface residues outside of the boreal growing season and that earthworm surface casting also has a role in residue burial. However, the increase of incorporation by *L. terrestris* activity, interrupted by winter conditions, was moderate and did not lead to marked exposition of soil surface by experimental end, even at those plots with the highest *L. terrestris* foraging. The incorporation rate estimates may have been unrepresentative due to the exceptionally late harvest during the study period. Investigations covering the whole year from multiple growing seasons are needed for a comprehensive assessment of earthworm impacts on crop surface residue dynamics.

Keywords: *Lumbricus terrestris*, cereal residues, bioturbation, casting, residue burial

Introduction

The earthworm *Lumbricus terrestris L.*, commonly present in temperate and boreal agricultural soils, can be a key species influencing residue incorporation in no- or reduced-tillage agroecosystems where their abundance is often high [1], with densities up to 30 *L. terrestris* middens m^{-2} measured in Boreal no-till fields [2] (a midden is a mixed heap of collected litter and surface casting at the opening of the permanent burrow of this species). *L. terrestris* is a deep burrowing epi-anecic species, with the physical ability to forage coarse organic matter from the surface into its middens and burrows for subsequent consumption [3-5]. *L. terrestris* foraging behaviour has unique effects on surface organic matter distribution in reduced tillage agroecosystems, where addition of the species can significantly alter the spatial distribution of mulches through aggregation within the middens [6]. Such redistribution of organic matter can have implications for soil surface properties, where increased exposure of the soil surface can increase soil crusting [7]. No-till environments with surface organic matter application are likely to enhance *L. terrestris* populations, where easily assimilated substances such as cereal residues can increase growth rate to maturity, further accelerating decomposition and residue burial [8].

The substantial effect which earthworm populations can have on the incorporation of organic matter in agroecosystems was demonstrated by Bohlen et al, [9], who estimated that 840 kg ha^{-1} yr^{-1} of surface applied corn residues could be incorporated by earthworms under a temperate climate. In their field experiment, the remaining 10% of surface litter was present in *L. terrestris* middens indicating that the disappearance of litter was mediated by foraging of this species. These results were supported by Shuster et al. [6], where inoculations of *L. terrestris* decreased surface residue cover compared with non-inoculated enclosures. The corn fields used in both studies underwent spring tillage management, whereas under no-tillage systems, *L. terrestris* densities and consequently the residue mass incorporated could be even higher. For instance, in a global study synthesis where different reduced tillage systems were compared with ploughing, no-till was the most favourable management for earthworms [1]. In biomass, to which *L. terrestris* contributes strongly due to its large size, no-till was at least twice as beneficial as the different reduced tillage regimes studied. In field mesocosms under conservation tillage, the decomposition rate of straw was higher in the presence of *L. terrestris* compared with treatments with subsurface feeding earthworm *Aporrectodea caliginosa*, collembolans (*Folsomia candida)* and nematodes (*Aphelenchoides saprophilus)* [10-11]. From research on an extensively managed temperate grassland, it is known that *L. terrestris* activity and burrows

constitute a rapid way for fresh carbon (C) transport into deep soil horizons although that does not substantially increase subsoil carbon stocks due to rapid C turnover [12].

In addition to foraging and burial of surface residues, casting on the soil surface and on the residues by earthworms can have implications for organic matter burial and subsequently on decomposition and the assimilation of nutrients within agroecosystems. Earthworm casts are granular aggregates high in soil porosity and moisture [13], have high nutrient concentrations [14] and microbial activity [15-16] which enhances decomposition of integral organic matter [17]. Over time, surface casting by *L. terrestris* and other earthworms may enhance residue burial and decomposition alongside burial by foraging. It was recently estimated that in temperate no-till field soil, the total earthworm cast production was 549 g dwt m^{-2} yr^{-1} which was four times higher than in mouldboard ploughed soil [18]. A main contributor to the high bioturbation under no-till was the elevated abundance of *L. terrestris.* The rate of surface casting varies greatly, but annual estimates are typically tens of tonnes of castings per hectare [19]. Although the role of earthworm casts on organic matter decomposition and nutrient cycling have been widely studied [13, 20-21], exploration of surface casting as a form of residue burial is, to our knowledge, yet to be fully investigated in field settings.

The importance of *L. terrestris* for residue dynamics in northern no-till farming, where winter conditions interrupt all earthworm surface activity, has remained unstudied. To address this knowledge gap, a field experiment was designed to explore the effects of *L. terrestris* density on the incorporation rate of cereal residues between autumn harvest and spring sowing in boreal no-till farming. Focus on this period was to learn the extent that *L. terrestris* foraging can diminish the amount of surface residue prior to spring sowing where ample residue cover, useful for erosion control outside of the growing season, can physically hamper sowing and constitute a source of *Fusarium* infection for the following crop. Specific aims of the study were: (i) To investigate incorporation rate of harvest residues in no-till fields relative to *L. terrestris* abundance, the main hypothesis being an increased rate with species presence; (ii) To study the importance of surface casting by *L. terrestris* and other earthworms on residue burial, and; (iii) To relate *L. terrestris* presence with densities of other ecological groups of earthworms.

Materials and Methods

Study sites

The study was conducted in south-western Finland over the winter of 2015-2016 on three direct drilled (no-till) cereal field sites with differing soil properties. These were two of Luke's (Natural Resources Institute Finland) experimental fields in Jokioinen (Ojainen and Kotkanoja sites), and a no-till field under practical cultivation at Kiikoinen (Tab. S1).

At the Ojainen site, different tillage methods and direct drilling have been compared since 1999, mainly under spring cereal cultivation. The soil is a sandy clay and individual study plots measure 18 m x 40 m. Two direct drilled plots were selected, based on all earthworm and *L. terrestris* midden abundance records collected over several years (no other residue-foraging and midden-producing earthworm species were present at this or the two other study sites). One plot contained *L. terrestris* (LT+), whilst this species was entirely absent from the other (LT-). This difference was possibly due to initial spatial variation in the field and/or varying immigration rates of *L. terrestris* into the different parts of the field over the course of the experiment. The distance between LT+ and LT- plots was approximately 50 m. Based on earlier observations, other earthworm species present were *Aporrectodea caliginosa* (Sav.), *A. rosea* (Sav.) and *Lumbricus rubellus* (Hoffm.) (Luke, unpubl.).

