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A REVIEW OF EARTHWORM RESEARCH IN LANCASHIRE

Abstract: *Earthworm-related research began at the University of Central Lancashire in 1994. This was initially on life history investigations of UK species, and use in soil restoration schemes, both long-term activities. Interspecific interactions became an interest, as did the use of various organic materials as a source of food. Collaborations with Finland, Poland and the USA led to investigations in boreal agroecosystems, mountain forests and cropping systems, respectively. Lumbricus terrestris was often a key species and, along with ecosystem service provision, its behaviour - mating, foraging, midden construction and settlement – was examined with novel use of visual recording. Field investigations were supported by laboratory experiments and the ability to maintain cultures of soil dwelling (endogeic and anecic) species was a vital element in research growth. Realisation that large species could be maintained and reproduce in small culture vessels was an important breakthrough. It allowed detailed knowledge of specimens with respect to origin, age, and reproductive status to be collected, which was used in a variety of investigations including DNA analysis linked to mating of cryptic species. Meanwhile, further collaborations were established in the field, particularly with Forest Research UK, where earthworm-tree interactions were investigated in a range of contexts. Other long-term monitoring was set up at Manchester Airport and at Down House in Kent, with many projects undertaken in Scotland, either on reclaimed industrial sites or on the Isle of Rum. Further laboratory work led to the development of a method for tagging earthworms, and interactions of earthworms with forest fungi was investigated. Ecotoxicological work also looked at the potential harm of silver nanoparticles in the soil. Throughout this time, solutions were sought to practical problems in research with the development of ideas such as Earthworm Inoculation Units and polyurethane casting of burrows. This period led to the completion of 20 PhDs and publication of over 150 peer-reviewed papers. Earthworm conservation is now under investigation through breeding of red-listed species and investigating the potential to hold cocoons in a "frozen ark". With several Departmental/University name changes, the initial Earthworm Research Group has now become Ecological Engineering, at the University of Lancashire.*

Keywords: Behaviour, Conservation, Ecosystem services, Interactions, Soil restoration

PRZEGLĄD BADAŃ NAD DŻDŻOWNICAMI W LANCASHIRE

Abstrakt: *Badania nad dżdżownicami rozpoczęły się na Uniwersytecie Central Lancashire w 1994 roku. Początkowo koncentrowały się na badaniach cyklu życiowego gatunków brytyjskich oraz na wykorzystaniu ich w programach rekultywacji gleby, co stanowiło działania długoterminowe. Zainteresowanie budziły interakcje międzygatunkowe, a także wykorzystanie różnych materiałów*

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organicznych jako źródła pożywienia. Współpraca z Finlandią, Polską i Stanami Zjednoczonymi doprowadziła do badań odpowiednio w borealnych agroekosystemach, lasach górskich i systemach upraw. Dżdżownica Lumbricus terrestris była często gatunkiem kluczowym, a świadczenia usług ekosystemowych, jej zachowanie – gody, żerowanie, budowę kanałów i osiedlanie się – badano za pomocą nowatorskiego wykorzystania rejestracji wizualnej. Badania terenowe były wspierane eksperymentami laboratoryjnymi, a możliwość utrzymania kultur gatunków glebowych (endogeicznych i anektycznych) była kluczowym elementem rozwoju badań. Odkrycie, że duże gatunki mogą być utrzymywane i rozmnażane w małych naczyniach hodowlanych, stanowiło ważny przełom. Umożliwiło to zebranie szczegółowej wiedzy o okazach pod względem pochodzenia, wieku i statusu reprodukcyjnego, co wykorzystano w szeregu badań, w tym w analizie DNA związanej z kojarzeniem gatunków. W międzyczasie nawiązano dalszą współpracę w terenie, w szczególności z Forest Research UK, gdzie badano interakcje dżdżownic z drzewami w różnych kontekstach. Inne długoterminowe systemy monitoringu utworzono na lotnisku w Manchesterze i w Down House w hrabstwie Kent, a wiele projektów zrealizowano w Szkocji, na zrekultywowanych terenach przemysłowych lub na wyspie Rum. Dalsze prace laboratoryjne doprowadziły do opracowania metody znakowania dżdżownic, a także zbadano interakcje dżdżownic z grzybami leśnymi. Prace ekotoksykologiczne dotyczyły również potencjalnej szkodliwości nanocząsteczek srebra w glebie. W tym czasie poszukiwano rozwiązań praktycznych problemów badawczych, rozwijając takie koncepcje, jak jednostki inokulacji dżdżownic i poliuretanowe odlewy ich korytarzy i nor. W tym okresie ukończono 20 doktoratów i opublikowano ponad 150 recenzowanych artykułów. Ochrona dżdżownic jest obecnie przedmiotem badań poprzez hodowlę gatunków z czerwonej listy i badanie możliwości przechowywania ich kokonów w „zamrożonych kapsułach". Po kilku zmianach nazw wydziału, Earthworm Research Group pracuje obecnie na Wydziale Inżynierii Ekologicznej Uniwersytetu Lancashire.

