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Re-wilding - An investigation of its effects on earthworm abundance, diversity and their provision of soil ecosystem services

By

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DECLARATION OF OWN WORK

I declare that this thesis 'Re-wilding - An investigation of its effects on earthworm abundance, diversity and their provision of soil ecosystem services' is entirely my own work and that where any material could be construed as the work of others, it is fully cited and referenced, and/or with appropriate acknowledgement given.

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ABSTRACT

Ecosystem services are defined as the benefits humans derive from processes and functions within natural ecosystems. Many ecosystem services crucial to human health, welfare and prosperity are being altered and managed by humans for the benefits they provide. Intensive agricultural practices have been and continue to be a major contributor to global biodiversity loss, which in turn threatens the provision of these services.

Agri-environment schemes were introduced in the 1980s in response to this. These schemes offer payments to farmers to carry out environmentally friendly management practices, such as re-wilding, in the hope this will mitigate and reverse the degradation of ecosystems, the biodiversity they hold and the services they provide.

Re-wilding is a revolutionary environmental management practice that aims to restore ecosystem processes to a near Neolithic state through naturalistic disturbance and grazing regimes.

Earthworms tend to be the most abundant animal biomass within most soil ecosystems. Their behavioural ecology modulates a number of soil ecosystem services. For this reason, this study decided to investigate the effects re-wilding has had on earthworm composition along a chronological sequence as an indirect indicator of changes in a number of soil ecosystem services.

Earthworm abundance and species diversity were recorded using the hand-sorting and mustard extraction methods. Soil characteristics were measured alongside earthworm samples. Regression analyses were carried out to examine correlations between these variables.

Statistically significant positive correlations were observed between the number of years re-wilded and both earthworm species diversity and abundance. It also observed significant correlations between earthworm composition and changes in some soil characteristics which are directly linked to the provision of soil ecosystem services.

This suggests that agri-environemnt schemes, through the application of naturalistic grazing and disturbance regimes, have the ability to support the restoration of ecological functions and processes within degraded agricultural landscapes.

Re-wilding - An investigation of its effects on earthworm abundance, diversity and their provision of soil ecosystem services

INTRODUCTION

Ecosystem services are defined as the benefits humans derive, directly or indirectly, from processes and functions within natural ecosystems (Costanza et al. 1997; Reid et al, 2005; POST, 2007; UKNEA, 2011). They are a product of complex biogeochemical and physical processes that develop as biological organisms interact with one another and their surrounding environment (Swift et al, 2004; Jax, 2005). In the last 20 years, they have become established as a conceptual framework for identifying and acknowledging the historically unappreciated goods and functions that nature provides (Reid et al, 2005; Fisher et al, 2009; Carpenter et al, 2009).

At the most general level, they can be categorised into four groups; provisioning (food, fibre, fresh water *etc.*), regulating (pollination, water purification *etc.*), supporting (primary production, nutrient recycling *etc.*) and cultural services (educational, spiritual etc.) (Reid et al, 2005).

Many ecosystem services are crucial to human health, welfare and prosperity (de Groot, 1987; Matson et al. 1997). In a world where an increasing number of natural ecosystems are being altered and managed by humans for the services they provide, it has become vital to understand and quantify how these ecosystems and their associated services are responding to anthropogenic activity. This study aimed to do this by focusing on earthworm composition as an indirect indicator of changes in a number of services within a particular type of ecosystem, an agricultural ecosystem (agro-ecosystem) in Southern England that underwent a change in management from intensive agricultural production, to the restoration of a stable 'natural/historic' system.

Agro-ecosystems, in common with all ecosystems, both provide and consume ecosystem services. In an anthropogenic context, agro-ecosystems are well recognised for some of their provisioning services (e.g. provision of food, fibre, pharmaceuticals and bioenergy (Power, 2010)). Other types of services agro-ecosystem provide include; supporting services (e.g. maintenance of soil fertility), regulating services (e.g. the regulation of the population dynamics of pests) as well as cultural services (e.g. recreational hunting).

In turn, agro-ecosystems depend on an array of services themselves; including supporting (e.g. soil structure) and regulating services (e.g. pollination) (Swinton et al, 2007). These are brought about and regulated by biota in surrounding ecosystems, whether native or managed (Tilman, 1999; Swift et al, 2004; Zhang et al, 2007; Power, 2010; Blouin et al, 2013).

Soil is a natural resource with the capability to support a diversity of biota providing a suite of ecosystem services (Edwards, 2004; Pulleman et al, 2012). Earthworms are a key component of this biota and their transformative effects on soil formation, structure and fertility provide ecosystem services (Mackay et al, 1982).

Intensive agriculture intended to produce high crop yields has also produced disservices (effects to ecosystems that are deemed undesirable) such as agro chemical contamination, pesticide poisoning of non-target species and nutrient runoff. These disservices have led to the loss of key ecological functions and processes through habitat degradation. (Tilman, 1999; Zhang et al, 2007; Swinton et al, 2007).This has triggered the conversion from natural and complex to less diverse homogenous ecosystems (Tilman, 1999; Benton et al, 2003) which in turn has led to a decline in farmland biodiversity throughout much of the UK and many other parts of the world (Krebs et al, 1999; Robinson & Sutherland, 2002; Benton et al, 2003 Kleijn et al, 2009).

There is little doubt that loss of biological diversity jeopardises the long-term sustainability of natural ecosystems, as well as agro-ecosystems, by threatening the provisioning, supporting and regulating services upon which these systems rely (Russell, 1989; Matson et al. 1997; Tilman, 1999; Smith et al, 2008a; Power, 2010). It seems clear that natural ecosystems lie in a complex web of interdependent services and dis-services that it consumes and provides.

Developments in agriculture, technology and trade over the last 250 years, have led to the most significant increase in human population in history (Krautkraemer, 1994). Currently, it is estimated that there are over seven billion people on earth, more than 500 million of whom inhabit Europe (EUROSTAT, 2013a). These figures are expected to continue rising (EUROSTAT, 2013b; World Bank, 2013).

Currently, agricultural landscapes cover approximately 45% of Europe (Busch, 2006) and more than 70% of the UK (Defra, 2012). Growth in population and consumption has, and will continue to, result in large-scale land-use changes, primarily due to an increase in the demand for agro-ecosystem provisioning services (i.e. food, fibre and energy) (Kleijn et al, 2006; Verburg et al, 2006; Godfray et al, 2010). To meet this demand, intensive agricultural practices have proliferated to the point where it has become essential for agro-ecosystem management to account for their effects on surrounding ecosystems. Without this accountability the services upon which natural ecosystems, including agro-ecosystems, rely are set to deteriorate or be at risk of disappearing completely. Thus, a conscious balance needs to be struck between the exploitation of ecosystem services and the sustainable management of the functions and processes that underpin them.

In light of this pressure, during the 1980s in Europe, the Common Agricultural Policy (CAP) adopted provisions for its member states to engage in Agri-Environment Schemes (AES). These are schemes of environmental management intended to reverse the decline in biodiversity throughout the European agricultural landscape by financially incentivising farmers and other landowners to adopt environmentally sensitive farming practices. Examples of these schemes include the Environmentally Sensitive Areas (ESA) which aimed to maintain and enhance the biodiversity of farmland species and habitats and the Countryside Stewardship Scheme (CSS) which encouraged the creation of field margin strips among several other things (Ovenden et al, 1998; Lobley & Potter, 1998; Morris et al, 2000 Herzog, 2005; Kleijn et al, 2006).

Over the past decade, research has recommended that the centre of gravity of agro-environmental management be moved from the level of species and habitats, to that of landscapes and ecosystems, in the expectation that this will promote a broader awareness and better understanding of the relationships between biodiversity management and ecosystem services (Bengtsson et al, 2002; Benton et al, 2003; Tscharntke et al, 2005; Barrows, 2013).

In 2005, a new AES called Environmental Stewardship (ES) expressing this shift in focus was launched. These are a set of schemes acknowledge the requirement of an 'ecosystem goods and services approach' towards environmental management (Carpenter et al, 2009; Berry et al, 2011; Reed et al, 2013). They have enabled the development and implementation of re-wilding; a revolutionary environmental management practice that aims to restore ecosystem processes using naturalistic disturbance and grazing regimes, at a landscape-level (Bignal & McCracken, 2009; Brown et al, 2011; Navarro & Pereira, 2012).