Kotkanoja site is an experimental leaching field established in 1975 on heavy clay soil with four adjacent 33 m x 140 m field strips [22]. *L. terrestris* was initially absent but introduced using the Earthworm Inoculation Unit technique [23] at the up-slope end of the field in autumn 1996 [24]. Through gradual population growth and spread, gradients of *L. terrestris* abundance have been formed in two direct drilled strips of the field, separated by a ploughed strip. Prior to this study, the whole site had been under spring cereal cultivation from 1996, except for a set-aside period during 2002-2008. Based on field observations of *L. terrestris* distribution in 2013 [25], areas of high population density (LT+) and areas without *L. terrestris* (LT-), i.e., beyond the leading edge of dispersal, were chosen from both direct drilled strips. The distance between LT+ and LT- areas was 100 m. Other earthworm species in the field are *A. caliginosa*, *A. rosea*, *Lumbricus castaneus* (Sav.), *L. rubellus* and *Dendrobaena octaedra* (Sav.) [25].

The Kiikoinen site is an arable field on loam soil under long term direct drilling of spring cereals. For almost two decades, this field had been under direct drilling with some intermittent years of shallow disc harrowing (5 cm deep, the most recent disk harrowing conducted in 2013). After the harvest in

late October 2015, the abundance of *L. terrestris* was surveyed in the field by observing the spatial variation of midden density on the soil surface. Based on these observations, areas of high (LT+) and low (LT-) abundance were selected, separated by 50 m, with LT- situated at a slightly sloping part of the field. There was no prior information on the species composition of the earthworm community.

Weather data for the sites were obtained from the Finnish Meteorological Institute's (FMI) open data sources. For Ojainen and Kotkanoja, data from of FMI's Jokioinen Observatory was used.For Kiikoinen, data was from FMI's Kokemäki/Tulkkila weather station (Tab. S1).

Experimental design

Start of the experiment. The experiment was set up as soon after autumn harvest as feasibly practical (Tab. S1). Due to exceptional growth and harvest conditions in 2015, this was unusually late at all three sites: for instance, at Ojainen and Kotkanoja, the harvest dates were 28th and 29th September, respectively, while the median harvest date during the preceding five years (2010-2014) had been 3rd and 4th September.

Experimental design was similar on all sites except that the number of treatment replicates varied. Plot positions were first marked within LT+ and LT- areas. At Ojainen, five plots, separated by 5 m, were positioned along linear transects through the two treatments. At Kotkanoja, four plots were marked in rectangular configurations with minimum plot interval of 3.5 m in both LT+ and LT- areas in both direct drilled strips (treatment total N=8). At Kiikoinen, five plots with a minimum distance of 5 m were marked in an irregular configuration within the two areas.

Studies of earthworm impacts on litter and residue dynamics typically use litter bags filled with residue of standard size and mass, with mesh sizes either allowing or excluding earthworm access [26-27]. Despite the obvious advantages of litter bags, we eschewed this approach by providing residues freely on the soil surface. The rationale was that even if the mesh size would allow the entrance of *L. terrestris,* which do not consume residues *in situ* on the soil surface, they would find it difficult to effectively grab and remove residues from a mesh bag. This is supported by our unpublished field test at a separate LT+ area, which showed that the incorporation rate of 3 cm straw confined in a mesh bag with 10 mm mesh size was 18% less compared with similar straw available freely on the soil surface. The potential for underestimation of residue incorporation was emphasized in the present experiment because we wanted to study the impact on residues representing the complete size

variation as spread on the soil surface by the combine harvester. The greatest lengths of cereal straw and leaves (>10 cm) would have been particularly difficult for *L. terrestris* to remove from litter bags.

At each plot position, a square of 0.25 m^2 was delineated with a wooden frame. The stubble (and weeds where present) was cut close to the soil surface and removed. The harvest residue was then manually collected from the soil surface into paper bags by hand and using forceps, carefully avoiding the inclusion of soil. Collection only left the smallest residues, such as awns and husks on the soil surface (Fig. S1A). If moss was present on the soil surface, it was removed and discarded. After clearance, plots were covered with 50 cm x 50 cm metal mesh cages, with a height of 5 cm and mesh size of 8 mm. Cages were firmly attached to the ground by two metal rods pushed through the mesh at opposite corners. Simultaneously, a large additional batch (approx. 2 kg) of residues was collected from areas close to the experimental plots.

Plot residue samples were taken to the laboratory and kept in open paper bags for four days at +60 °C. The additional collected residue was dried in the same way. The plot residue samples were then weighed and mean dry mass of residue (g dwt 0.25 m^{-2}) for each site was determined. A corresponding amount of the separately collected and dried residue from the site was weighed in paper bags and taken to the field for the start of the experiment (Tab. S1). An estimate for the ash free dry weight (AFDW) was determined from a milled residue samples (first dried at 105 °C and subsequently ashed at 550 °C; [28-29].

In the field, mesh cages were removed, and the determined amount of dried residue added evenly on the soil surface (Tab. S1). The plot was then re-covered with a cage and a coded tag attached. Each plot position was marked with a 1 m tall pole adjacent to the cage to allow location during times of snow cover, if necessary.

End of the experiment. The experiment was terminated in the spring of 2016, as close as possible before sowing of the fields (Tab. S1). For each plot, the mesh cage was removed and residues remaining on the soil surface collected carefully into paper bags. The technique and accuracy of collection was closely aligned to the initial clearing of the plots in the autumn (Fig. S2). If pieces of residue were partially buried into *L. terrestris* burrows, only the above ground parts were collected by cutting. In the case of middens, which were counted, “trimming” of the midden residue with scissors was necessary. To guarantee equal efficiency of sampling, residue collection was conducted by the same researchers (authors), simultaneously collecting from a particular plot. To document consistency

in residue collection at experimental end, images were taken of every plot at two points throughout the sampling process (1 – residue before removal; 2 – soil surface after residue removal; Fig. S2).

In the laboratory, the residue samples were dried at 60 °C for four days. Soil crumbs attached to the residues were subsequently removed from the samples by gentle moving and shaking the residue on a 2 mm mesh and collecting the detached soil. Brushes and forceps were used to remove crumbs that remained attached to the residue thereafter. Typically, the largest crumbs removed from residues were particularly easy to recognize as earthworm castings (Fig. S3). Total mass of soil detached from the residues was determined for each sample. The dry mass (40 ^{o}C for 48 hours) of the cleaned residue was then determined. Ash Free Dry Weight (AFDW) of the residue was determined (550 ^{o}C for 5 hours) for each plot from a milled residue sample and the mass of the remaining residue in the plot converted to AFDW.

Earthworm sampling. Immediately after residue collection, earthworms were sampled from within the plots, delineated by a metal frame hammered into the soil. A mustard suspension (60 g mustard powder thoroughly mixed in 10 L of water) was poured on to the plot [30]. The amount of suspension used depended on infiltration rate, maximally 20 L for the 0.25 m^2 area was applied. In many cases the emergence of *L. terrestris* – the main target of the sampling – was slow which is typical in local spring conditions and therefore collection of earthworms was continued for up to 50 minutes. Earthworms were put into fresh tap water and were separated into three classes: *L. terrestris* (juveniles identified by the unique pigment gradient on the dorsal side), epigeic earthworms (small to medium sized, uniformly darkly pigmented individuals) and endogeic earthworms (unpigmented specimens). The mass of *L. terrestris* individuals was determined with a field balance. For epigeic and endogeic earthworms, only the individual count was recorded.