Słowa kluczowe: zachowanie, ochrona, usługi ekosystemowe, interakcje, regeneracja gleby

I. INTRODUCTION

The Earthworm Research Group (ERG) came into existence when the first author joined the University of Central Lancashire in 1994, with the second author appointed the following year. Collaboration between these two, and other researchers from institutions in many countries, has led to the body of work described here. Earthworms have been considered as model organisms and examined in numerous ways due to their tremendous influence in soil processes by provision of ecosystem services (Blouin et al., 2013). Thirty years ago, much of what we now take for granted for certain types of earthworms was still to be learned, such as how they could be maintained in the laboratory and monitored in the field. Rather than setting out a chronology of events, this review is topic-based, with cross-referencing as appropriate.

The aim of this publication is to present life histories and interactions, soil restoration and soil life research, forest research, behavioural research, agroecosystems, ecotoxicology, DNA analysis and microbial survival, long-term monitoring and history, conservation and the future of research in our group.

II. METHODOLOGY

A review of our research was conducted. Published scientific papers were collated, and the presented topics were generated from subject-specific areas and research objectives. The work presented includes original peer-reviewed publications and specific review articles. Although the focus is on research in Lancashire, this work includes collaborations with numerous research centres from around the world.

III. RESULTS

Life histories and interactions

Early work of the ERG focussed on the life cycles of soil dwelling earthworms, i.e., those that require mineral soil. These were not the small, darkly pigmented litter dwelling (epigeic) species such as *Eisenia fetida* (the brandling or tiger worm) – which live within and consume rich organic matter such as animal waste, extensively studied in the 1980s (Edwards, 1988). By contrast, these were either unpigmented, shallow working (endogeic), geophagous species such as *Allolobophora chlorotica* and *Aporrectodea caliginosa* (the green and grey worms, respectively) or larger deep burrowing (anecic) species such as *Lumbricus terrestris* and *Aporrectodea longa* (the dew worm/nightcrawler and black-headed/long worm, respectively). All of these require a soil medium supplemented with organic matter (OM) as food material. Provision of temperature-controlled settings (incubators) was an early requirement and effects of temperature on growth, reproduction and cocoon development were extensively investigated (Butt et al., 1994; Butt, 1997).

