Earthworms in past and present agricultural landscapes of Hebridean Scotland

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Abstract

The Hebrides of Scotland constitute a unique set of island environments with a long history of human settlement and agriculture. Earthworm community surveys were undertaken in selected agricultural landscapes of Inner (Isle of Rum) and Outer (North and South Uist) Hebrides. On North Uist, earthworms were sampled from areas of Blackland (organic, anthropic, acidic agricultural soils) and on South Uist in machair (sandy, fertile, low-lying grassy pasture). Specific grassland and cultivated areas with various organic additions - including dung and seaweed - were targeted, using hand-sorting of soil for earthworms plus mustard vermifuge extraction. Work on Rum investigated earthworms in ridge and furrow (lazybed) agricultural systems, abandoned almost 200 years ago and since uncultivated, but grazed by ungulates. On the Uists, nine earthworm species were identified, representing all three ecological categories, but dominated by the epigeics, *Dendrobaena octaedra* and *Lumbricus rubellus*. Densities and biomasses across Blackland soils ranged from 10 to 130 ind. m^{-2} and 2.3 to 33.7 g m^{-2}, respectively. Here, 5 species were present, and management had a significant effect on species richness and abundance with most earthworms present in recently restored lazybeds. In the machair soils, the corresponding measurements were 4 to 220 ind. m^{-2} and 0.8 to 89.0 g m^{-2}. Significantly higher earthworm densities and biomasses were recovered below cattle dung pats compared with dung-free areas. Cultivated areas in machair were less diverse and had lower earthworm densities than uncultivated. On Rum, ridge and furrow abundances did not differ clearly with 24-102 and 34-112 ind. m^{-2} respectively and biomasses of 7.4 – 26.3 and 8.8-30.8 g m^{-2}. Here, *Aporrectodea caliginosa* (49%), *L. rubellus* (23%) and *Dendrodrilus rubidus* (19%) dominated of the seven species found. Further research on earthworms in the Hebrides is warranted.

Keywords: Blacklands, fertiliser, lazybeds, machair, ridge and furrow, seaweed

1. Introduction

The Inner and Outer Hebrides comprise a diverse group of islands skirting 300 km of coast along the west of Scotland (Figure 1). More than eight thousand years ago, people visited these remote islands initially to collect minerals, such as the bloodstone from Rum for arrowhead production [1] and to hunt deer and gather birds and their eggs for food. Thereafter, Hebridean agriculture developed with human settlement from the Mesolithic period [2]. These islands experience a temperate maritime climate, with mild winters, cool summers and heavy rain all year. Meteorological data, derived from South Uist (Outer Hebrides) and Colonsay (Inner Hebrides - a proxy for Rum), show 30-year (1981-2010) average max and min temperatures (°C) of 16.6 (July/August) and 3.1 (February) and average annual precipitation (mm) of 1,178 [3].

The soils across the Hebrides present a diverse range, from peaty podsols, through anthropogenic black soils to the contrasting fertile machair shell sands. All are a function of numerous factors not least the geology, which is complex, with ancient sedimentary rock, in places overlain with volcanic intrusions [4, 5] and effects of more recent glaciation [6]. Combined with high annual rainfall up to, for instance, 1,800 mm on the Isle of Rum [7], these soils require management to make them viable for crop production. Many coastal soils were amended with brown seaweeds (kelp and fucoids) [8] produced in abundance in the littoral zone and collected from the shore, often after storm dislodgement [9]. In some areas this marine bounty was simply applied directly to the land or may have been composted first, perhaps with the addition of animal dung [10]. On some islands, where waterlogging posed a problem, a ridge and furrow (lazybed) system was developed with planting in parallel ridges, several metres across, and narrower furrows dug out by hand for drainage [11, 12].

It is likely that with agriculture, earthworms were introduced - accidentally or deliberately - with some species having known associations with human agricultural system [13, 14]. A survey of the earthworms of the Hebrides was undertaken by Boyd [15-17], which recorded the species present in given habitats on specific islands. Some effects of soil type and grazers were addressed, but no data were presented from Rum and very little from the Uists. Little focus was given to the specific features of Hebridean agriculture such as fertilisation of soils using seaweeds.

The aims of this investigation were to gather specific data on the earthworms present at selected current and/or previous agricultural sites in the Hebrides where seaweed was, or is still, used as a fertiliser. The Isle of Rum with historical lazybed formations (Figure 2a) was chosen to complement ongoing soil ecological research on the island [9, 14, 18-20]. Two further, contrasting locations were selected: organic, anthropic, agricultural soils (Blacklands) of North Uist and sandy, fertile, low-lying grassy pasture (Machair) of South Uist (Figures 2b and 2c respectively). Specific objectives were to determine earthworm species richness, abundance and biomass across sub-sections of the sites and relate these to selected soil properties and current or historical soil management.

2. Methods

All field work took place under spring conditions (in either May 2011 or March 2014) when soil moisture and temperature allowed earthworm activity in the topsoil. To sample for earthworms, a combination of digging with hand-sorting of soil and application of a mustard vermifuge was used [21]. At each sampling point, an area of 0.1 m^2 was excavated to a depth of approximately 0.2 m and the soil placed on plastic sheeting. The soil was broken up by hand, inspected closely and any earthworms located were preserved in 4% formaldehyde. A suspension of 50 g of mustard powder in 10 litres of water [22] was poured into the hole created by soil removal to extract any deep burrowing species. Any earthworms extracted were combined with those obtained from hand-sorting of soil. Sample number was 5 per location to obtain representative abundance and biomass data and allow as much as possible to be investigated in the given time frame. Preserved earthworms were returned to the laboratory for species identification, using the key of Sims and Gerard [23], and for biomass determination.