Environmental conditions

Soil temperature (0-7 cm) and moisture (0-15 cm; TDR-measurement) during earthworm sampling was recorded each day to verify that sampling was done under conditions favorable for earthworm activity in the topsoil. The ranges of temperatures and soil moisture percentages, respectively, for the three sites were: Ojainen, 7.6-9.8 °C, 35.2-48.2%; Kotkanoja, 8.1-11.6 °C, 37.2-51.8%; Kiikoinen 14.0-15.2 °C, 24.9-38.4%. Conditions at all sites were therefore suitable for successful earthworm extraction.

Temperature and precipitation over the experiment and the averages of the reference period are shown for Jokioinen in Fig. S4. Over the experimental period, the number of days with minimum temperature > 0°C was 60 -73 days at the sites (highest at Kiikoinen), while the period of permanent snow cover was practically equal at the sites (Tab. S1).

Statistical analysis

To evaluate the success at assigning the experimental plots to LT+ and LT- treatments, and to compare *L. terrestris* density, biomass and midden counts within sites, the abundances for each study site were compared with a one-way ANOVA, by first assuring that assumptions of normality and equal variances were met. Where data did not follow normal distribution, non-parametric Mann-Whitney U tests were applied to compare the treatments within a site. Reduction in residue mass was converted into a percentage for each plot. A one-way ANOVA was applied to study the effect of *L. terrestris* density (LT+ and LT-) on residue mass reduction at each site. Where data did not follow a normal distribution, non-parametric Mann-Whitney U tests were again applied. Results were also analysed as continuous data, where multiple linear regressions were applied to study how different *L. terrestris* abundance indicators and field site explained the changes in residue mass. The relationship of *L. terrestris* density with epigeic and endogeic earthworms was assessed by Spearman's correlation coefficient. Statistical analyses used SPSS v28 software.

Results

L. terrestris abundance in LT+ and LT- areas

For each site, all five indicators of *L. terrestris* abundance were higher in LT+ than in LT- plots ($p < 0.001$; Tab. 1) indicating successful assignment of plots in the treatments. However, the sites differed with Ojainen having no *L. terrestris* at all in LT-, Kotkanoja having some individuals and Kiikoinen with clearly the highest relative individual counts in LT-. The total *L. terrestris* density at Kiikoinen was high compared with the other two sites (Tab. 1) due to an abundance of juveniles, whereas Kotkanoja and Ojainen had a larger proportion of adults.

Residue mass reduction rate

The highest overall decline in surface residue mass was recorded at the Ojainen site, with the rate intermediate at Kotkanoja and lowest at Kiikoinen (Fig. 1). At Ojainen and Kotkanoja sites, the mean

297 reduction rate was significantly higher in LT+ treatments compared with LT- treatments (Fig. 1; one-
298 way ANOVA; $p < 0.05$): at Ojainen the rate at LT+ was 19% higher than in LT- (means: LT+, 29.6% vs.
299 LT-, 24.8%) and at Kotkanoja 59% higher than at LT- (means: LT+, 16.7% vs. LT-, 10.5%). At Kiikoinen
300 the mass decline rates were equally low in both treatments.
301
302 The multiple regression model for surface residue decline rate with *L. terrestris* density and site as
303 independent variables was statistically significant ($F_{2, 33} = 74.74$, $p < 0.001$, $R^2 = 0.819$). The decline
304 rate increased significantly with increasing density of *L. terrestris* and was site-dependent (Tab. 2): the
305 rate increase was obvious at Ojainen and Kotkanoja sites but not at Kiikoinen (Fig. 2).
306
307 *Surface casts on residues*
308
309 At Kiikoinen, the mean dry mass of soil removed from residues was 52% higher in LT+ compared with
310 LT- plots (one way ANOVA; $p < 0.05$; Fig. 3). At the two Jokioinen sites there were no corresponding
311 differences between the treatments, but the total soil removed at Kotkanoja was generally higher
312 than at Ojainen. Apart from *L. terrestris*, endogeic earthworm species likely contributed to the casting
313 on surface residues. The highest endogeic densities were recorded at Kiikoinen (Fig. 4B) where means
314 in LT+ and LT- were 25 ± 3 and 11 ± 3 ind. 0.25 m^{-2} respectively. No epigeic species were present at
315 this site. At the end of the Kiikoinen experiment, abundance of surface castings not associated with
316 middens was recorded suggesting endogeic origin (also by appearance Fig. S3).
317
318 The multiple regression model for mass of soil removed from residues was statistically significant ($F_{2,}$
319 $_{33} = 76.70$, $p < 0.001$, $R^2 = 0.823$). The amount of soil removed increased with increasing density of *L.*
320 *terrestris* and the site effect was also significant (Tab. 2). Plots of *L. terrestris* density, endogeic species
321 density and total earthworm density with the dry mass of soil detached from residues show that the
322 mass increased with increasing earthworm density for all three variables (Fig. 4A-C).
323
324 *Species abundance relationships*
325
326 Analysis of covariation between total *L. terrestris* density and total ecological group density indicated
327 a positive correlation between total *L. terrestris* density and total endogeic density (Fig. 5A; $r_s = 0.849$;
328 $p < 0.001$) and negative correlation between *L. terrestris* density with total epigeic density (Fig. 5B, r_s
329 $= -0.517$; $p < 0.001$). All variables describing *L. terrestris* abundance had statistically significant positive
330 correlation with total endogeic density (Tab. 3).

Discussion

Influence of L. terrestris *abundance on decline rate of surface residues*

The results showed that in boreal no-till farming, the presence of *L. terrestris* can notably increase residue incorporation during the period outside of the growing season. There was, however, considerable variation between the experimental sites, ranging from no effect of *L. terrestris* to a 19-59% increase in the decline rate of surface residue mass. Further, despite the impact of *L. terrestris,* the decline of residue mass always remained moderate, and at none of the sites did the residue foraging and incorporation result in discernible exposition of the soil surface by experimental end.

L. terrestris behaviour is affected by light conditions, temperature, and soil moisture [31-33]. In boreal conditions, the autumn season with its dark night periods (for instance at Jokioinen daylength declines from 14.5 hrs in early September to 8.5 hrs in late October), cool air temperatures (Figure S4) together with related moist topsoil conditions define a period of particularly favourable conditions for *L. terrestris s*urface activity. In S-W Finland, this period typically extends from late August to early November. Considering that harvest dates at the study sites were three weeks late compared to a more typical autumn, the most favourable surface foraging period of *L. terrestris* was correspondingly shortened. Therefore, the present estimates for residue mass decline impact by *L. terrestris* may be considerably lower than during an average year. Over the experimental period, the minimum temperature remained above 0°C during a third of the nights only, which must be the definite lower limit for surface activity. This underlines how short the favourable conditions are for earthworm surface foraging outside of the growing season in the prevailing conditions.