Although the importance of AES in supporting above-ground farmland biodiversity has been well documented, few studies have investigated the effect of AES below ground on soil invertebrate communities (Hole et al, 2005; Smith, et al, 2008a; Smith et al, 2008b; Taylor & Morecroft, 2009; Roatry & Schmidt, 2013; Blouin et al, 2013). As earthworms are a major component of these communities and important providers of ecosystem services throughout a variety of ecosystems, it is essential that research addresses this lack of knowledge.

The objectives of this study were to assess the effects re-wilding has had on earthworm abundance, diversity and their provision of a number of soil ecosystem services in Southern England. The study was carried out in the Knepp Castle Estate (Knepp hereafter); an agro-ecosystem located in West Sussex that has introduced a significant change in management over the last 15 years, from intensive agricultural production to a large-scale landscape-level re-wilding project. The study made full use of the fact that the estate had introduced fields into the re-wilding project in an annual chronological sequence (chrono-sequence). Changes in earthworm abundance diversity and provision of several chosen soil ecosystem services were investigated along this chrono-sequence.

Literature review

This literature review has been divided into two sections. The first section explores the literature that has contributed to our understanding of the functional role earthworm composition has within the soil on ecosystem processes and the provision of selected soil ecosystem services.

The second section reviews background literature on the main contributing factors of the global 'biodiversity crisis' and then briefly explores the history of the techniques used in conservation biology to address this crisis. Given the underwhelming empirical data quantifying actual or potential benefits restoration management practices such as re-wilding have had on below-ground biodiversity, the section necessarily finishes by focusing on the theory behind the use of these practices to conserve soil biota.

EARTHWORMS AND SOIL ECOSYSTEM SERVICES

Earthworms are present in the soils of almost every terrestrial ecosystem throughout the world (Lee, 1985) and they tend to be the most abundant animal biomass within these ecosystems (Lavelle & Spain, 2001). Despite earthworms being recognised as an important component of soil biota for many years (Edwards, 2004), their contribution to the modification of ecosystem processes and the subsequent provision of ecosystem services has not been explored in depth until recently (Blouin et al, 2013).

Earthworm burrowing, consumption and egestion activities directly modulate soil ecosystem services such as soil formation, structure and nutrient cycling. They also indirectly influence other services such as soil aeration, water regulation and primary production (Darwin, 1881; Lavelle et al, 2004; Edwards, 2004). It is for these reasons that earthworms have been identified as 'ecosystem engineers' (lavelle, 1996; lavelle, 2002; van Eekeren et al, 2010; Blouin et al, 2013).

The interactions between the services earthworms modulate are extremely complex and dynamically interlinked, thus it is difficult to consider one service alone without acknowledging how it influences or is influenced by other closely related services (Brown & Doube, 2004; Natural England, 2012). In this light, it must be noted that the categories used below necessarily oversimplify and underestimate the extent to which the boundaries between these services overlap.

- ***Soil formation***

It has long been an established fact that the behavioural ecology of earthworms affects soil formation (Darwin, 1881). Earthworms consume organic matter produced by plants and other heterotrophic organisms. The organic matter consumed by earthworms is mixed with soil mineral particles to form water-stable aggregates and reduced in size through comminution. These aggregates are then deposited either within the burrows or on the soil surface, where they improve the moisture loading capacity of the soil (Edwards, 2004). As different earthworm species have different ecological strategies, the exact type of organic matter consumed depends on the species of earthworm concerned. Some prefer decaying organic matter and others only feed on inorganic fractions of soil.

There are numerous studies that have investigated the relationship between soil formation and earthworm abundance. Kubiena (1953) showed that in some part of Europe, earthworms are responsible for forming up to half of the aggregates in the surface layer of the soil. Other studies Hendrix et al (1992) investigated the abundance and distribution of earthworms throughout different agro-ecosystems in Georgia, U.S.A. Their results showed a positive relationship between earthworm abundance and standing stock of organic matter.

Earthworm species are generally categorised into three ecological groups; epigeic, endogeic and anecic (Bouché, 1977; Lavelle et al, 2004).

- Epigeic earthworm species typically reside and forage within the litter layer accumulated on the soil surface and tend not to burrow into soil.
- Endogeic species of earthworm form branched, horizontal burrows in the soil. They usually reside within the upper 15cm layer of the soil and feed on decomposed plant matter.
- Anecic earthworm species create deep vertical burrows in the soil and influence soil organic matter (OM) by consuming decaying surface organic residues, which they drag down into their burrows (Shipitalo & Renee-Claire, 2004).

Poier & Richter (1992) examined the spatial distribution of earthworms under winter barley and sugar beet. They found significant positive correlations between both the abundance and biomass of the anecic earthworm species *Lumricus terrestris* (*L.terrestris*) and the organic carbon content in top 30cm of the soil (Ap-horizon). They also found a significant positive relationship between aggregate density in the Ap-horizon and the abundance of the endogeic earthworm species *Aporrectodea caliginosa* (A.*caliginosa*).

- ***Soil structure***

As previously mentioned, earthworms comprise several functional groups, thus the relationship between soil structure and earthworm activity varies, depending on the species of earthworm concerned (Figure 1). Their activities alter the physical, chemical and biological properties of the soil and in turn modulate the availability of resources to other organisms. There are numerous papers that have investigated the effect earthworms have on soil water infiltration rate throughout different agricultural ecosystems (Clements, 1982; Bouché & Al-addan, 1996; Shipitalo & Renee-Claire, 2004; Blouin et al, 2013).

Burrows formed by earthworms act as tubular pathways which facilitate the movement and storage of water, leading to improved drainage (Bardgett et al, 2001). Clearly, the degree to which this is the case depends on the type of soil, the diameter and connectivity of the burrows in question (Kretzschmar, 2004).

In 1991, Clements et al showed that an experimentally induced absence of earthworms over a 20 year period within plots of a sward sown to perennial ryegrass in England, led to a significant reduction in soil moisture content and soil water infiltration rate. Similarly, Katsvairo et al (2007) found a statistically significant positive correlation between soil water infiltration rate and earthworm population densities in a conventional peanut/cotton rotation system in Florida.

Willoughby & Kladivko (2002) introduced *L.terrestris* into no-till fields that were absent of earthworms in Indiana. Unsurprisingly, they found a statistically significant positive relationship between the number of *L.terrestris* and soil water infiltration rate.

Others papers have been more specific in their approach, linking the spatial distribution patterns of particular species of earthworm with underlying soil hydrological characteristics. For example, Cannavacciuolo et al (1998) conducted a geostatitical approach to characterise the spatial variability of *L.terrestris* and *A.caliginosa*, in a temperate grassland system in Brittany, France. Their results showed that the total biomass of adult earthworms from both species correlated positively with soil hydrology.

- ***Nutrient Cycling***

Through the aforementioned burrowing, consumption and egestion activities, earthworms accelerate the rate at which organic matter is decomposed by increasing the surface area of organic matter available to microbial activity (Seeber et al, 2008). According to Edwards (2004), earthworms simulate microbial activity by an order of magnitude during feeding. In addition to this, during feeding, key nutrients within organic matter such as nitrogen, phosphorous and potassium are converted into a form that is available to plants (Edwards, 2004; Bityutskii et al, 2002).

Earthworms affect numerous soil nutrient cycling processes (Bohlen et al, 2004). James (1991) showed that the concentration of mineral nitrogen in earthworm casts, throughout a single year, accounted for approximately half of the annual plant phosphorous uptake and 12% of the annual plant nitrogen uptake in a prairie grassland system in the Kansas. Eriksen-Hamel & Whalen (2007) investigated the effects earthworms have on soil nitrogen pools and plant growth in maize and soybean agro-ecosystems. They found a strong linear relationship between earthworm abundance and the concentration of both soil mineral nitrogen and microbial biomass nitrogen.