However, prior to gaining life cycle knowledge, there was a need to optimise some of the culture requirements of these earthworms. As the name suggests, deep burrowing species normally occupy burrows to a depth of 1 m or more under field conditions. This was not practical in the laboratory, but we soon learned that such depth requirements were unnecessary and it was possible to keep e.g., *L. terrestris* in containers of 15-30 cm depth (Butt et al., 1994). Knowledge of the lifestyle of the two groups also suggested that provision of food (OM) needed to be tailored to the given ecological groups. Deep burrowers could be fed from the soil surface – dragging down the material as required – whereas the shallow workers needed the OM to be incorporated into the mineral soil. We also found, for example, that 24 h darkness encouraged activity and that adequate moisture was necessary, and made simpler after a "standard" soil was chosen. For the past thirty years, we have used Boughton/Kettering loam, obtained in pre-sterilised form, as a basis for experimentation, unless experimental design dictated otherwise. To save on citations and words, an often referred to review paper can be accessed which covers most of the basics on soil dwelling earthworm husbandry (Lowe & Butt, 2005). In addition, a book chapter (Lowe et al., 2023) presents potential benefits that can be gained from earthworm culture.

After examining monocultures of earthworms, it seemed natural to combine species in culture and consider interactions, whether positive (between ecological groupings - shallow workers and deep burrowers) or negative (within ecological groupings). This showed that incorporation of organic matter into the soil by surface feeding of the deeper burrowers appeared to benefit the shallow workers. Work here led to numerous papers (e.g., Butt, 1998; Lowe & Butt, 1999, 2003) which also examined the way in which deep burrowing species such as *L. terrestris* may exhibit a shallow working lifestyle in early life, until a given mass is reached and deep burrow construction begins (Lowe & Butt, 2002).

Soil restoration and soil life

Learning about the basic biology and life history of more common earthworm species may be good science, particularly if novel manipulations are required. But could this knowledge be put to good practical use? We have always strived to be involved with applied aspects of research, so the life history traits were explored to enable earthworm production for use in soil amelioration projects. Large areas of land are despoiled by human intervention and legislation dictates that soil restoration should be included in any reclamation work. Historically this involved provision of a shallow layer soil-like material and perhaps a seeding of grass or even planting of a few trees. We have always argued that this was inadequate and perhaps the restored system needed a "kick-start" and addition of earthworms was a good way to enable some ecosystem services to be returned to a soil (e.g., Butt, 2008).

From the 1990s we were involved with working on semi-restored landfill sites. One of these, Calvert in Buckinghamshire, was a proving ground for a technique which evolved from the laboratory-based work described above. The Earthworm Inoculation Unit (EIU) technique was a method for growing earthworms in plastic bags of soil with food but ensuring that the starter culture of mature worms (of e.g., 2 species) were then maintained so that they reproduced, and some of the cocoons hatched, to give all 3 earthworm life stages. EIUs were then taken to the field and inserted, without disruption, into an appropriately sized hole after the plastic bag was removed (reviewed by Butt, 2011). Survival, spread and population/ community development was then recorded over time. This technique was probably never explored/exploited to its full potential and may still have merit for research in the future. We undertook work in collaboration with Forest Research at Calvert (Butt et al., 2004; Moffat et al., 2008) and envisaged that a system which used EIUs perhaps with the inclusion of a tree, could be a positive step towards a more holistic view of soil restoration, particularly if appropriate microbes were also incorporated. Scope for further research certainly exists here.

EIUs were also utilised by the Strathclyde Greenbelt Company (a commercial enterprise) at a reclaimed steelworks site at Hallside, in Scotland. We were involved in assisting with the set-up of the EIUs and monitoring thereafter. For numerous reasons (see Bain et al., 1999; Butt, 2008) this was not a great success but was a site that we returned to sample after a period of 20 years. Long term monitoring of sites (see below) is advocated and can lead to some very interesting results, as here. Even within a very stony substrate comprised mainly of colliery spoil, earthworms managed to survive and we found a community of 16 species after more than two decades. This was in part due to the initial inoculation and some natural colonisation (Butt & Quigg, 2021). Throughout restoration research, there was a need to consider the use of organic materials to enhance soil status and act as a food for earthworms. This continues to be an ongoing strand of our research (e.g., Butt, 1999; Bentley & Butt, 2026).