Kiikoinen site differed notably from the two others with its small decline in surface residue mass and with no differences in the rate of residue decline between LT+ and LT- treatments despite the high density of juvenile *L. terrestris*. This may have been partly affected by the late harvest date (11-18 days later than in the other sites) shortening further the period of most favourable conditions for surface activity. This might have been compensated by the higher number of experimental days with minimum temperature > 0 °C at Kiikoinen. However, usage of this temperature limit may not capture sufficiently air temperature effects, as *L. terrestris* activity may be significantly lowered already at higher temperatures.

Numerous factors may have contributed to the indiscernible difference between the LT treatments at Kiikoinen. First, there is evidence that oat residues may not be a preferred food source for *L. terrestris*

363 [34] and it has been noted that oat residues can have a negative effect on midden construction [35].
364 The size of residue particles can influence the feeding and decomposition rate of *L. terrestris*, but
365 residue size distribution was not recorded in this study. Positive effects of small particle size on *L.*
366 *terrestris* growth have previously been noticed [36]. The effect was, however, present only when very
367 small residue [< 3 mm] was used, whereas in our case even the smallest residues were more than 1
368 cm long. Further, Kiikoinen had the highest presence of *L. terrestris* at the LT- treatment which may
369 have interfered with the detection of *L. terrestris* effects. Kiikoinen also had the highest proportion of
370 small, juvenile *L. terrestris,* with a biomass less than 1 g, that are known to inhabit sub-surface soil and
371 may not incorporate surface organic matter [37].

372 Foraging of *L. terrestris* is undoubtedly a major factor in the surface residue mass decline at the two
373 Jokioinen sites, where their impact on no-till residue incorporation had also been qualitatively
374 observed over several years preceding the experiment. However, other factors not accounted for
375 here, will have affected the general decline rates and the differences between LT+ and LT- treatments.
376 These include differences in microbial community composition and decomposition rates in addition
377 to the likely differences in surface residue-consuming micro-, meso- and macrofaunal communities of
378 the sites. The cereal species may also differ as a resource base for the soil community as it is known
379 that even the cultivars of the same crop and their combinations may affect earthworm growth [38].
380 Residues of different crops differ anatomically and chemically [39] and in their decomposition rates.
381 The highest residue decline rate was observed at Ojainen site with barley residue. This may relate to
382 the reportedly higher decomposition rate of barley compared with wheat [40-41] which was cultivated
383 at the Kotkanoja site and had an intermediate residue mass reduction rate. We are not aware of any
384 studies where the decomposition rate of oats (the crop at Kiikoinen) has been compared with barley
385 and wheat.

386 *Residue burial by surface casting*

387 More soil was removed from surface residue samples originating from experimental plots with high
388 earthworm abundance. While not all casts were deposited on top of the residue, field observations
389 indicated the importance of the casts in the burial of the residue. Also, the variation between the sites
390 was large and only at Kiikoinen could the phenomenon clearly be related to the LT+ treatment. Whalen
391 et al. [42] recorded that 90% of *L. terrestris* casts are deposited on the soil surface and a higher mass
392 of removed casts at the Kiikoinen site was likely related to relatively high densities of *L. terrestris*.
393 However, in addition to *L. terrestris*, other species may have contributed to soil addition on residues
394 through surface casting. A notable species in this respect is *A. caliginosa* – the most common endogeic
395 species in Finnish arable systems [43] - which commonly cast within their burrow system but also on

396 the soil surface [20, 42, 44-45]. Endogeic species differ in their bioturbation activity [46] and
397 differences in endogeic community composition may have resulted in variation of surface casting
398 activity between the sites. Observations made at experimental end at the Kiikoinen site indicated
399 abundant endogeic surface casting and the high accumulation of casts on the residues will have
400 resulted from combined action of *L. terrestris* and endogeic species.

401 The variation in the rates of casting between the sites was likely affected by variation in their
402 environmental conditions. The two Jokioinen sites were on clay soils and Kiikoinen was on loam. Loam
403 soil is a more favourable environment for earthworms than clays [43, 47-48] and the loam soil may
404 have allowed more extensive burrowing and casting at Kiikoinen. Variation in other soil physical and
405 chemical properties may have also affected the casting rates. However, to our knowledge, the effects
406 of soil properties, such as texture on casting rate, have not been widely studied, unlike its influence
407 on the qualitative properties of the casts (e.g., [49]; but see [50]). The differences between the sites
408 may also have been affected by different exposition of soil surfaces to rain and thaw water eroding
409 the casts.

410 *Covariation of species abundances.*
411
412 The enhanced physical movement of organic matter into the soil profile by *L. terrestris* activity could
413 increase food availability for endogeics [51] and the observed positive correlation of *L. terrestris*
414 abundance with endogeic earthworm density could imply facilitative species interactions. The
415 experimental findings on the inter-specific effects between *L. terrestris* and endogeic species is,
416 however, contrasting. In laboratory cultures there was an indication that the presence of *L. terrestris*
417 adults may facilitate *A. chlorotica* growth to maturity [52] but reduce the growth rate of *A. caliginosa*
418 [53] with negative effects increasing with earthworm density [54].

419 The negative correlation between *L. terrestris* and epigeic earthworm densities could result from the
420 efficient residue collection and incorporation by *L. terrestris* reducing the availability of the litter layer
421 habitat of epigeics [8]. It is, however, also possible that *L. terrestris* populations benefit epigeics
422 through the development of a midden, where previous studies have recorded elevated epigeic
423 densities [53]. A high density of juvenile *L. terrestris* was recorded within LT+ treatments at Kiikoinen
424 which could have increased food competition, where both juvenile *L. terrestris* and epigeics species
425 can forage in *L. terrestris* middens [53]. Due to the low occurrence of epigeic earthworms in the
426 present study, as in many other agroecosystems, a representative impact of *L. terrestris* populations
427 on epigeic earthworms would require a more comprehensive investigation.

Concluding remarks

Studies on soil faunal impacts in plant residue decomposition typically use a method where standard sized plant material is placed in litter bags with varying mesh sizes allowing or preventing the entry and foraging of different sized soil invertebrates (e.g., [26-27, 34, 55-56]). We used a 'free residue' approach where the litter was not confined in bags to allow the analysis of residue removal in a more natural setting, where *L. terrestris* foraging behaviour and the usage of inherent size variation of residue was less compromised. This approach has its shortcomings which include the close contact of the residue with the soil surface complicating the collection of the residue at experimental end and the labour intensity of the collection process. Despite the challenges, we consider that the approach can be useful when the aim is to obtain a realistic measure on the impact of a large, litter-hoarding detritivore such as *L. terrestris* in its natural environments.