As shown above the behavioural ecology of earthworms directly modulates soil ecosystem services such as soil formation, structure and nutrient cycling. It also indirectly modulates other services, such as water regulation, primary production and the creation of habitats for microbial communities. Consequently, earthworm activities influence the provision of many environmental goods and functions that humans and many other organisms benefit from.

Burrows formed by earthworms alter the porosity of soil. This in turn affects soil water infiltration rate which is an essential process for water regulation (Gómez-Tagle, 2009). According to the UK National Ecosystem Assessment (UKNEA), water regulation is an extremely important ecosystem service, particularly in the light of climate change, as it provides humans with flood protection and erosion control (Georgina et al, 2011).

Bardgett et al (2001) explains that improvements in soil porosity due to earthworm burrowing activity allow plant roots to proliferate and exploit larger areas of the soil profile for water, thus increasing their retention and/or uptake of water.

Both earthworm burrowing and egestion activities indirectly create habitats for a suite of microbial communities by altering soil structure and stimulating soil formation. Kretzschmar (2004) explains that the dynamics of microbial activities are closely related to the concentration gradients of solutes, water and gases present in earthworm burrows. Moreover, earthworm burrows are lined with both protein and carbon rich mucus which create favourable environments for microbial and plant communities (Brown & Doube, 2004).

RE-WILDING

Currently, there are over seven billion people inhabiting the earth, a figure which is projected to exceed nine billion by 2050 and cause a 70-100% increase in the demand for food (Godfray et al, 2010; U.N. Population Division, 2013; U.S. Census Bureau, 2011; Tscharntke et al, 2012). Estimates suggest agricultural production will have to be doubled or even trebled in order to meet this future demand and it is likely that any significant increase in agricultural production will involve further conversions of currently unproductive land (Green et al, 2005, Tscharntke et al, 2005; Brussaard et al, 2010 Sunderland 2011).

The conventional approach to achieve food security has been to convert complex, heterogeneous wild lands, into intensively managed, homogenous agricultural landscapes (Green et al, 2005). Such conversions have been the principal driver of global biodiversity loss and have led to the degradation of many ecosystems and the services they provide (Tscharntke et al, 2005; Pimentel et al, 2007; Godfray et al, 2010; CBD, 2010; IUCN, 2010; Sunderland, 2011). A prime example of this loss is the rapid decline in numerous populations of farmland birds throughout Europe as a result of the post-war agricultural intensification (Tscharntke et al, 2005). There is no doubt that a conversion-driven agricultural expansion will continue to have a detrimental effect on natural ecosystems and the biodiversity they hold (Norris, 2008; Sunderland, 2011; Tscharntke et al, 2012).

In response to this biodiversity crisis, conservationists have long been debating whether agricultural production and conservation land management ought to be separated (land sparing) or integrated (land sharing). Although these approaches focus on different facets of biodiversity, both schools of thought have their merits. However, it would take decades of controversial debates before these merits would be acknowledged and incorporated together into conservation policy (Dobbs & Pretty, 2004).

Land sparing has been the dominant view in nature conservation for many years, ensuring biologically diverse regions are kept safe from encroachment of agriculture, through the establishment of protected areas (PAs). The first PA was set up in the Unites States in 1872. Since then, the number of PAs around the world has been rising sharply and exceeded 140,000 in 2005 (Chape et al, 2008).Although PAs plays an essential role in safeguarding threatened species whom do not stand a chance of surviving in agricultural landscapes, recent studies have shown that the global network of protected has been unsuccessful in halting the global biodiversity loss (Coad et al, 2009; Mace et al, 2010).

This is primarily because over 50% of all species exist outside of the current network of protected areas, mostly within agro-ecosystems (Blann, 2006; Scherr & McNeely, 2008; Guerrero et al, 2011) For example, Tscharntke et al, (2005) point out that protected areas in Germany only hold around 25% of endangered species, whereas agricultural landscapes hold the remaining 75%. To make matters worse, both the protected areas and the assessments used to evaluate their success appear to be concerned largely with biodiversity patterns (i.e. taxa and land classes) and pay little attention to the underlying processes that have shaped these patterns of biodiversity (Rouget et al, 2003; Mortiz et al, 2005). Moreover, PAs follow an exclusionary top-down approach that often fails to consider important socio-economic and political issues of surrounding communities (Andrade & Rhodes, 2012).

It soon became evident 'land sparing' was not going to be the silver bullet for the conservation of biodiversity that Myers et al (2000) had suggested and is even further from a solution in times of unpredictable climate change and increased competition for land (Tscharntke et al, 2005; Brussaard et al, 2010; Godfray et al, 2010; Tscharntke et al, 2012).

Consequently, during the 1980s in Europe, conservationists, policy makers and land managers began addressing the negative relationship between biodiversity and agricultural intensification through 'land sharing' approaches (often referred to as 'wildlife-friendly farming' (Fischer et al, 2008)) such approaches included agri-environment schemes (AES) (Lobley & Potter, 1998; Ovenden et al, 1998; Kleijn & Sunderland, 2003; European Commission, 2005; Mashall et al, 2006). AES are voluntary agreements designed to financially incentivise farmers to adopt environmentally sensitive management practices that protect and enhance farmland wildlife (Herzog, 2005; Natural England, 2009).

The first agri-environment scheme to be rolled out in England was the Environmentally Sensitive Areas Scheme (ESA) in 1987. The primary focus of this scheme was to financially encourage the conservation and enhancement of particular regions within the country which had a high landscape, wildlife or historic value (Natural England, 2002). ESA was shortly followed by the Countryside Stewardship Scheme (CSS) which was rolled out in 1991 in order to promote the adoption of a wider range of environmentally beneficial management practices in other important areas that were not been covered by ESA. By 2003, more than 1.1 million hectares (~13%) of agricultural land in England were under either an ESA or a CCS (Marshall et al, 2006).

Although these schemes recognised the fact that farmers and other land owners have the potential to contribute to biodiversity conservation, the extent to which this potential was actualised through these schemes on a national scale was insufficient (Bignal & McCracken, 2009; Natural England, 2009). The problem was that both ESA and CCS incentivised the widespread implementation of low-effort management practices on a local scale and paid little attention to the spatial distribution of biodiversity at the landscape-scale. (Tscharntke et al, 2005).

Reviews of these schemes in 2003 suggested that they were failing to maintain and restore high quality wild lands (Natural England, 2009). It recommended that the best elements of these schemes should be combined into a single scheme called Environmental Stewardship (ES), whose scope would consider both biodiversity patterns as well as biodiversity processes (Bengtsson et al, 2002; 2003; Benton et al, 2003; Tscharntke et al, 2005; Barrows, 2013).

ES is a comprehensive national scheme composed of three distinct tiers; Entry Level Stewardship (ELS) scheme, Organic Entry Level Stewardship (OELS) shceme and Higher Level Stewardship (HLS) scheme. ELS are very similar to the CCS and ESA mentioned above in that it incentivises straightforward environmental management practices which attempt to address declines in farmland wildlife. In contrast, HLS reward higher standards of environmental management, including the protection of landscape character and features identified by the European Landscape Convention (2000)- an international treaty whose primary focus is the protection, management and enhancement of European landscapes and the systems within them (Natural England, 2009).

It has become increasingly clear that management of biological organisms at the level of landscapes, as opposed to that of genes, species and habitats, is necessary to maintain the long-term sustainability and resilience of ecosystems and the services they generate (Tscharntke et al, 2005). The HLS schemes recognises this by financially stimulating the design and implementation of ecological restoration practices such a re-wilding, that adopt flexible and open-ended limits to ecological change, as opposed to management practices that set rigid habitat or species targets to reach a desired ecological 'state' (Hodder & Bullock, 2009; Hughes et al, 2011).

In contrast to the active management approaches funded by ES schemes, re-wilding is the passive management of ecological succession which requires little or no human intervention. The aim of re-wilding is to restore ecosystem processes within large, connected, self-sustaining ecosystems by managing keystone species through naturalistic disturbance and grazing regimes (Pykälä, 2000; Navarro & Pereira, 2011; Brown et al, 2011). Re-wilding sets the complex and heterogeneous 'primeval' landscapes of the pre-Neolithic period as the benchmark for nature conservation rather than agricultural man-made landscapes that had previously been used. Thus re-wilding sets the context for natural processes to evolve, giving conservation biologists and land managers a wider temporal perspective of these processes and information which is valuable when designing conservation policy (Vera, 2009).