Soil samples were also collected from locations where earthworms were sampled. These were taken from the upper 5-10 cm, removing roots of growing plants, as necessary. Soils were subjected to standard analyses for moisture, soil organic matter and pH [24], factors known to directly affect earthworms [25, 26].

2.1 Isle of Rum (Inner Hebrides)

During May 2011, earthworms were collected from two locations at Harris, on the SW coast of Rum. Each site location was determined from maps detailing the historical lazybed configurations on the island [27]. No cultivation had occurred here since 1826 when the islanders were removed as a part of the "Highland Clearances" [28]. One site (A) was on a hillside above Harris Lodge where the lazybeds had been dug sloping downhill (56.976015, -6.386383; 56 m asl) and the second (B), close to a bridge over the Harris River (56.974400, -6.372717; 30 m asl). At each, earthworms were collected from five pairs of ridge and furrow positions on the lazybeds. Mean ridge centreline interval was 4.2 m at site A and 2.5 m at B. Mean differential between ridge and furrow height was 21 and 25 cm at sites A and B, respectively.

2.2 Uists (Outer Hebrides)

Earthworms were collected from two locations in late March 2014. These were the Blackland soils of North Uist and the machair of South Uist. Anthropogenic Blackland soils were historically fertilised with seaweeds gathered from the coast [8]. The machair plots studied, ploughed in autumn to less than 10 cm, were originally set up to examine the effects of grazing regimes, rotational cropping and fertiliser type on habitat-specific flora and fauna, particularly birds. This globally significant and threatened habitat is listed on Annex 1 of the EU Habitats Directive [29].

2.2.1 Blackland (North Uist, Grimsay)

Sampling was undertaken on historically cultivated areas of Blackland soils, based on information provided by a crofter (farmer) at Grimsay. Three sub-sections were investigated: “Old Lazybeds” - hand dug formations, formerly fertilised with seaweed and abandoned by the 1960s (57.485809, -7.229138); “New Lazybeds” - similar formations, but re-dug by hand in 2013 and fertilised with hand-cut brown seaweed (*Ascophyllum nodosum)* (57.486008, -7.232486 – foreground of Figure 2b); and “Mown Grassland” - arable fields previously ploughed for growing oats and hay until the 1960s and since mown for silage (57.484630, -7.233500).

2.2.2 Machair (South Uist, Askernish)

Sampling in this area of alkaline, shell sand soils involved several approaches. First, comparisons were drawn across Machairlife + experimental plots (2,000 m^2 in area) [29] where rotations of fertilisation were in progress (57.180847, -7.414632). Rotted kelp is spread during late winter before cultivation and shallow ploughing which helps to prevent soil erosion. In spring 2014, all of the plots examined were in pasture production. Comparison was made of an artificially (NPK) fertilised area (plot 33) and to an area (plot 35) where kelp was used at an application rate of 15 t ha^{-1} (this amount of composted seaweed meets the crop requirement for both N and K but with a shortfall of P [29]). Here, earthworms obtained from quadrats under the two fertiliser strategies were compared directly (n=10 per plot).

The effect of dung was included in an additional comparison, because grazing cattle and hence dung pats were present, and some species of earthworms are known to be attracted to dung [30, 31].

Here, artificial fertiliser (plot 34) was again compared with kelp addition (plot 36), but 5 quadrats were sampled in each from below an area with recent dung addition paired with another (within 2 m) with no evidence of recent dung deposits (see figure 2c).

Additionally, quantitative sampling was undertaken on a nearby uncultivated wetland machair area, where *Phragmites australis* (reed) was growing (Nat. Grid Ref. 57.183772, -7.412200), and on two uncultivated dune ridges towards the coast (Nat. Grid Ref. 57.185029, -7.414970). A qualitative investigation for earthworms was also employed on yellow dunes sloping down to the sea (57.187198, -7.422051).

2.3 Data analyses

Earthworm densities and masses were converted to values per square metre for statistical analyses using Minitab® 19. Where direct comparisons were made of earthworm numbers and biomasses or soil properties between different areas within the three main study sites, either a t-test or a one-way analysis of variance (ANOVA) was used, as appropriate, when conditions of normality and homogeneity were met, with Tukey-Kramer pairwise comparisons. On Rum, with two sites and ridge and furrow comparisons and in the machair plots where dung presence/absence was examined with the fertilizer treatment comparison, a two-way ANOVA was employed. The p-values less than 0.05 were considered statistically significant.

3. Results

3.1 Isle of Rum

Sampling of the lazybeds revealed the presence of seven earthworm species of which *Aporrectodea caliginosa*, *Lumbricus rubellus* and *Dendrodrilus rubidus* comprised more than ninety percent (Figure 3). No difference was found between the number of earthworms in the ridge and furrow positions of the abandoned lazybeds ($F_{(1, 16)}$=0.204, p=0.65, Table 1), but a difference was found between the two formations sampled, with those above Harris Lodge (Site A) containing significantly more than those close to the Harris River (Site B) ($F_{(1, 16)}$=12.416. p=0.002). No earthworms were extracted with vermifuge applied to the sampling pits. Biomass data revealed a similar pattern (Table 1). The lazybed formations, although still clearly visible, were overgrown with vegetation mainly comprised of grazed grasses although ling heather (*Calluna vulgaris*) was established in small patches, particularly on the ridges. As expected, there was significantly more moisture in the furrows than the ridges (overall means of 58 and 44%, respectively) with Site B significantly ($F_{(1, 8)}$ =32.901, p<0.001) wetter than Site A. In addition, organic matter content in furrows was significantly higher in than ridges (overall 29 and 21% respectively) with more at Site A than at the lower lying Site B ($F_{(1, 8)}$ =11.699, p=0.009). Acidic soils, around pH 5 were present at both sites. Soil data is summarised in Table 2.