The earthworm impact on residue burial occurred predominantly by active foraging and related incorporation, but results suggest that surface casting on residues by *L. terrestris* and other earthworms can also contribute to the phenomenon. The importance of the latter was not quantified in terms of residue burial rate, but it seems reasonable to suggest that along with the foraging-related litter incorporation, casting on residues serves to bring fresh litter into close contact with the soil and may thereby contribute importantly to the initiation of decomposition.

The experiment was conducted outside the boreal growing season which is mostly unsuitable for earthworm surface activity. Maximally, the decline of surface residue over the experiment was approximately one third of the initial mass in treatments where *L. terrestris* was present, the lowest decline rate being less than one tenth of the initial residue mass. Field observations at the two field experiments at Jokioinen over several years preceding the experiment have shown that no accumulation of residues on the soil surface occurs. It is therefore evident that a large proportion of surface residue incorporation and decomposition takes place during the growing season. While the present results likely underestimated the incorporation due to earthworm activity, they may have given a realistic picture of a relatively minor earthworm impact outside of the growing season. This can be taken as positive news for the maintenance of erosion-preventing residue cover on the soil surface outside the growing season. A more comprehensive understanding of bioturbation by earthworms in residue incorporation will require experimentation covering the whole annual cycle from multiple years, and consider the effects of temporal and spatial variation in environmental conditions.

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Tables

Tab. 1. Mean values (± S.E.) of *L. terrestris* abundance indicators at high (LT+) and low (LT-) density plots for each field site. All values are given per 0.25 m^2. Values denoted with a different letter within a site are statistically different at $p < 0.001$ level (one-way ANOVA; df = 1). (ind. = number of individuals, n = number of middens).

L. terrestris	Ojainen		Kotkanoja		Kiikoinen	
	LT+	LT-	LT+	LT-	LT+	LT-
Total density (ind.)	5.0 ± 1.4[a]	0.0[b]	6.5 ± 1.7[a]	0.4 ± 0.3[b]	22.8 ± 2.0[a]	6.0 ± 1.3[b]
Adult density (ind.)	0.8 ± 0.5[a]	0.0[b]	2.0 ± 0.8[a]	0.0[b]	1.8 ± 0.5[a]	0.6 ± 0.4[b]
Juvenile density (ind.)	4.2 ± 1.0[a]	0.0[b]	4.5 ± 1.4[a]	0.4 ± 0.3[b]	21.0 ± 0.5[a]	5.4 ± 1.1[b]
Total fresh mass (g)	5.1 ± 2.4[a]	0.0[b]	9.0 ± 2.9[a]	0.2 ± 0.1[b]	11.1 ± 2.1[a]	3.3 ± 1.3[b]
Midden density (n)	6.6 ± 1.1[a]	0.4 ± 0.2[b]	6.8 ± 0.6[a]	0.3 ± 0.2[b]	3.2 ± 0.6[a]	1.8 ± 0.7[b]

Tab. 2. The results of the multiple regression analyses with the residue decline rate (above) and mass of soil removed from residue (below) as independent variables and *L. terrestris* (L.t.) total density and study site as explanatory variables.

Residue decline rate

Independent variable	Slope	95% CI		t	Sign.
		Lower	Upper		
L.t. total density	.28	.09	.49	2.90	.007
Site	-11.69	-13.77	-9.60	-11.40	<.001
Constant	37.23	33.41	41.05	19.81	<.001

Mass of soil removed

Independent variable	Slope	95% CI		t	Sign.
		Lower	Upper		
L.t. total density	.51	.30	.71	4.20	<.001
Site	6.95	4.78	9.12	6.51	<.001
Constant	-5.85	-9.83	-1.86	-2.99	.005

Tab. 3. Correlation (r_s) between different variables describing *L. terrestris* abundance and endogeic and epigeic earthworm total densities. No other anecic species were recorded in the fields. N=36. Statistically significant correlations are marked with asterisk ($p < 0.05$).

Earthworm Group	*Lumbricus terrestris* factor			
	Total density (ind. 0.25 m^{-2})	Biomass (g 0.25 m^{-2})	Adult density (ind. 0.25 m^{-2})	Juvenile density (ind. 0.25 m^{-2})
Endogeic (ind. 0.25 m^{-2})	0.849*	0.732*	0.56*	0.852*
Epigeic (ind. 0.25 m^{-2})	-0.517	-0.388	-0.334	-0.512

Figure legends

Fig. 1. Mean (± S.E.) reduction in mass of surface residue (% AFDW) at each site in LT+ and LT- areas. For Ojainen and Kiikoinen, N=5; for Kotkanoja, N=8. Statistically significant differences at sites ($p < 0.001$) are represented by different letters.

Fig. 2. Relationship between *L. terrestris* total density (ind. 0.25 m^{-2}) and decline in surface residue mass (% AFDW) at each site. For each site the least squares line has been fitted.

Fig. 3. Mean (± S.E.) dry mass (g) of soil detached from surface residues at experimental end at high and low *L. terrestris* densities for each field. Statistically significant difference between LT+ and LT- at each location is indicated by different letters (one-way ANOVA; $p < 0.05$). N=5 (Ojainen and Kiikoinen); N=8 (Kotkanoja).

Fig. 4. Total *L. terrestris* density (A), total endogeic density (B) and total earthworm density (C) plotted against the dry mass of soil removed (g 0.25 m^{-2}) from remaining surface residue at the end of the experiment.

Fig. 5. Correlation (r_s) between *L. terrestris* density with (A) endogeic species density and (B) epigeic species density (ind. 0.25 m^{-2}) at the end of the experiment.