Despite its potential for biodiversity conservation, only a few re-wilding projects have been set up in England. One of them is at the Knepp Castle Estate in Sussex, where an area of approximately 1,220ha has been put under a re-wilding project ('Wildland project') (Taylor, 2009). Until the 21st century, the Knepp Castle Estate formed a typical English estate, with in-hand and let farmland. Since 1990, Knepp has taken part in numerous agri-environment schemes. In 2001, with support from AES, a plan to put a large part of the estate under a landscape-scale restoration project commenced. By 2006, all fields within the Southern Block had been put under the 'Wildland Project'. Although the re-wilding project was not initiated to stimulate research, it has provided a unique opportunity to investigate the effects restorative management approaches, such as naturalistic grazing and disturbance have on soil. It has been implemented by substituting extinct European megafauna with free grazing, extant species such as Long Horn cattle, Exmoor ponies and Tamworth pigs (Greenaway, 2006).

As earthworms are a major component of these communities and important providers of ecosystem services throughout a suite of ecosystems, they are likely to be excellent indicators for the impact of environmental factors and helpful when monitoring land use transformations such as re-wilding. Currently, no studies have investigated the effects re-wilding has below ground on soil invertebrate communities (Hole et al, 2005; Smith, et al, 2008a; Smith et al, 2008; Blouin et al, 2013). Thus, it is crucial that research addresses this lack of knowledge, which this aim of this study.

Materials and Methods

SITE AND PLOT DETAILS

The Knepp Castle Estate (51.006491°N, 0.335335 °W) is an 11th century estate located in lowland England south of Horsham, West Sussex. The estate lies on Wealden Clay and is approximately 3,600 acres. The estate has been divided up into three distinct sections; the Northern Block, Middle Block and Southern Block (*Figure 1*).

Figure 1: *The Knepp Castle Estate is comprised of the Northern (red), Middle (orange) and Southern Block (white)*

The majority of the study was conducted in the Southern Block (*Figure 2*). However, since all the fields within the Southern Block had been taken out of agricultural production, control sites that were still under intensive agricultural production outside of The Knepp Estate (*i.e.* zero years re-wilded) were used. All of these control sites were located within Prior's Byne Farm, West Sussex. This primarily because the agricultural practices used on this farm are very similar to those used in the Southern Block prior to the re-wilding project. Both study sites (Southern Block and controls) are within 2.5km one of each other and share the same underlying geology.

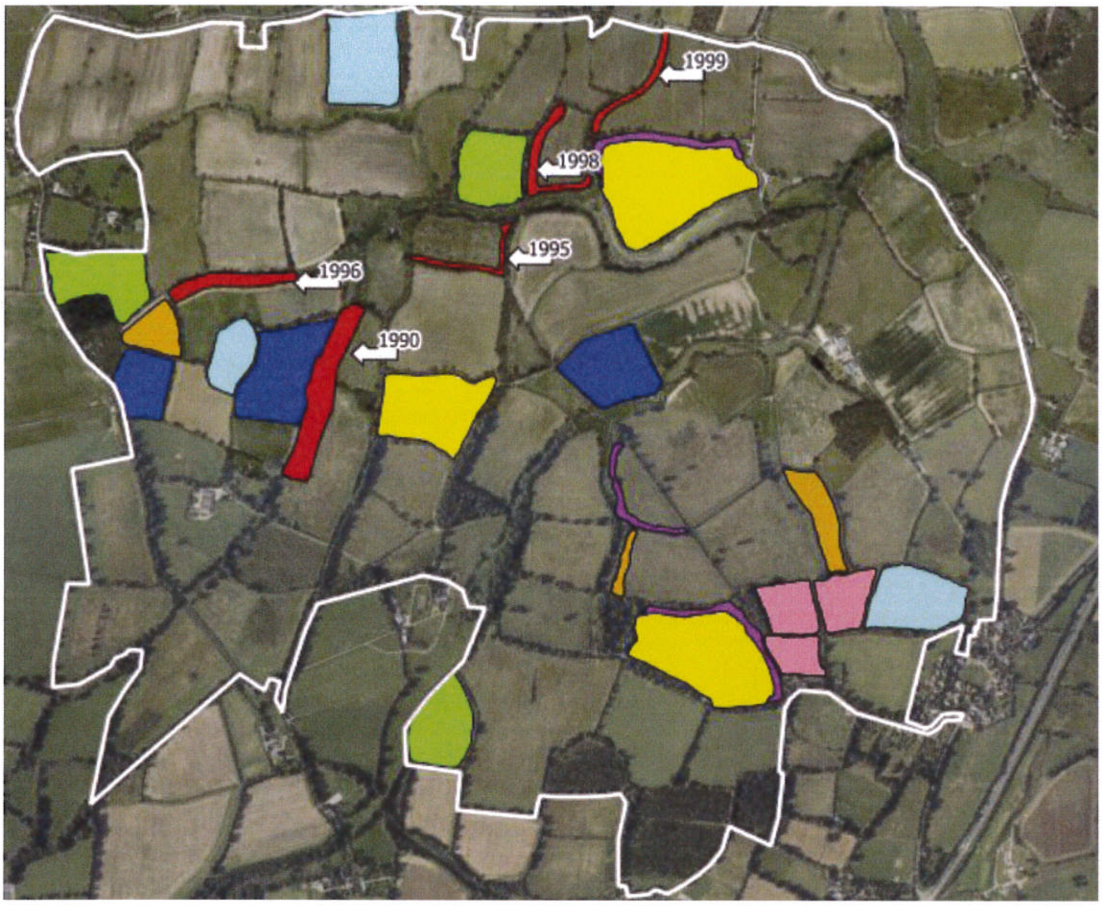

Figure 2: *The Southern Block and the fields sampled. The fields which were not part of a triplet have been highlighted in red and are marked by the year in which they were set aside. Fields re-wilded in: 2000 (pink), 2001 (purple), 2002 (orange), 2003(green), 2004 (light blue), 2005(yellow) and 2006 (dark blue).*

EXPERIMENTAL DESIGN

In order to make full use of the chronological sequence of re-wilding within the Southern Block, data was collected from fields that had been re-wilded in consecutive years between 1990 and 2006.

Where possible, three field replicates were chosen for each year along the chronological sequence. Single replicates were used for years in which only single fields were re-wilded. There were also some years in which no fields were re-wilded. Naturally, these could not be included in the study. A total of 29 fields were sampled from the Knepp Estate and Prior's Byne Farm. Three replicates were chosen for the years: 2000, 2001, 2002, 2003, 2004, 2005, 2006 and 2013 ('before control'). The single replicate years were: 1990, 1995, 1996, 1998 and 1999. In order to minimise the effects of temporal variation, sampling was stratified throughout the whole sampling period.

EARTHWORM SAMPLING

Sampling took place between the May 20th and June 28th 2013. In order to maximise sampling efficiency, a combination of two earthworm sampling methods were used at every sampling point (Pelosi et al, 2008). These were (1) the passive hand sorting method and (2) the behavioural mustard extraction method (Eisenhauer et al, 2008; Valckx et al, 2011).

1. *Hand sorting*

This involved sampling a known volume of soil for earthworms. In each field, a 25m^2 sampling area was marked out using a set of 30cm tape measures. Six sampling points were chosen at random within the 25m^2 area. A single 25 cm x 25 cm x 10 cm deep block of soil (monolith) was excavated at each sampling point. The monolith was placed on a tray so that earthworms could be hand sorted on site into pots containing 80% alcohol.

2. *Mustard extraction*

In contrast to the active hand sorting method described above, this sampling technique relies on the activity of a chemical expellant in mustard powder, allyl isothiocyanate (AITC), to oust earthworm from the soil (Gunn, 1992). Both the hand sorting and mustard extraction techniques were carried sequentially. Once a monolith had been extracted for hand sorting, a mustard solution was evenly poured into the pit and any earthworms that emerged over a 30 minute period were collected.