Forest Research

The work at Hallside (above) included planting of willow trees into the colliery spoil/sewage sludge substate but needed more careful management (coppicing) if it was to have been successful. One organisation – Forest Research (FR) – the research arm of the UK Forestry Commission has a close association with the ERG. We originally worked together on the Calvert restoration site – see above (Butt et al., 2004) and have more recently been the academic partner for several PhD projects. One of these was also related to soil restoration and involved fieldwork in Essex (Ashwood et al., 2018). This looked at specific tree species and their suitability (with earthworms) to survive and prosper in hostile soil conditions (Ashwood et al., 2017). Another project investigated experimental work on landfill sites looking at historical use of paper pulp, earthworms and tree planting (Lampert, 2023). This demonstrated that the legacy of inputs from slow-release action of the organic matter, earthworm activity and tree growth remained after decades.

Another project examined the role of earthworms in soils associated with Short Rotation Coppice (SRC) tree growth (Rajapaksha et al., 2013a). Here, the focus was on field work with earthworms found below different tree species. Parallel food choice of tree litter was examined in the laboratory by development of a "cafeteria-type" set up of experiments (Rajapaksha et al., 2013b), which was very successful and has been repeated by other researchers (e.g. Ashwood et al., 2017; Bentley & Butt, 2026) with other earthworm food materials. Further FR projects are ongoing (see below).

Tree-covered mountainous areas of Europe have also formed a backdrop to research from our group. In association with the University of Rzeszów, earthworms were investigated within the forests of the Bieszczady National Park in Poland. This built on previous work undertaken by the Polish partner and involved earthworm collection and culture of selected species in the ERG laboratory (Kostecka & Butt, 2001; 2015; Kostecka et al., 2019). More recent work has examined survival strategies adopted by earthworms during winter conditions in these forests with low temperatures and snow-covered soils (Butt et al., in prep. ISEE13a). Within the Black Forest of southern Germany, research with the University of Freiburg has examined the ecology and behaviour of the very large earthworm *Lumbricus badensis*. This species can reach 40 g (some 10 x the size of *L. terrestris*) and has a major impact within the forests where it is found, with burrows down to 2 m. Our research to date, has looked primarily at the activities of this species at the soil surface (Butt et al., 2021; 2026), but further laboratory-related investigations of life history, for example, are ongoing (Butt et al., in prep. ISEE13b).

Behavioural Research

Use of video cameras has enabled us to record earthworms at the soil surface. This began by examination of *L. terrestris*, an earthworm known to feed (by collection of leaves) and to mate at the soil surface, whilst retaining its tail in its own burrow (Butt & Nuutinen, 2005). This work has mainly been undertaken under controlled laboratory conditions in collaboration with Natural Resources Institute Finland (Luke) and examined the effects of resource distribution, daylight duration and type of food available on feeding and mating (Butt et al., 2003; 2005; Nuutinen et al., 2014). More recently other surface-active species such as *Lumbricus friendi* have been recorded individually and with *L. terrestris* (Butt & Nuutinen, in prep. ISEE13), as has *L. badensis*. The latter (see above) was recorded in the field with HD nighttime cameras, adapted to run on 6V batteries overnight. Further observational research has used more basic, but effective equipment such as glass-sided wormeries. Also known as 2D-mesocosms or Evans' Boxes, these have allowed information to be gathered on cocoon deposition and the behaviour of adult *L. terrestris* by provision of OM in the vicinity of the unhatched cocoon (Grigoropoulou et al., 2008) – a form of parental care? There is still much to learn of intra-specific behaviour with this species. Field research has also revealed that intra- and interspecific behaviours occur with other earthworms within the middens of *L. terrestris* (Butt & Lowe, 2007a).