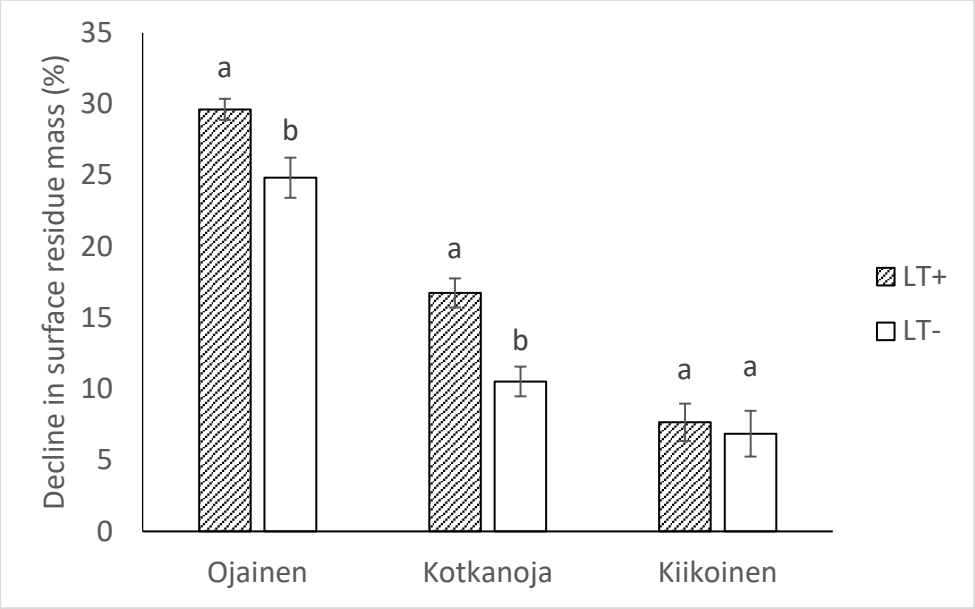

Decline in surface residue mass (%)
35
30
25
20
15
10
5
0
a
b
a
b
a
a
LT+
LT-
Ojainen
Kotkanoja
Kiikoinen

Fig. 1.

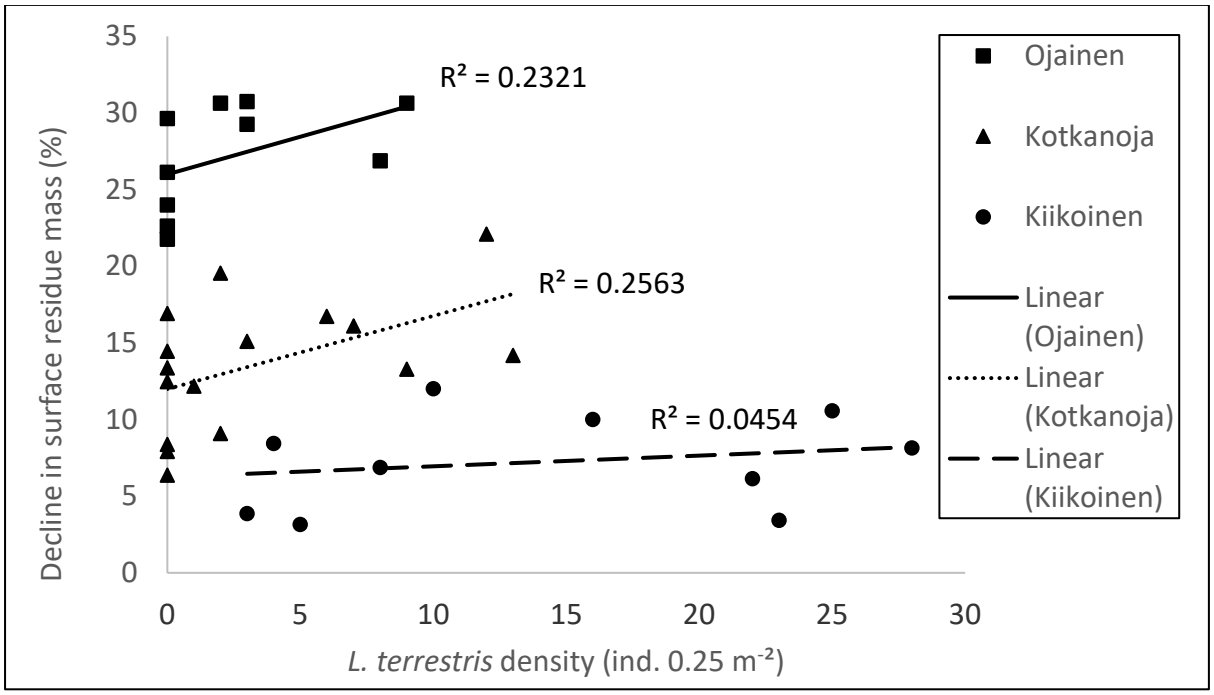

35
30
25
20
15
10
5
0
0
5
10
15
20
25
30
Decline in surface residue mass (%)
L. terrestris density (ind. 0.25 m-2)
R² = 0.2321
R² = 0.2563
R² = 0.0454
Ojainen
Kotkanoja
Kiikoinen
Linear (Ojainen)
Linear (Kotkanoja)
Linear (Kiikoinen)

Fig. 2.

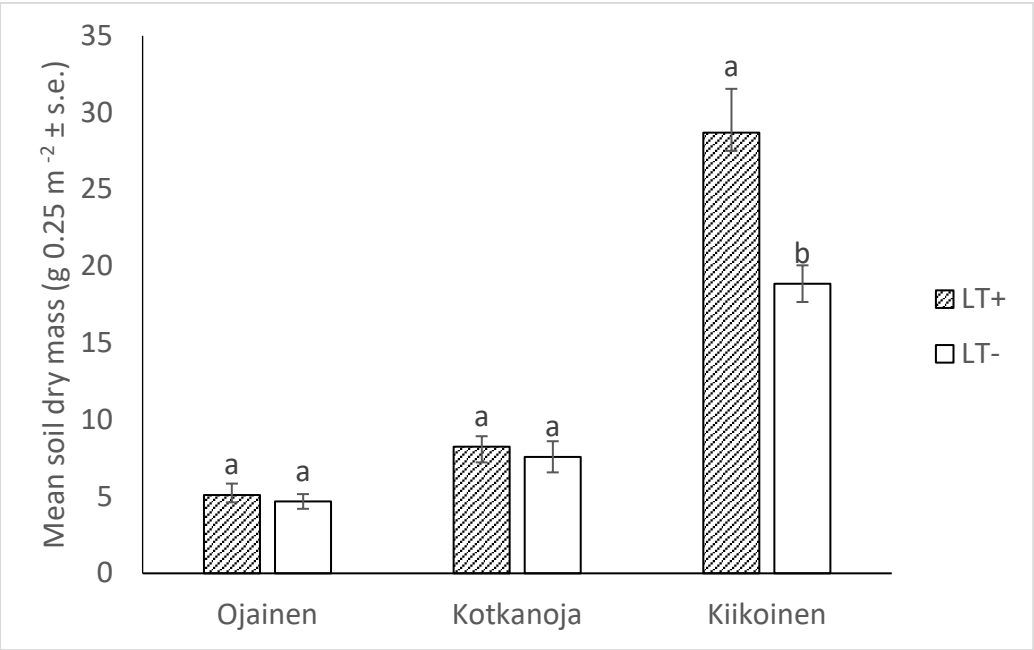

Mean soil dry mass (g 0.25 m -2 ± s.e.)
35
30
25
20
15
10
5
0
a
a
a
a
a
b
LT+
LT-
Ojainen
Kotkanoja
Kiikoinen

Fig. 3.