The preparation of the final mustard was based on the procedure described by Lawrence & Bowers (2002) and involved two steps:

- ***(i)*** 570g of Colmans mustard powder was mixed with 1.140 L of water to form a preliminary mustard solution and
- ***(ii)*** 25ml of the preliminary solution was further dilute into 1.25L of water to form the final mustard solution.

This final mustard solution was used in a single pit, thus the two-step process outlined above was repeated another five times to create six mustard solutions. A total of 174 final mustard solutions were created in order to sample the 29 fields. All of these steps were carried out in the laboratory shortly before sampling to ensure that the active chemicals in the suspension did not lose their irritating activity (Pelosi et al, 2009).

In order to avoid pseudoreplication for earthworms and environmental variables, all data collected from pits dug on the same field were averaged. This meant that each field entered into the analyses as a single datum point, creating a dataset for the analysis, with 29 spatial replicates.

SPECIES IDENTIFICATION

Earthworms were identified to species level using Sims & Gerard (1999). Only adult earthworms could be identified. Immature (juvenile) worms were counted but not identified. Species identification data were used to calculate both the species richness and abundance of earthworms.

ECOLOGICAL GROUPS

As juveniles could not be identified to species level, they were assigned to a functional group, based on the criteria of Bouché (1977) (see literature review). Adult earthworm species were also assigned to functional groups.

ENVIRONMENTAL VARIABLES

Data on numerous abiotic soil parameters were collected at every sampling point and averaged out across the six sampling points in each site. Air temperature (°C) was recorded using a thermometer that had been carefully situated out of direct sunlight. Soil moisture readings were collected in the 5-10cm layer below the soil surface using Delta-T Moisture meter with an attached SM300 moisture sensor (Delta-T Devices Ltd). This measured volumetric moisture content in cubic metres of water per cubic meter of soil ($m^3.m^{-3}$). Soil pH was recorded using a PH-220S soil pH meter (Lutron Electronic). Soil penetration resistance readings ($kg.cm^{-2}$) were collected using a Delrin™ pocket penetrometer (Geo-Enterprise Inc). Shear torsion readings ($kg.cm^{-2}$) of topsoil were collected using a Torvane® shear torsion meter (Geo-Enterprise Inc). Soil cores were ($126cm^3$) were collected alongside each pit and were left to dry for a week. Once dry these cores were then weighed in order to calculate their relative bulk density ($g.cm^{-3}$). Soil infiltration rate ($L.s^{-1}$) was recorded determined collected by timing how long it took for the final mustard solution to fully penetrate the soil at the bottom of the pit.

STATISTICAL ANALYSIS

Multiple regression analyses were conducted in R (R Development Core Team 2012) to examine the effects re-wilding has had on earthworm abundance and species richness. These models were used to test whether the abundance and diversity of earthworms was associated with variation in the environmental variables recorded. All factors and interactions of interest were fitted to a maximal model. The maximal model was simplified to a minimum adequate model by the removal of non-significant variables, interactions, and non-linear terms.

Redundancy analysis (RDA) was carried out to illustrate relationships between environmental data, earthworm abundance species richness and changes in functional group composition using the CANOCO 5 software programme (ter Braak & Šmilauer, 2012). RDA is an ordination method that was used to examine the association between linear combinations of environmental variables and earthworm composition. In the case of RDA the analysis assumes that underlying environmental gradients have linear relationships with individual species abundances. The statistical significance of these relationships was analysed using Monte Carlo permutation tests. All non-significant explanatory variables were removed as RDA is a constrained ordination method able to select the best explanatory variables to fit graphically (Roatry & Schmidt, 2013).

Results

A total of 1988 earthworms were sampled, comprising 616 adult earthworms and 14 species. The most abundant species was *Aporrectodea rosea* with 143 individual. The percentage of juvenile epigeic, endogeic Anecic earthworms were 21.2%, 39.5% and 8.2% respectively. Only one of these species, (*A.c.nocturna*), was represented by a single individual.

Table 1: earthworm species, the ecological group they belong to and the percentage they comprise of the total.

Earthworm Species	Ecological group	Percentage composition
Aporrectodea rosea	Endogeic	23.2
Allolobophora chlorotica	Endogeic	22.1
Lumbricus rubellus	Epigeic	14.1
Aporrectodea caliginosa	Endogeic	11.0
lumbricus castaneus	Epigeic	6.7
Lumbricus terrestris	Anecic	5.7
Aporrectodea longa	Anecic	5.5
Apporectodea icterica	Endogeic	2.9
Satchellius mammalis	Epigeic	2.8
Lumbricus festivus	Epigeic	2.4
Murchieona muldali	Endogeic	1.8
Octolasion tyrtaeum	Endogeic	1.3
Eiseniella tetraedra	Epigeic	0.3
Aporrectodea caliginosa (nnocturna)	Endogeic	0.2

EARTHWORM ABUNDANCE

The minimum adequate regression model showed earthworm abundance was strongly positively correlated with years re-wilded (t=4.94, d.f=27, p<0.001) (*Figure 3 and 4*). This relationship remained statistically significant when fields represented by a single replicate were removed from the analysis (t=7.18, d.f=27, p<0.001). The minimum adequate model also showed earthworm abundance was also positively correlated with air temperature (t=2.38, d.f=27, p<0.05).

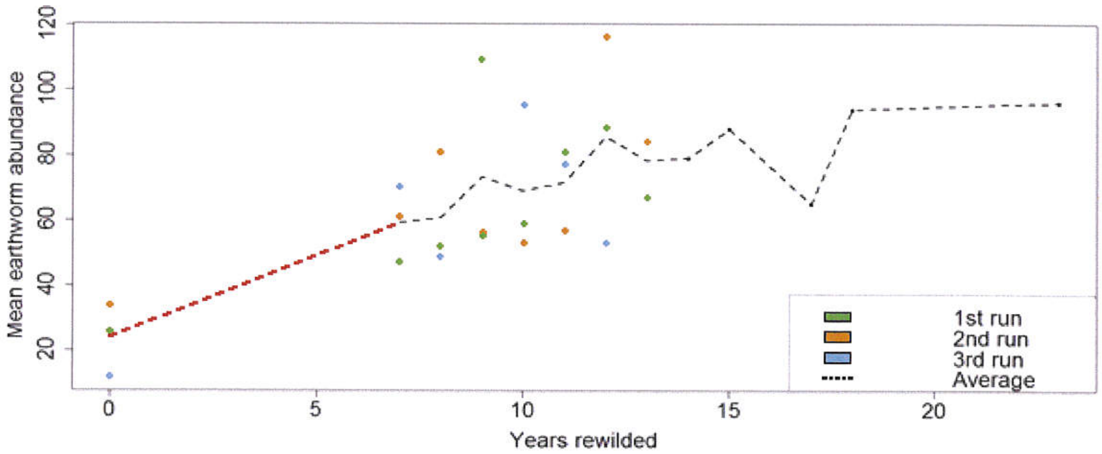

Figure 3: *Mean earthworm abundance per individual run during different stages of re-wilding. The red dashed line indicates that this portion of the graph has been inferred and may not be a true reflection of the relationship between the variables shown.*

(B)

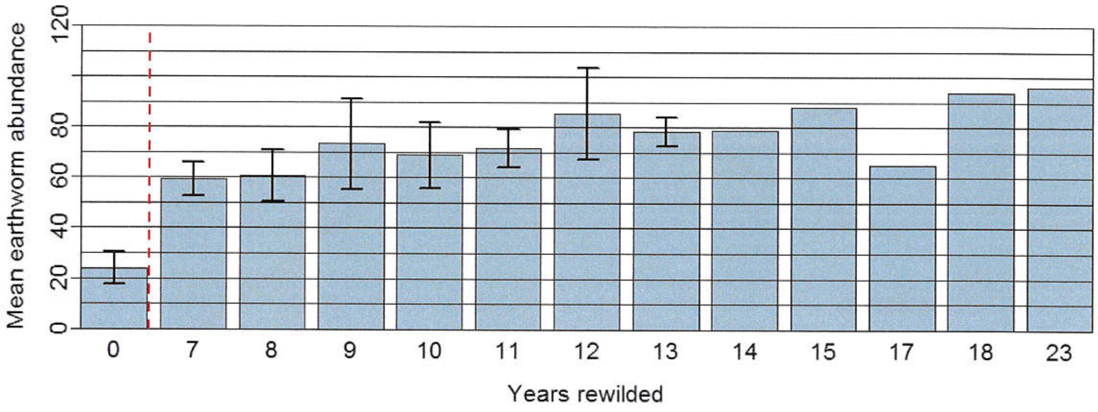

Figure 4: *Overall means of abundance of earthworm communities throughout different stages of re-wilding. Error bars show the standard error. Absence of error bars indicates that only one replicate was available for that given year.*

The Redundancy Analysis (RDA) revealed that years re-wilding was significantly positively correlated with earthworm abundance (p<0.001). The RDA showed that *A.caliginosa*, *A.longa* and *A.chlorotica* were strongly correlated with years re-wilded, whereas *L.terrestris* was negatively correlated with years re-wilded. The RDA showed no correlation between year re-wilded and *L.rubellus*, *A.c.nocturna and E.tetraedra.* The RDA also revealed that *A. rosea* and *L.castaneus* did not appear to be correlated with years re-wilded but were positively correlated with topsoil shear torsion.