3.2 Blackland (North Uist)

In the Blackland soils, five earthworm species were found with *Dendrobaena octaedra* and *L. rubellus* in each of the three agroecosystems sampled. *A. caliginosa* was only present in the mown grassland systems where it represented 60% of earthworms. In the newly dug lazybed soils*, D. rubidus* and *Eisenia veneta* were recorded, representing 31% and 7% of community numbers. The largest contribution was from *D. octaedra* (53%). Lowest earthworm community density was in the difficult to dig, *C. vulgaris*-dominated old lazybeds, where *L. rubellus* accounted for 82%. Earthworm densities were significantly different ($F_{(2, 21)}$ =4.39, p=0.035) but biomasses across the three agroecosystems were not significantly different ($F_{(2, 21)}$ =1.80, p=0.191) (Figure 4). No deep burrowing earthworms were present. The largest individual earthworm found was a mature *E. veneta* with a mass of 1.39 g.

Soils in the old lazybeds were highly organic and had the lowest recorded pH (4.46) of this study and the whole area was very wet. In the new lazybeds, organic matter had been added in the form of fresh and composted seaweed, which increased loss on ignition compared with the grassland soils (Table 2).

3.3 Machair (South Uist)

Comparison of earthworm numbers from kelp-fertilised (plot 35) and artificially fertilised (plot 33) plots showed low abundances in general, but significant differences (t=2.31, p=0.036) with 4 ± 2.21 and 14 ± 3.71 ind. m^{-2}, respectively. Similar differences (t=2.7, p=0.021) were shown between biomasses for kelp and artificial additions at 0.81 ± 0.42 and 4.09 ± 1.14 g m^{-2}, respectively. Most earthworms collected were *L. rubellus* (78%) with *Allolobophora chlorotica* comprising the remainder. The machair soils were much more alkaline (around pH 8) than the Blackland soils (Table 2). A major difference in soil moisture content of kelp and artificially fertilised was noted (13.4 and 23%, respectively; Table 2).

A two-way analysis, drawn across kelp (plot 36) and artificially (plot 34) fertilised plots with sampling subdivided between "with dung" and "without dung" revealed that recently deposited dung led to significantly more earthworms ($F_{(1, 16)}$=19.692, p<0.001), a greater than 10-fold increase present under dung (Figure 5a) and with a significantly greater biomass ($F_{(1, 16)}$=17.315, p<0.001; Figure 5b). Here, the type of fertiliser treatment had no significant effect on either earthworm number or biomass and there was no significant interaction in either case between fertiliser and dung treatments. *L. rubellus* was again dominant and accounted for more than 95% of all earthworms under dung. The remainder were *A. chlorotica* and *A. caliginosa*.

On uncultivated dune ridges, four earthworm species were present. Here, community density was higher than in similar cultivated areas at 151 ± 26.1 earthworms m^{-2}. *A. chlorotica* was dominant by number, comprising 34% of the total, *A. longa*, *L. rubellus and A. caliginosa* represented 31, 25 and 9%, respectively. Community biomass was 76.5 ± 15.4. g m^{-2}, of which *A. longa* accounted for 62%. In seaward yellow dunes, only few earthworms were located. Those found were either *L. rubellus* or *A. caliginosa,* with the former mainly associated with dung pats. Here, organic matter content of the very sandy substrate was minimal (Table 2).

An uncultivated, wetland area of the machair, with *Phragmites* as the dominant vegetation, produced 220 ± 49.3 earthworms m^{-2}, dominated (52%) by *Aporrectodea rosea*. *A. caliginosa* and *Eiseniella tetraedra* each accounted for a further 14% of total numbers. The remainder were *A. chlorotica*, *Aporrectodea longa* and *L. rubellus* with 7, 4 and 3% respectively. This was the highest abundance of earthworms found during the survey on South Uist. Overall community biomass was 59.5 ± 30.3 g m^{-2}.

4. Discussion

Compared with recent world-wide estimates of earthworm community metrics by Phillips et al. [32], these Hebridean arable environments lie in the mid to upper end of the scales, with (as determined here) local earthworm richness of 3-7 species and abundance ranges of 4-220 individuals and biomasses 0.8-60 g earthworms m^{-2}. The global study also showed that precipitation is a key regulator of earthworm communities and recognized north-western parts of Europe among the global hotspots of earthworm diversity and abundance. In the Hebrides, the relatively high and steady annual precipitation and absence of prolonged droughts all support earthworm population growth. Humans are important dispersers of earthworms and the long human settlement on Rum and the Uists with their active interaction with the mainland have likely contributed to the relatively high local diversity in the arable habitats. The grass-dominated cultivation of the study sites with high input of organic matter and relatively low physical disturbance further enhance earthworm diversity and abundance [26].

4.1 Isle of Rum (Inner Hebrides)

Almost 200 years since last cultivated at Harris by 400 crofters, the ridge and furrow pattern can still be clearly seen on all flat ground close to the sea and on adjacent slopes [27, 28], although the lazybeds have likely flattened out after their management ceased. Earthworm species found were a sub-section of those previously recorded at Harris (Butt and Lowe, 2004) with the addition of *A. longa*. An overall mean earthworm community density of 68 ind. m^{-2} was less than the 104 ind. m^{-2} previously recorded in different lazybeds at Harris. The differential shown from sites A and B indicate the variability among these systems and higher abundances in up-slope positions under more well-drained conditions. A consistency with earlier results was the dominance of *A. caliginosa* and the proportion of *L. rubellus* and *D. rubidus*, the other two abundant species [14].