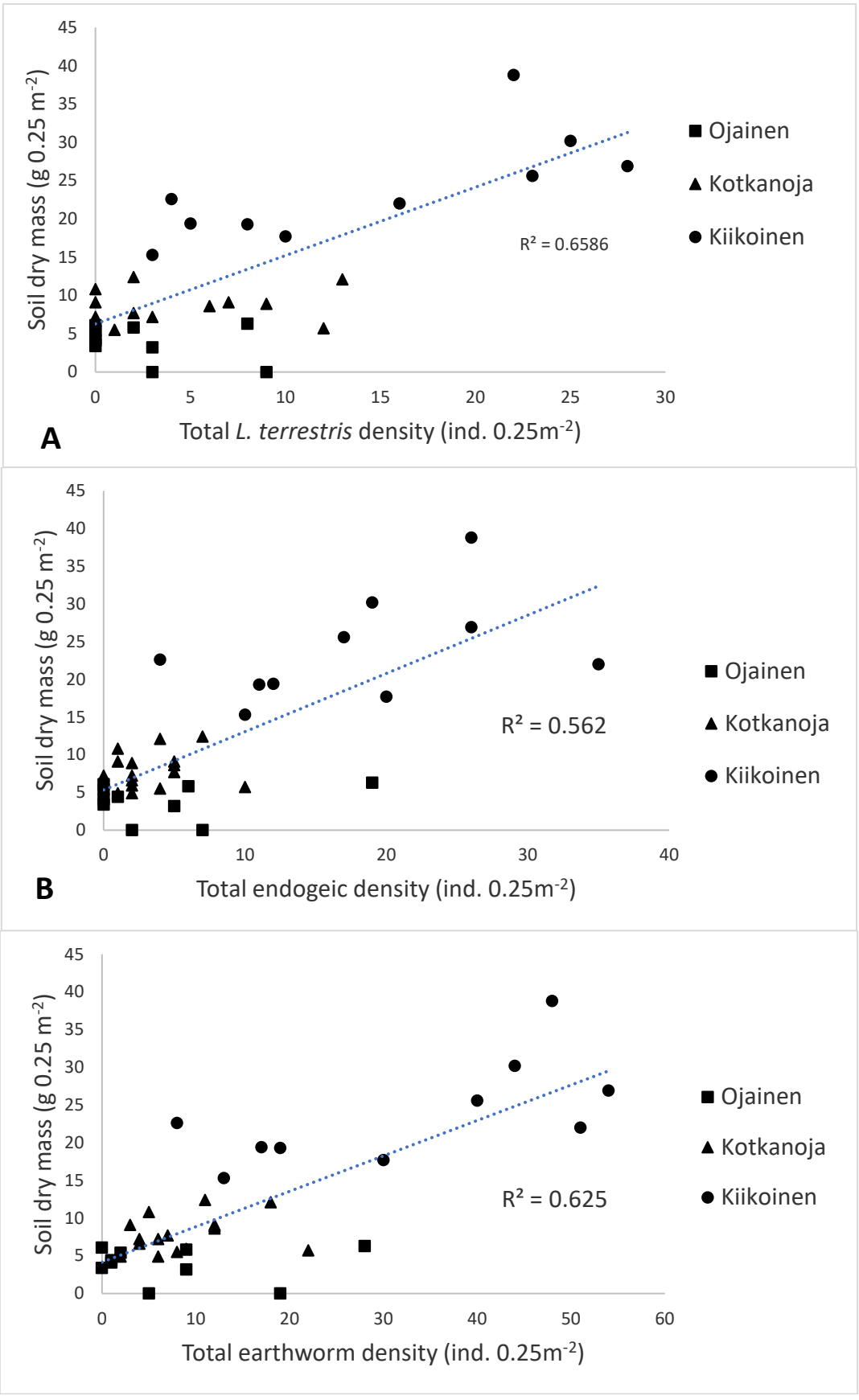

Soil dry mass (g 0.25 m-2)
Total L. terrestris density (ind. 0.25m-2)
R² = 0.6586
Ojainen
Kotkanoja
Kiikoinen
A
Soil dry mass (g 0.25 m-2)
Total endogeic density (ind. 0.25m-2)
R² = 0.562
Ojainen
Kotkanoja
Kiikoinen
B
Soil dry mass (g 0.25 m-2)
Total earthworm density (ind. 0.25m-2)
R² = 0.625
Ojainen
Kotkanoja
Kiikoinen

Fig. 4.