The RDA also showed that juvenile earthworm abundance was significantly positively correlated with years re-wilded (p<0.001), soil moisture (p<0.05) and topsoil penetration resistance (P<0.05). The RDA biplot in *Figure 5* clearly shows a negative correlation between soil moisture and the abundance of juvenile endogeic earthworms and the absence of a correlation between years re-wilded and the abundance of juvenile endogeic earthworms. The RDA also shows a positive correlation between years re-wilded and the abundance of juvenile epigeic and anecic earthworms.

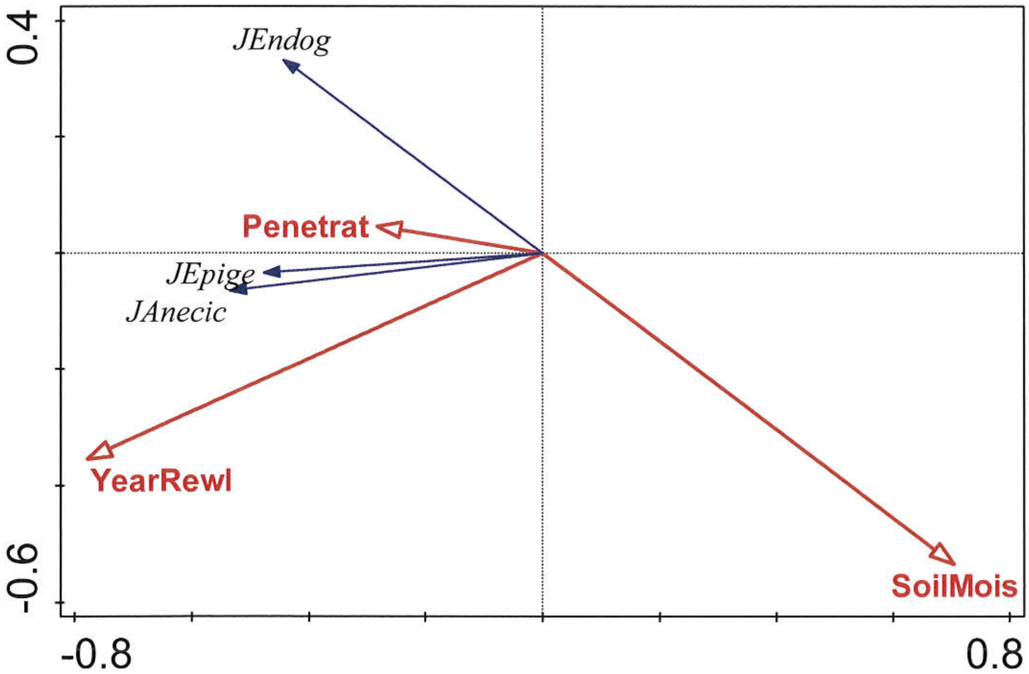

Figure 5: *RDA biplot showing the correlation between environmental variables (red arrows) and abundance of juvenile earthworms (blue arrows). The first two RDA axes explain 53% of the variability in earthworm species abundance. Environmental variables accounted for 27.9% of the total variability. Abbreviations: top soil shear torsion (ShearTors) number of years re-wilding (YearRewl), juvenile epigeic (JEpige), juvenile anecic (JAnecic), juvenile endogeic (JEndog).*

EARTHWORM SPECIES DIVERSITY

The minimum adequate regression model showed earthworm species diversity was strongly positively correlated with years re-wilded (t=3.056, d.f=27, $p<0.05$) (*Figure 6 and 7*). This relationship remained statistically significant even after fields represented by a single replicate were removed from the analysis (t=4.62, d.f=27, $p<0.01$). The model also showed there was a statistically significant positive relationship between earthworm species diversity and air temperature (t=3.15, d.f=27, $p<0.01$).

(A)

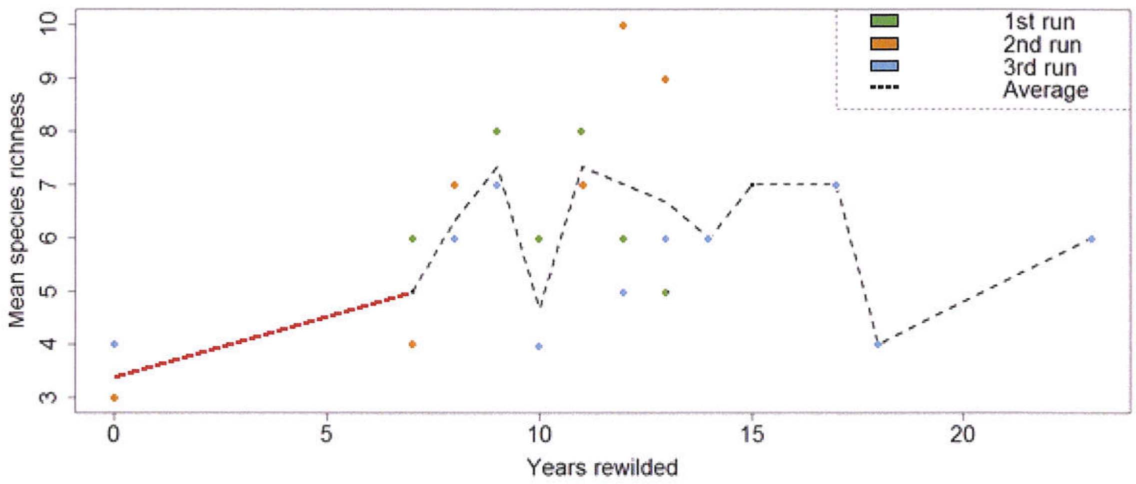

Figure 6: *Mean earthworm species richness per individual run during different stages of re-wilding. The red dashed line indicates that this portion of the graph has been inferred and may not be a true reflection of the relationship between the variables shown..*

(B)

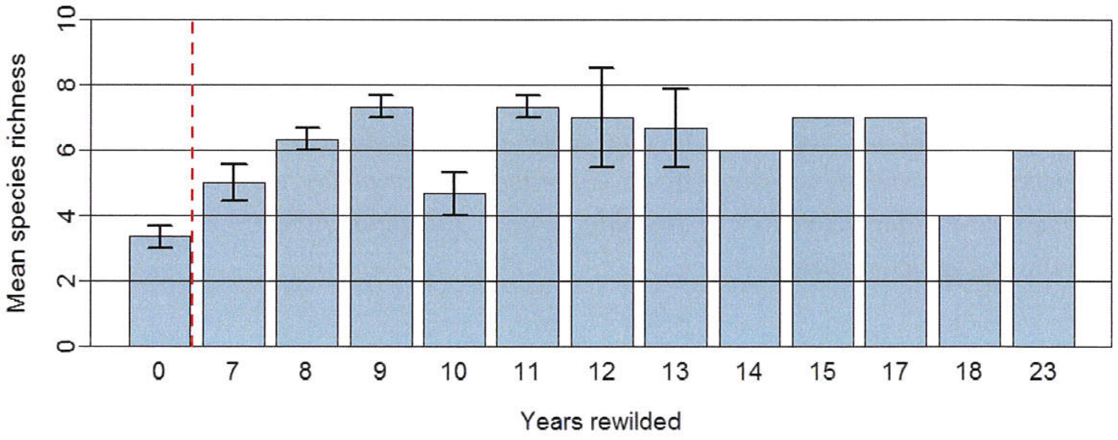

Figure 7: *Overall means of earthworm species richness throughout different stages of re-wilding. Error bars represent the standard error. Absence of error bars indicates that only one replicate was available for that given year. Red line signifies the six year gap in the chrono-sequence.*

ECOLOGICAL TYPES

The Redundancy Analysis (RDA) indicated there was no correlation between the abundance of anecic earthworm species and the number of years re-wilding. However, there was a strong, significant positive correlation between years re-wilded and the abundance of both endogeic and epigeic species of earthworm (P<0.05) (*Figure 8*).