No significant difference in earthworm numbers and biomasses between ridge and furrow components was unexpected, as the soils of the furrows were moister and contained more organic matter than the ridges. The abundance and activity of earthworms in the furrows might also have been expected to be higher and lead to greater bioturbation, as reported by Cannon and Reid [33], for similar formations in Cumbria. However, population growth and activity in the furrows may be offset by standing water often seen at Harris on level lazybeds in spring. The more favourable drainage at the ridges may therefore balance the potential benefits of higher organic matter content in furrows.

The similar, acidic pH values in both lazybed components might suggest that only acid-tolerant species *sensu* Satchell [25] would be found, yet both were dominated by rather acid-intolerant *A. caliginosa* for which Sims and Gerard [23] suggest a lower limit of approximately pH 5.9. It is possible that dominance of *A. caliginosa* at these sites relates to the earlier agricultural management and improvement of soils which otherwise could mainly support more acid tolerant epigeic species. Deeper soils of the ridges, necessarily present due to their construction, appeared not to influence earthworm numbers. This may relate to the scarcity of deep burrowing, anecic species and to the absence of deep droughts and frosts which would necessitate deep burrowing in the subsoil by endogeic species [34].

4.2 Blackland (North Uist, Grimsay)

Four of the five earthworm species collected in Blackland were previously recorded on North Uist (Boyd, 1956), the exception was *E. veneta*. This anthropic species was found in the "New Lazybeds" and associated with recent addition of seaweed and organic matter from compost heaps. The re-digging of these beds, primarily using *A. nodosum* as fertiliser, was an attempt to re-establish historical techniques for crop production [8]. However, the contribution of *E. veneta* by number (7%) in the lazybeds was small compared with the other earthworm species and almost certainly represented animals introduced with the composted organic matter. Presence of only epigeic species *sensu* Bouché [35] in the new lazybeds confirmed that the high organic matter content of these systems, as recently dug and provisioned, may have attracted earthworms from the surrounding grassland and bolstered numbers. Earthworms are known to be attracted to concentrations of organic matter on the soil surface [16, 31]. The dominance of *D. octaedra* and *D.*

rubidus reflected the nature of these soils as both species are known for inhabiting wet soils, such as peats, with a high organic content and acidic nature [23].

Vegetation on the sampled “Old Lazybeds” was dominated by *C. vulgaris*, and without locally supplied information of former use, these areas, hidden by long-stemmed heather, may have been considered as uncultivated moorland. The paucity of earthworms reflected this, with less than 20 ind. m^{-2}. These numbers were however double those found in non-agricultural, heather-dominated soils by Butt and Lowe [14] on the Isle of Rum. Satchell [25] considered *L. rubellus,* which dominated in the old lazybeds, to be ubiquitous and able to tolerate acidic soils. The species was recorded by Boyd [16] in peat bogs and by Svendsen [36] in *Calluna*-dominated moorland, although the latter suggested that *L. rubellus* preferred more mull-like soils. The very wet nature of the Old Lazybeds on Uist may have contributed to earthworms being located relatively close to the soil surface, although Boyd [16] suggested that both *L. rubellus* and *D. octaedra* may also inhabit the deeper peat. It was of no surprise that endogeic, “geophagous” earthworms were not found in the habitat as their soil requirement for nutrition - quality organic matter and a mineral base - were not met.

The “Mown grasslands” were dominated by endogeic *A. caliginosa*, the only member of this ecological category found in Blackland soils. As on Rum, an ability of this species to tolerate pH levels into the acidic range was critical. The presence of *L. rubellus* and *D. octaedra*, each at close to 20% by number, demonstrated the high organic matter content of the soils. The absence of deep burrowing species in this system (or anywhere in Blackland soils) indicated that they are not suited to these anthropogenic, acidic soils, even though depths to 1 m are present.

Although the Blackland systems examined would all have historically received seaweed fertiliser, information provided showed that, apart from the “New Lazybeds” which were an experimental set up [8], this had not taken place for over 50 years. A comparison with earthworms from unadulterated local moorland might have been useful, but was not possible, as by their very nature, the local highly organic, Blackland soils are all human modified for agriculture.

4.3 Machair (South Uist, Askernish)

Due to its coarse textured shell sand soil, machair is not a favourable habitat for earthworms which often reach their maximum abundances in medium textured loamy soils [37, 38]. Nevertheless, the uncultivated wetland area of machair, with its high soil organic matter content and water table showed the potential of machair to support abundant and diverse earthworm communities.

In cultivated parts of the machair, earthworm abundances were at the lowest level observed in the survey. Without an unfertilized control, it is difficult to judge if kelp application has any positive effect on earthworms in a field cultivation setting. In any case, our results suggest that artificial fertiliser encourage earthworms by comparison to kelp additions. The unexplained higher soil moisture under artificial fertilisation may partly explain the difference.