Agroecosystems

Earthworms have long played a role in agricultural systems, so it was appropriate to investigate these areas. Some early work in the USA examined earthworms in maize fields and specifically examined water movement, mediated by *L. terrestris* burrows (macropores). Working with the United States Department of Agriculture (USDA), we developed a novel technique for finding the dimensions of earthworm burrows by filling them with polyurethane resin and then extracting the burrow impression intact (Shipitalo & Butt, 1999). Further work conducted in Finland with Natural Resources Institute Finland has spanned most of the ERG duration. Several projects have been undertaken to look at aspects of *L. terrestris* ecology (e.g., Nuutinen & Butt, 2003; 2009; 2019) but perhaps one project that stands out relates to inoculation, using the EIU technique. A selected field (Kotkanoja) has been monitored over almost 30 years, assessing the colonisation of *L. terrestris* and potential effects on soil properties, other soil fauna and the drainage of the field (Nuutinen et al., 2011; 2017; 2026). More recently research has been conducted with BOKU University in Vienna, Austria. Here aspects of earthworms and use of cover crops have been examined (Euteneuer et al., 2020) and several investigations have used and developed new techniques (Euteneuer et al., 2024; Euteneuer & Butt, 2025). More standard investigations have also considered fertilisers, cropping systems and cultivation with earthworm monitoring and enhancement of *L. terrestris* numbers (Simon et al., 2025; Euteneuer et al., 2026; Sturm et al., 2026).

A Scottish Island

The Isle of Rum, a National Nature Reserve in the Inner Hebrides, has provided a setting for long-standing research on earthworms. The general infertility of the acidic soils means that most of the 105 km^2 island contains only a few epigeic, acidophilic species (*Bimastos rubidus*, *Dendrobaena octaedra* and *Lumbricus rubellus*). Nevertheless, interventions by humans over centuries have created areas of soil fertility that lend themselves to earthworm research. Survey work over several years allowed us to produce generic information (Butt & Lowe, 2004) which then led to more specific investigations. These included evidence of marine organic inputs to high altitude "greens" by Manx shearwaters (Callaham et al., 2012), very large *L. terrestris* in remote wooded areas (Butt et al., 2016), soil signals from cultivation by crofters removed from the island two centuries ago (Butt & Nuutinen, 2021; Parkes, 2025) and use of seaweed as a food for earthworms (Butt et al., 2020). And there are still opportunities for more research on this remote island.

Ecotoxicology

Due to their intimate contact with the soil, earthworms have been the subject of ecotoxicological testing of soils for decades with new development occurring (e.g., Forbes et al., 2020). One of our major inputs to this type of work has been to propose the use of soil dwelling species, rather than the widely adopted epigeic *E. fetida*, as they are better models for the way in which soil-based toxins may act (Lowe & Butt, 2007a; Lowe et al., 2016; Bart et al., 2018). In addition to having "the right type of worm", we also felt that the right type of test was necessary. Rather than using lethal dose (e.g., LD50) tests, it seemed more appropriate to consider behavioural tests such as avoidance (Lowe et al., 2017). Here, gradients of contaminated soils were prepared and earthworms inserted at chosen points. After a given time, the animals were retrieved and their new positions noted. Investigations have included the use of biochar (Brami et al., 2017) and silver nanoparticles (Kister et al., 2023). Within some of these trials, individual earthworms were marked with Visible Implant Elastomer (VIE) tags to allow for recognition. Development and use of VIE tags in this and other earthworm experiments became commonplace with researchers in our lab over the years (Butt & Lowe, 2007a; Butt et al., 2009; Lowe et al., 2016; 2017) and in some fieldwork e.g., for identification of dispersing *L. terrestris* (Grigoropoulou & Butt, 2010). There is still great scope for further development of this technique in earthworm research. Another interesting area of research aimed to look at potential toxic aspects of human burial (associated with embalming fluids), with investigations for earthworms in freshly dug graves (Butt et al., 2014).