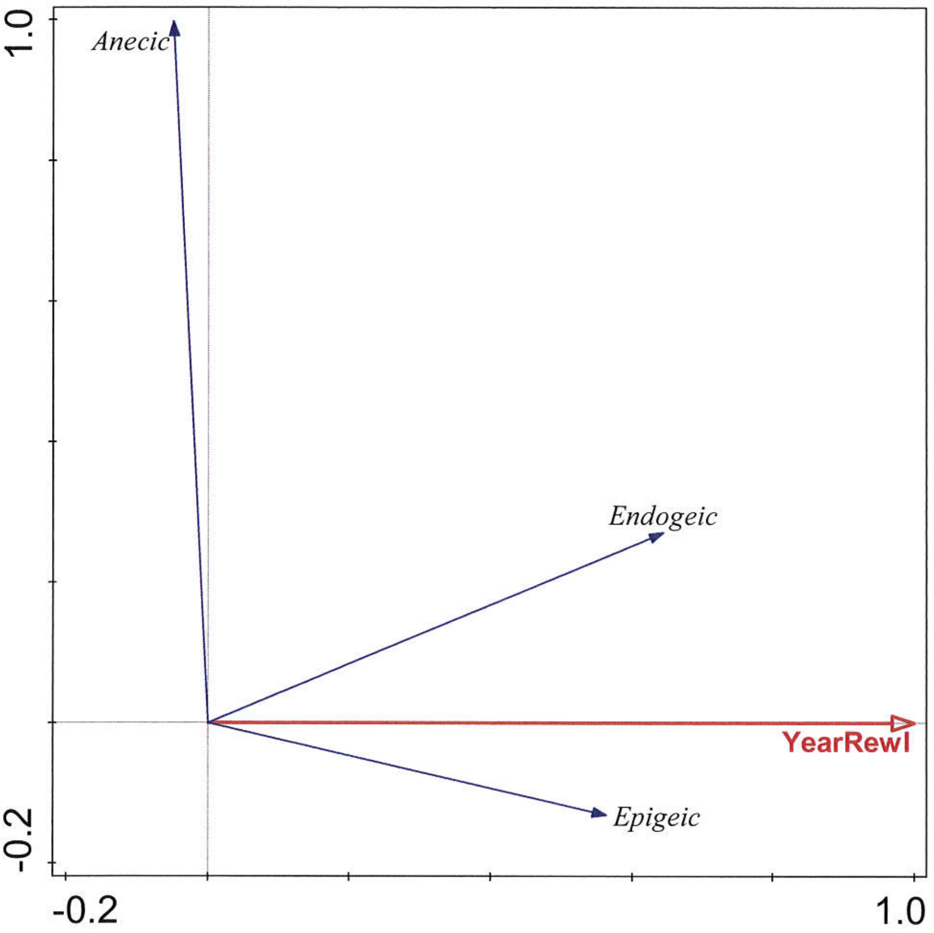

Figure 8: *RDA biplot showing the correlation between environmental variable (red arrow) and abundance of three ecological groups (adults + juveniles) (blue arrows). The first two axes explain 47.3% of the variability in abundance of the ecological groups of earthworms. Environmental variables accounted for 27.2% of the total variability. Abbreviations: number of years re-wilding (YearRewl), juvenile epigeic (JEpige), juvenile anecic (JAnecic), juvenile endogeic (JEndog).*

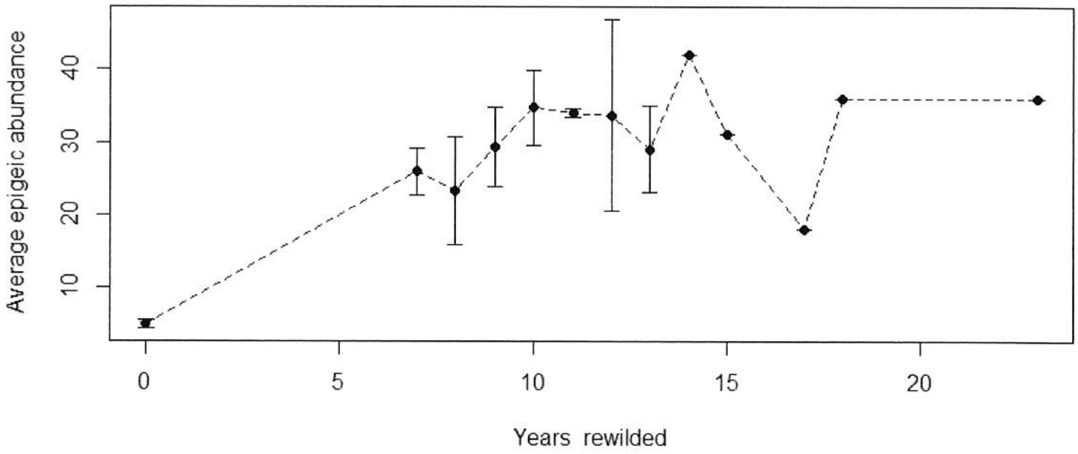

Figure 9: *Mean abundance of epigeic earthworm species throughout different stages of re-wilding. Error bars represent the standard error. Absence of error bars indicates that only one replicate was available for that given year.*

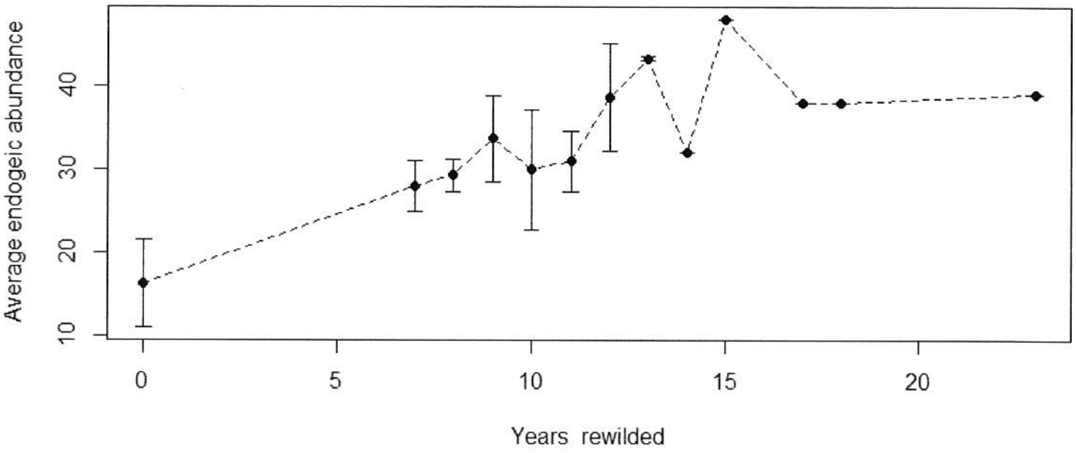

Figure 10: *Mean abundance of endogeic earthworm species throughout different stages of re-wilding. Error bars represent the standard error. Absence of error bars indicates that only one replicate was available for that given year.*