A comparison of fertiliser treatment, which accounted for the influence of dung pats, revealed the importance of grazing cattle on the presence of earthworms in machair: earthworm numbers and biomasses were more associated with the presence of cattle dung than the type of fertiliser used. Boyd [17] previously showed on the island of Tiree (Inner Hebrides), that larger numbers of earthworms, specifically *L. rubellus* and *D. octaedra*, were present below bullock dung, than in more open grassland habitat which contained more *A. caliginosa*. In machair, *L. rubellus* was dominant, particularly below dung, but *A. chlorotica* was also abundant. Dung is seen as a draw for earthworms and on these shell sand soils it leads to aggregation, particularly of epigeic species. It is known that dung attracts earthworms, as observed in permanent pasture [30] and in an experimental situation, where dung pats in pastures created temporary hot spots of earthworm abundance [31]. It was intriguing that earthworms were present – mainly in the dung pats – in the yellow sand dunes which delimit machair from the sea, only some tens of metres from the shore and under the effect of sea spray. It is noteworthy that no deep burrowing earthworms were found on these very sandy soils, a similar situation to sandy soils across successional sand dunes in Lancashire [39]. Addition of kelp can lead to an improved structure of the light machair, by physically trapping soil particles as well as the action of binding agents (the gel-like alginates and fucoidans) potentially reducing soil erosion by sand blow [29]. This effect may however be relatively superficial and too mild to make the soil suitable for the construction of permanent burrows of anecic earthworms.

5. Conclusions

In low input agricultural systems where fertilisation is organic, earthworms can notably increase plant yield through enhancement of nitrogen cycling and availability [40] and possibly by similar effects on soil phosphorus [41]. It has been recently shown that earthworms can feed on kelp [9], the main organic amendment used at our study sites, and potentially increase the mineralisation of plant nutrients from it. In the lazybeds, both abandoned and presently active, earthworms were present in sufficiently high numbers for effects on nutrient cycling and plant growth to be anticipated. Ongoing work is therefore examining the re-cultivation of lazybed systems with potential earthworm additions and their importance for crop growth conditions. This may reveal how ecosystem services of soil fauna have assisted the subsistence of the past crofting communities of the Hebrides. In machair soils, earthworm abundance was so low that their important effects on the high fertility soils – known from historical times – appear unlikely. In machair, future research interest could focus on the importance of cattle grazing and dung pats on earthworm movement ecology, population dynamics and the role of earthworms in dung decomposition.

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References

[1] C. R. Wickham-Jones, Scotland's First Settlers, Historic Scotland, Edinburgh, 1994.

[2] J. A. Love, Rhum's human history, in: T. H. Clutton-Brock, M. E. Ball (Eds), Rhum The Natural History of an Island, Edinburgh University Press, Edinburgh, 1987, pp. 27-42.

[3] Metoffice. https://www.metoffice.gov.uk/research/climate/maps-and-data/uk-climate-averages/, 2020 (accessed 29 June 2020).

[4] H. Jenny, Factors of soil formation: a system of quantitative pedology. McGraw-Hill, New York, 1941.

[5] Scottish Geology. https://www.scottishgeology.com/geo/, (2020) (accessed 25 May 2020).

[6] J. K. Charlesworth, The Late-glacial History of the Highlands and Islands of Scotland, *Trans Royal Soc Edin* 62 (1955) 769-928.

[7] T. H. Clutton-Brock, M. E. Ball, *Rhum The Natural History of an Island*, Edinburgh University Press, Edinburgh, 1987.

[8] O. Knox, T. Marsden, S. Warnick, G. Birch, M. Scherbatskoy, D. Wilson, B. Harvie, Improved sustainability and ecosystem services from seaweed additions to an old agricultural production system, J Ecol Envir Sci, 3 (2015) 28-37.

[9] K. R. Butt, C. Méline, G. Pérès, Marine macroalgae as food for earthworms: Growth and selection experiments across ecotypes. Envir Sci Poll Res (2020) https://doi.org/10.1007/s11356-020-07666-y.

[10] F. Darling, Crofting agriculture - its practice in the west highlands and islands, Edinburgh, Oliver and Boyd Ltd, 1945.

[11] H. Smith,, Middening in the Outer Hebrides: An ethnoarchaeological investigation, PhD, University of Sheffield, 1994.

[12] R. Dodgshon,, No Stone Unturned - A history of farming, landscape and environment in the Scottish highlands and islands, Edinburgh, Edinburgh University Press, 2015.

[13] P. H. Enckell, S. Rundgren, Anthropochorous earthworms (Lumbricidae) as indicators of abandoned settlements in the Faroe Islands. *Journal of Archaeological Science* 15 (1988) 439-451.

[14] K. R. Butt, C. N. Lowe, Anthropic influences on earthworm distribution, Rum National Nature Reserve, Scotland, Eur J Soil Biol 40 (2004) 63-72.

[15] J. M. Boyd, The Lumbricidae in the Hebrides II – Geographical Distribution, The Scottish Naturalist 68 (1956) 165-172.

[16] J. M. Boyd, Ecological Distribution of the Lumbricidae in the Hebrides, Proc. Royal Soc. Edinb. (B) 66 (1957) 311-338.

[17] J. M. Boyd, The ecology of earthworms in cattle-grazed machair in Tiree, Argyll, J Animal Ecol 27 (1958), 147-157.

[18] M. A. Jr Callaham, K. R. Butt, C. N. Lowe, Stable isotope evidence for marine-derived avian inputs of nitrogen into detrital foodwebs on the Isle of Rum, Scotland, UK, Eur J Soil Biol 52 (2012) 78-83.

[19] J. A. Gilbert, K. R. Butt, Effects of fertilisers on vegetation of ultrabasic terraces (1965-2010): Isle of Rum, Scotland. Glas Nat 25 (2012), 105-110.

[20] K. R. Butt, C. N. Lowe, M. A. Jr Callaham, V. Nuutinen, An oasis of fertility on a barren island: Earthworms at Papadil, Isle of Rum, Glas Nat (2015).

[21] C. Pelosi, M. Bertrand, Y. Capowiez, H. Boizard, J. Roger-Estrade, Earthworm collection from agricultural fields: comparisons of selected expellants in presence/absence of hand-sorting, Eur J Soil Biol. 45 (2009)176–183.