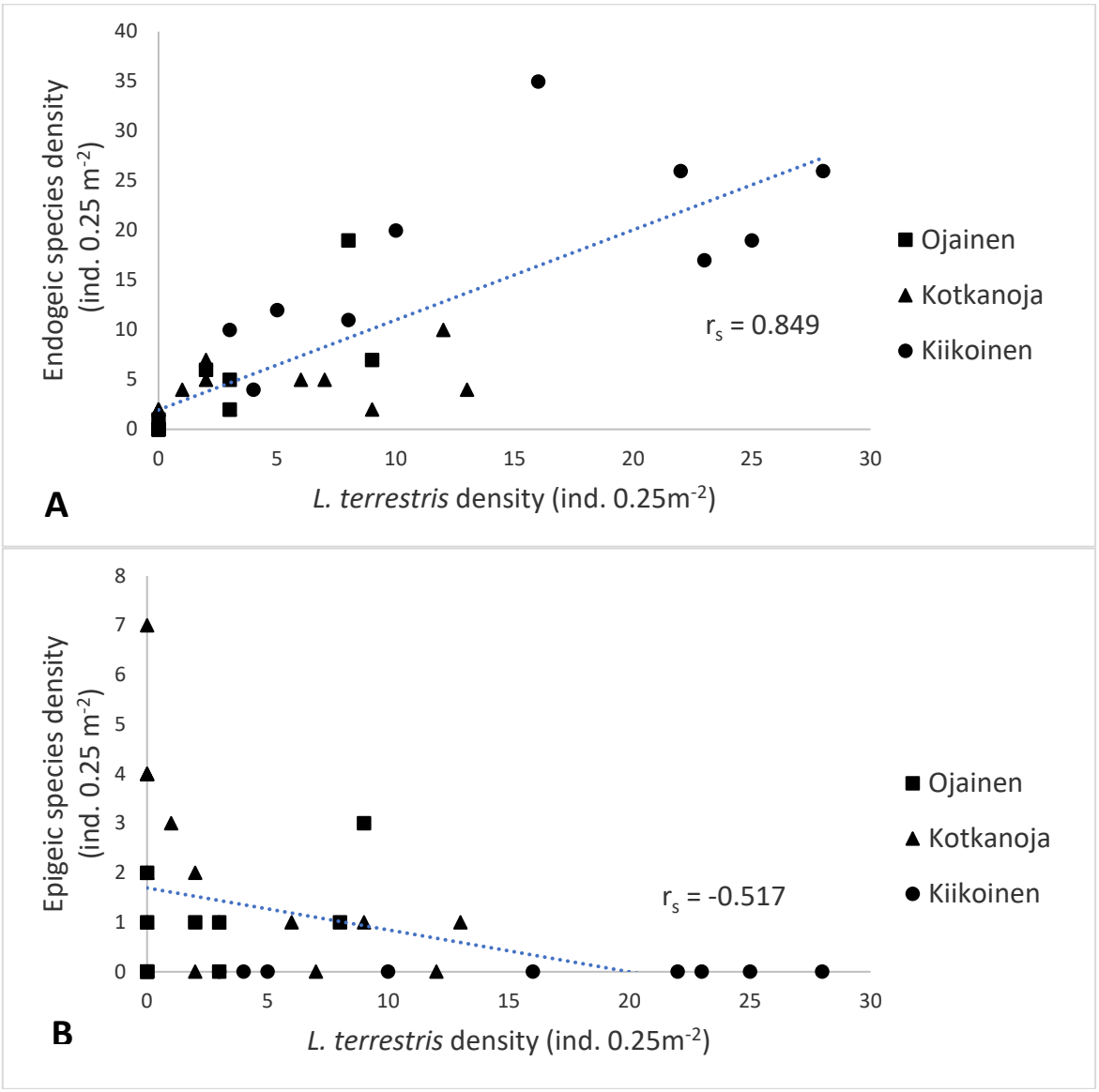

Endogeic species density (ind. 0.25 m-2)
40
35
30
25
20
15
10
5
0
0
5
10
15
20
25
30
rs = 0.849
Ojainen
Kotkanoja
Kiikoinen
A
L. terrestris density (ind. 0.25m-2)
Epigeic species density (ind. 0.25 m-2)
8
7
6
5
4
3
2
1
0
rs = -0.517
B
L. terrestris density (ind. 0.25m-2)

Fig. 5.

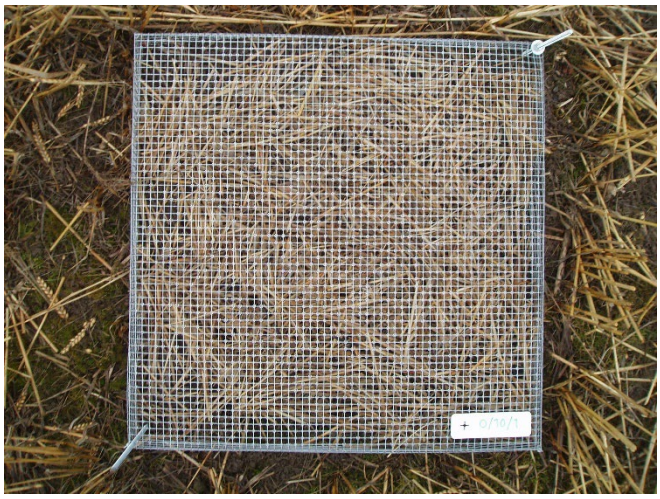
Supplementary material

Bentley et al. Two aspects of earthworm bioturbation: Crop residue burial by foraging and surface casting in no-till management

Table S1. Location of experimental sites, number of treatment replicates (N), type and quantity of harvest residue used, duration of the experiment and selected variables describing weather conditions over the experiment. Weather data: [1]Finnish Meteorological Institute (https://www.ilmatieteenlaitos.fi/avoin-data; [2]Jokioinen observatory (Ojainen and Kotkanoja), Kokemäki/Tulkkila station (Kiikoinen). DWT = dry weight.

Site	Latitude	Longitude	N	Residue	Residue DWT (g)	Experiment start date (2015)	Experiment end date (2016)	Duration of experiment (days)	Days minimum temp > 0 ^{o}C[1]	Snow cover (2016)[2]	Mean soil moisture at experimental end (% ± S.E.)
Ojainen	60.80371068	23.4650112	5	barley	80.0	16. Oct	29. April	198	63	4. Jan – 27. March	49 ± 0.9
Kotkanoja	60.81627106	3.51131225	8	wheat	110.0	23. Oct	3. May	194	60	4. Jan – 27. March	44 ± 0.2
Kiikoinen	61.41992185	22.65285768	5	oats	70.0	3. Nov	9. May	189	70	4. Jan – 24. March	36 ± 0.5

(A)



(B)

Fig. S1. (A) Soil surface at the start of the experiment, following manual residue removal from a 0.25 m^2 area; (B) Added residue under a cage at start of the experiment.

(A)

(B)

Fig. S2. Residue removal from an experimental plot at the end of the experiment. (A) Cereal residue cover at the end of the experiment before collection; (B) Soil surface of the plot after manual residue collection (LT-, plot 0/1/1, Ojainen, May 2016).

Fig. S3. Fresh earthworm casts on oat harvest residues at Kiikoinen site at the ending of the experiment.

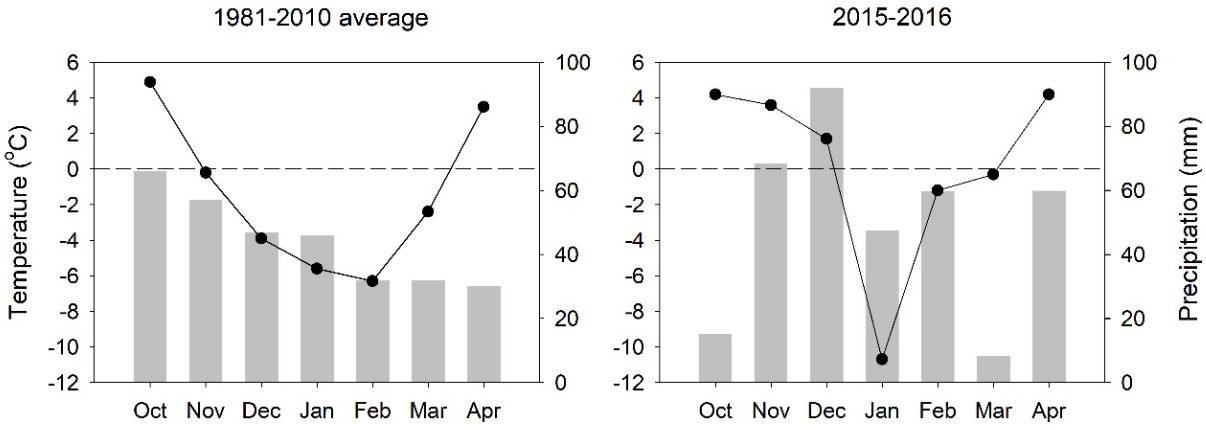


Fig. S4. Average October-April temperature and rainfall conditions at Jokioinen during 1981-2010 (the present official reference period) compared with the average monthly temperature and total precipitation during the 2015-16 experimental period. Source of data: Finnish Meteorological Institute.