DNA analysis and Microbial survival

An ability to successfully culture soil dwelling earthworms has meant that collaborative projects have developed linking our lab to others with diverse interests. One example is with researchers focusing on the potential spread of forest pathogens mediated by earthworms. Receiving a host of specific microbial-inoculated soils from the University of Padova, we maintained different earthworm species within them and collected casts on a regular basis for assessment of viability and identification of the microbes after gut-passage. Results of differential microbial detection and survival were revealing, with earthworm behaviours also assessed across the range of ecological groups utilised (Montecchio et al., 2015).

When considering the lineages proposed for *Allolobophora chlorotica* by King et al. (2010) it was thought that a closer examination of the molecular relationships could be undertaken and coupled with mating experiments. Therefore, in a series of experiments, unmated *A. chlorotica* were tested for their lineage and then, on maturity, mated in given groups. This allowed us to show the degree of breeding separation of this species (Dupont et al., 2011; 2022). This work grew from much earlier work in our laboratory examining the differences between the pink and green morphs of this species (Lowe & Butt, 2007b).

Long-Term monitoring and History

Several of our studies have been conducted over periods of decades, to allow for the potential slow pace of soil improvement/development to be assessed over more realistic time scales. One example was earthworm community development more than 20 years after translocation of grass turfs at a site near Manchester airport (Butt et al., 2022). Another project has examined the action of earthworms on the burial of flints in the grounds of Down House, Kent (the home of Charles Darwin) (Butt et al., 2016; in prep. ISEE13c). This specific project links with a more general investigation of the work of Darwin on earthworms (Darwin, 1881; Butt et al., 2008). A similar historical investigation is ongoing at the Wakes, in Hampshire and relates the contribution to earthworm science by Gilbert White (White, 1788; Butt, in prep.). Other long-term studies already mentioned relate to work on the Isle of Rum and at Hallside in Scotland, both covering periods of more than a quarter of a century. We feel that for field work where, for example, earthworm inoculation has taken place, effects of colonisation and soil development need to be measured over lengthy periods. This has certainly been the case at Kotkanoja field in Finland (see above).

Conservation

More recently, researchers have begun to realise that earthworms are more than active biomass in the soil. Their ecosystem services are still appreciated, but perhaps the earthworms themselves need closer scrutiny and something of their conservation status assessed, in terms e.g., of rarity, nativeness and specialisation (Gerard et al., 2025). The metrics that we currently use – abundance, biomass and species richness – may not be enough. Some earthworms have now been listed as red data species and may require close examination. One of these is *L. badensis* (see above) which is now part of a captive breeding programme in our laboratory (Butt et al., 2021; in prep. ISEE13c). Other European species, of which little is currently known, may also become the subject of investigation. An International Union for the Conservation of Nature (IUCN) group for earthworms was set up in 2025 (IUCN Earthworms n.d.) and we are a member of this. A further development in this area is the idea of creating a repository (seedbank) as for plants at Kew Gardens, London (Millennium Seedbank, n.d.). Here though, for earthworms, the approach is to examine the potential for creating a "Frozen Ark" by freezing earthworm cocoons for successful storage, thawing, and ultimately population recovery. This is an ongoing project with the Natural History Museum (London) (NHM, n.d.) and we have had some promising survival result to date.

The Future

Several research projects are ongoing. One of these, Landworm [n.d.], is a predominantly French group currently interrogating a large historical data set (e.g., Hoeffner et al., 2025; Phillips et al., 2025) and looking at concepts which will yield further insights into earthworm ecology. Further European links, as mentioned above, are also current and many of the long-term monitoring sites will be revisited. Current PhD projects with Forest Research are investigating earthworms and trees in UK urban settings and evaluating effects of natural colonisation vs tree plantation on soil fauna close to established forests. These will be completed over the next few years. There is always much to consider and investigate, with new ideas leading to new projects all the time. Whilst earthworms continue to act as ecosystem engineers and offer their ecosystem services, there will always be worthwhile reasons to study them.

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