[22] K. R. Butt, Earthworms of the Malham Tarn Estate (Yorkshire Dales National Park), Field Studies 9 (2000) 701-710.

[23] R. W. Sims, B. M. Gerard, Earthworms – synopses of the British Fauna no. 31 (revised). Field studies council, Shrewsbury, 1999.

[24] MAFF (1981) The analysis of agricultural materials, second ed, A manual of the analytical methods used by the agricultural development and advisory service (ADAS), HMSO, London, 1981.

[25] J. E. Satchell, Some aspects of earthworm ecology, in: D. K. Mc E. Kevan (Ed.) Soil Zoology), Butterworths, London, 1955, pp. 180-201.

[26] J. P. Curry, Grassland Invertebrates: Ecology, influence on soil fertility and effects on plant growth, Chapman and Hall, London, 1993.

[27] University of Glasgow, Ordnance Survey map of Rum (1:10,000), Ordnance Survey, London, 1972.

[28] J. A. Love, Rum - a landscape without figures, Birlinn, Edinburgh, 2001.

[29] MachairLife +. http://www.machairlife.org.uk 2013 (accessed 22 December 2020).

[30] D. Knight, P. W.Elliott, L. M. Anderson, D. Scholefield, The role of earthworms in managed, permanent pastures in Devon, England, Soil Biol Biochem 24 (1992)1511–1517.

[31] M. G. Bacher, O. Fenton, G. Bondi, R. E. Creamer, M. Karmarkar, O. Schmidt, The impact of cattle dung pats on earthworm distribution in grazed pastures, BMC Ecology 18 (2018) 59 https://doi.org/10.1186/s12898-018-0216-6.

[32] H. R. P. Phillips et al. (142 authors), Global distribution of earthworm diversity, Science 366 (2019) 480-485.

[33] P. Cannon, I. Reid, The influence of relic ridge-and furrow on the soil water regime and the plant community of an ancient meadow, Cumbria, England, Global Ecol Biogeo Lett 3 (1993) 18-26.

[34] V. Nuutinen, K. R. Butt, Worms from the cold: lumbricid life stages in boreal clay during frost, Soil Biol Biochem 41 (2009) 1580-1582.

[35] M. B. Bouché, Stratégies lombriciennes, Biological Bulletin (Stockholm) 25 (1977) 122-132.

[36] J. A. Svendsen, The distribution of Lumbricidae in an area of Pennine moorland (Moor House Nature Reserve), J Anim Ecol 26 (1957) 411-421.

[37] W. J. Mc L. Guild, The distribution and population density of earthworms (Lumbricidae) in Scottish pasture fields, J Anim Ecol 20 (1951) 88-97.

[38] M. Nieminen, E. Ketoja, J. Mikola, J. Terhivuo, T. Sirén, V. Nuutinen, Local land use effects and regional environmental limits on earthworm communities in Finnish arable landscapes, Ecol Appl 13 (2011) 3162–3177.

[39] E. J. Chamberlain, K. R. Butt, Distribution of earthworms and influence of soil properties across a successional sand dune ecosystem in NW England, Eur J Soil Biol 44 (2008) 554–558.

[40] J. W. van Groenigen, I. M. Lubbers, H. M. J. Vos, G. G. Brown, G. B. De Deyn, K. J. van Groenigen, Earthworms increase plant production: a meta-analysis. Sci Rep. 4 (2014) 6365.

[41] J. W. van Groenigen, K. J. van Groenigen, G. F. Koopmans, L. Stokkermans, H. M. J. Vos, I. M. Lubbers, How fertile are earthworm casts? A meta-analysis. Geod, 338 (2019) 525-535.

Figure 1 The major Hebridean Isles of Scotland (Adapted from http://www.geeoffshore.co.uk/images/maphebrides.png)

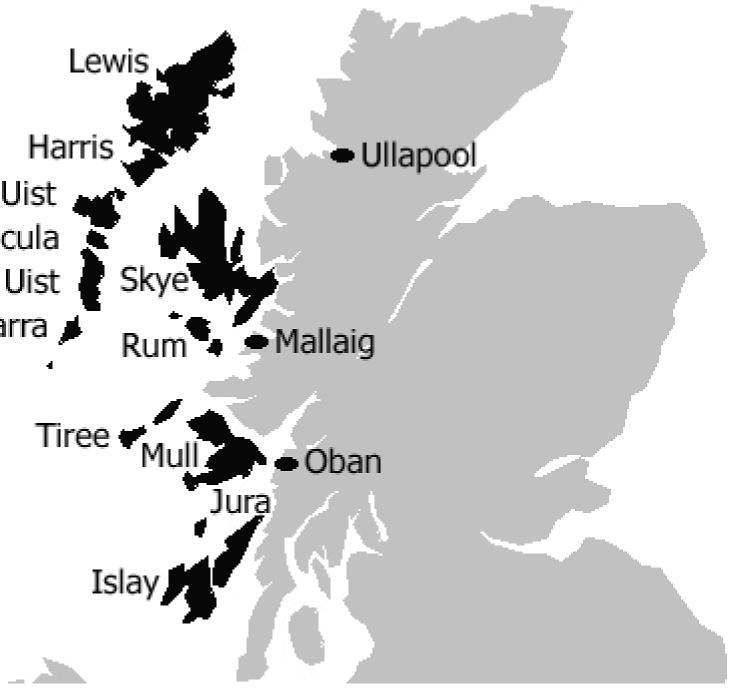


Figure 2 Agricultural areas of the Hebrides selected for investigation (a) Historic ridge and furrow (lazybed) formations at Harris on the Isle of Rum; (b) Blacklands (organic, anthropic soils) of North Uist, newly established lazybeds in the foreground; and (c) Machair (sandy, fertile, low-lying pasture) of South Uist.

(a)

(b)

(c)

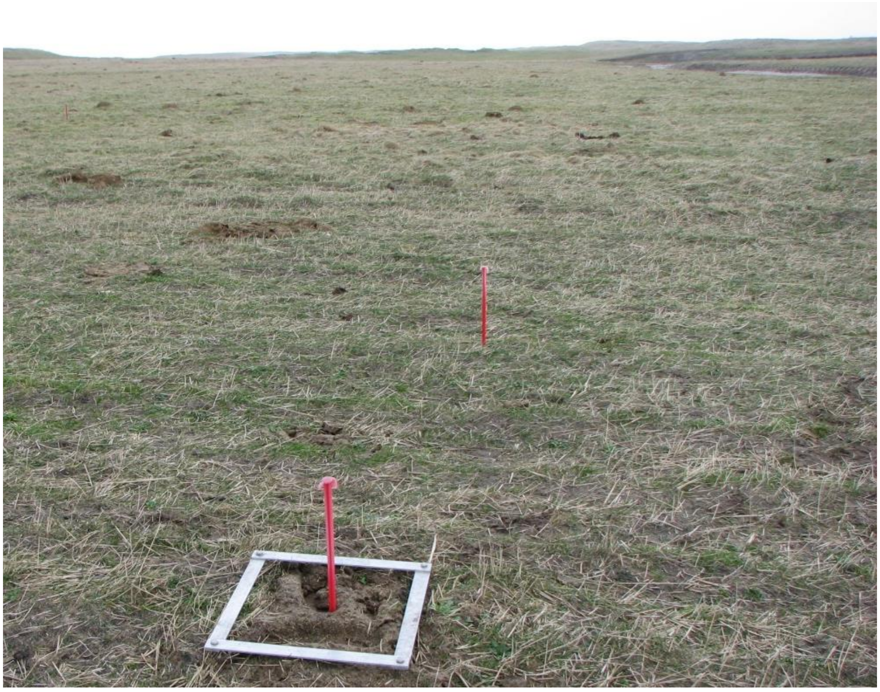


Figure 3 Population density of earthworms located from selected lazybed systems at Harris, Isle of Rum in May 2011. Numbers in brackets are % of total for that species: Ac – *Aporrectodea caliginosa* (41); Lr – *Lumbricus rubellus* (37); Dr – *Dendrodrilus rubidus* (15); Al – *A. longa* (2); Do – *Dendrobaena octaedra* (3); Ar – *A. rosea* (1); Achl – *Allolobophora chlorotica* (1).

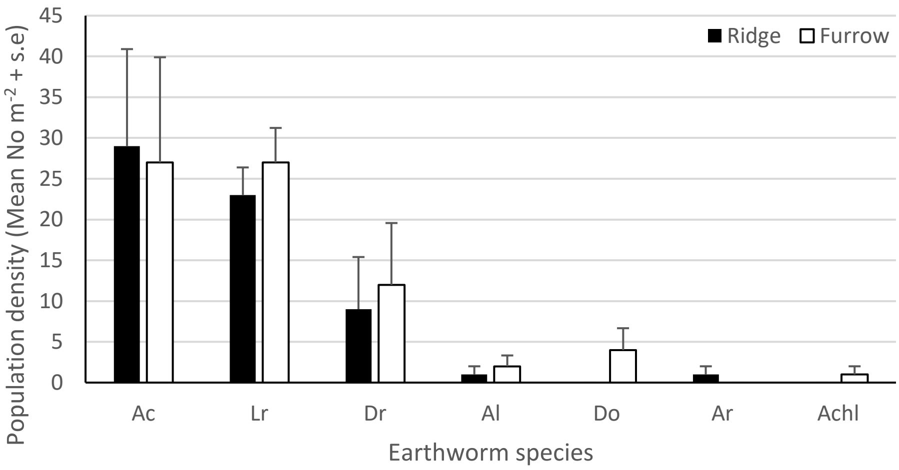


Figure 4 Earthworm community density and biomass from Blackland soil plots at Grimsay (North Uist) with differing histories relating to cultivation (see text for details). All density comparisons were statistically significantly ($p < 0.05$), biomasses were not significantly different in the three agroecosystems.

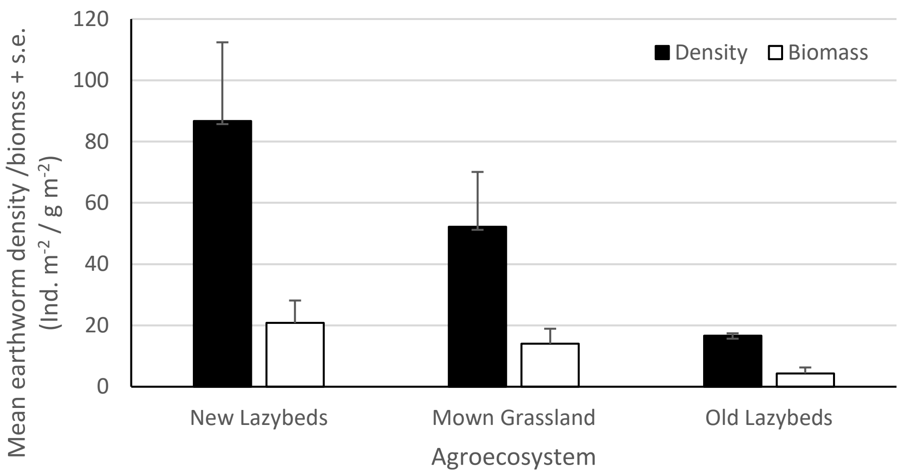
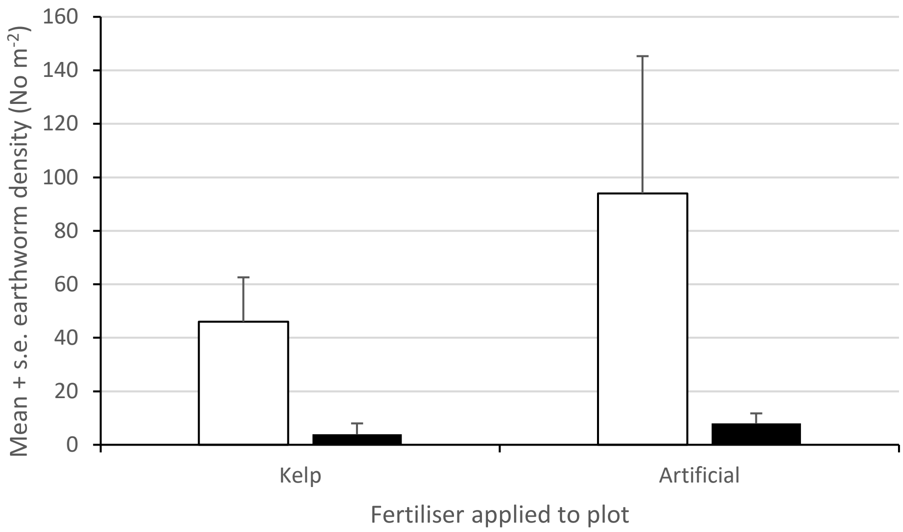


Figure 5 (a) Community density and (b) community biomass of earthworms from machair plots at Askernish (South Uist) with differing applications of fertiliser (Kelp or an artificial mixture) with sampling either below fresh cattle dung (white bars) or from an adjacent area with no recently deposited dung (black bars) (n = 5 per treatment). For both (a) and (b), the presence of dung led to significantly ($p < 0.001$) more earthworms with a greater biomass ($p < 0.001$), regardless of fertiliser type.

(a)


Mean + s.e. earthworm density (No m-2)
160
140
120
100
80
60
40
20
0
Kelp
Artificial
Fertiliser applied to plot

(b)

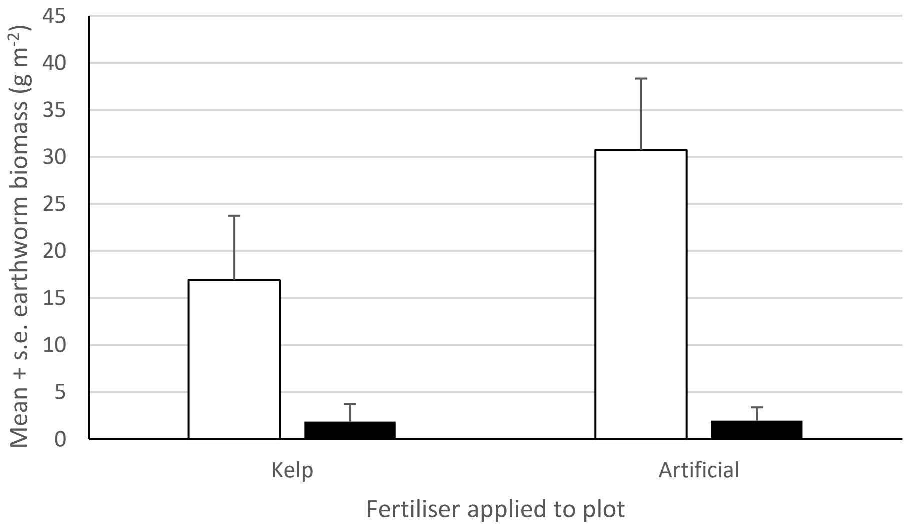

Mean + s.e. earthworm biomass (g m-2)
45
40
35
30
25
20
15
10
5
0
Kelp
Artificial
Fertiliser applied to plot

Table 1. Earthworm community abundance and biomass in ridge and furrow lazybed formations at Harris, Isle of Rur
same column indicate $p < 0.01$)

Location	Position	Density (Ind. m^{-2} ± se)
Site A. Above Harris Lodge (30 ° hill slope)	Ridge	102.0 ± 25.0 a
	Furrow	112.0 ± 34.7 a
Site B. Close to Harris River (Not freely draining)	Ridge	24.0 ± 7.48 b
	Furrow	34.0 ± 8.72 b

Table 2. Selected soil properties from areas sampled at sites on Rum, North UIst and South Uist (Hebrides, Scotland). (OM = Organic matter)

Island	Agroecosystem		Moisture (%)	OM (%)	pH
RUM	Site A	Ridge	50.1	23.7	5.07
(Harris)		Furrow	63.8	34.1	4.92
	Site B	Ridge	39.1	18.5	5.27
		Furrow	53.2	24.2	5.27
NORTH	New Lazybeds		82.9	87.9	5.37
UIST	Mown Grassland		70.2	66.2	5.49
(Blackland)	Old Lazybeds		85.2	94.4	4.46
SOUTH	Plot 33 (Artificial)		23.0	3.8	8.13
UIST	Plot 35 (Kelp)		13.4	4.2	8.15
(Machair)					
	Plot 34 (Artificial)		15.9	4.9	8.07
	Plot 36 (Kelp)		13.5	4.5	8.14
	Uncultivated ridge		23.8	8.8	7.93
	Wetland		50.9	13.6	7.79
	Yellow Dune		7.0	1.2	9.11