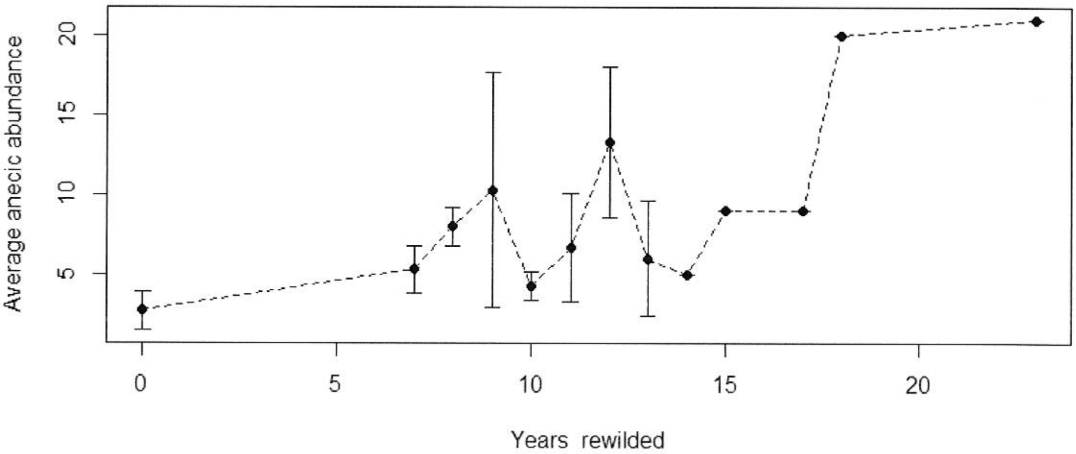

Figure 11: *Mean abundance of anecic earthworm species throughout different stages of re-wilding. Error bars represent the standard error. Absence of error bars indicates that only one replicate was available for that given year.*

ABIOTIC SOIL PROPERTIES

Regression analyses showed there was a significant negative correlation between years re-wilding and both soil moisture and top soil shear torsion (*Figure 12 and 13*). Regression analyses also showed a significant negative relationship between earthworm abundance and soil moisture (*Figure 12*). Although several other soil characteristics correlate with year re-wilded, the strength of these correlations was not statistically significant (Figure 14, 15 and 16).The results from these analyses have been summarised in *Table 2*.

Table 2: *Results of regression analysis of soil properties against years re-wilded, earthworm abundance and earthworm species richness. Abbreviations of soil properties: (PR) Penetration resistance, (ST) Shear torsion, (SD) Soil density, (SP) Soil pH, (SWIR) Soil water infiltration rate and (SM) Soil moisture.*

		PR	**TST**	**RSD**	**SP**	**SWIR**	**SM**
Years re-wilded	t-value	-1.593	**-2.291***	-0.997	1.186	-1.502	**-3.921*****
	Multiple R^2	0.086	0.163	0.035	0.049	0.077	0.036
	Adjusted R^2	0.052	0.132	-0.0002	0.014	0.034	0.339
Earthworm abundance	t-value	-0.473	-0.324	-0.019	0.408	0.435	**-2.544***
	Multiple R^2	0.008	0.003	1.275e-05	0.006	0.007	0.0193
	Adjusted R^2	-0.029	-0.033	-0.037	-0.031	-0.029	0.163

‘***’ $P<0.001$ ‘**’ $P<0.01$ ‘*’ $P<0.05$

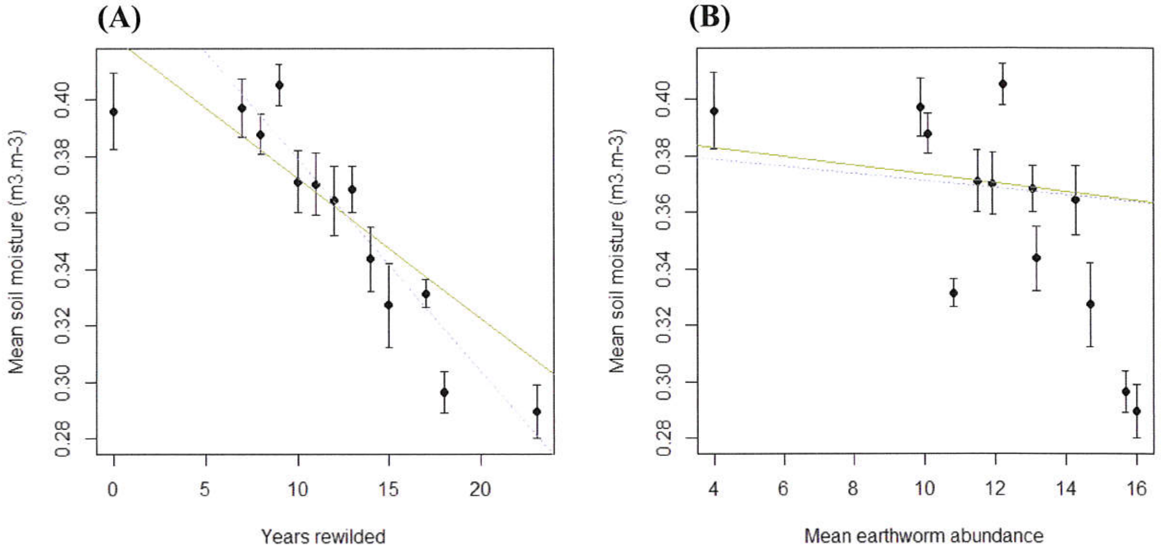

***Figure 12**: Mean soil moisture content as a function of (A) years re-wilding, with control (green) ($y = -0.004x + 0.42$), without control (blue) ($y = -0.007x + 0.45$) and mean soil moisture content as a function of (B) mean earthworm abundance, with control (green) ($y = -0.002x + 0.39$), without control (blue)($y = -0.001x + 0.38$).*

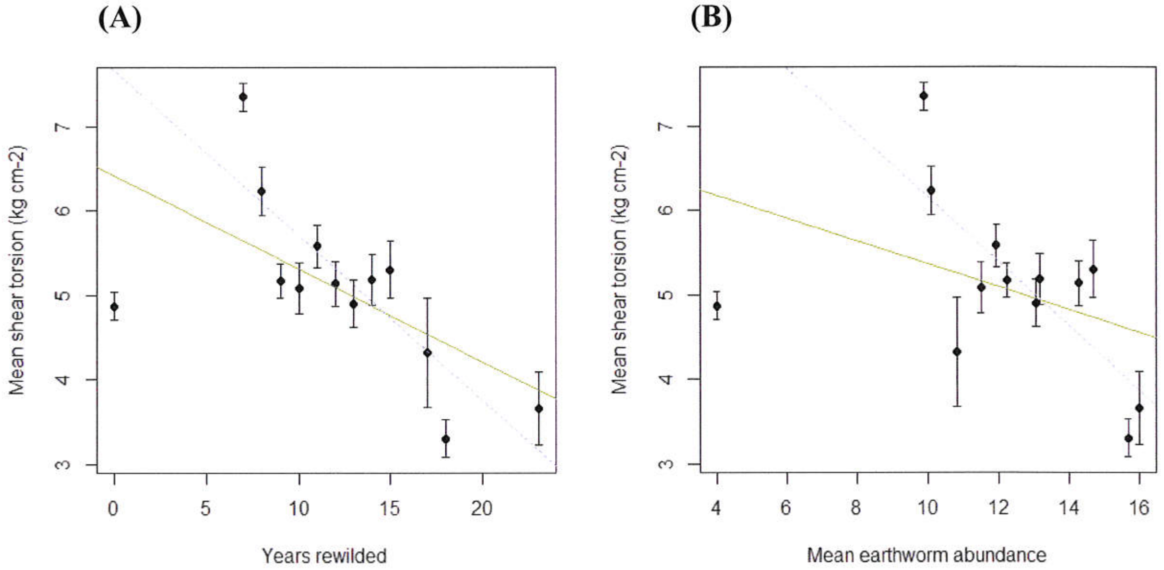

***Figure 13**: Mean top soil shear torsion as a function of (A) years re-wilding, with control (green) ($y = -0.11x + 6.4$), without control (blue) ($y = -0.19x + 7.7$) and mean top soil shear torsion as a function of (B) earthworm abundance, with control (green) ($y = -0.14x + 6.7$), without control (blue)($y = -0.38x + 9.9$).*

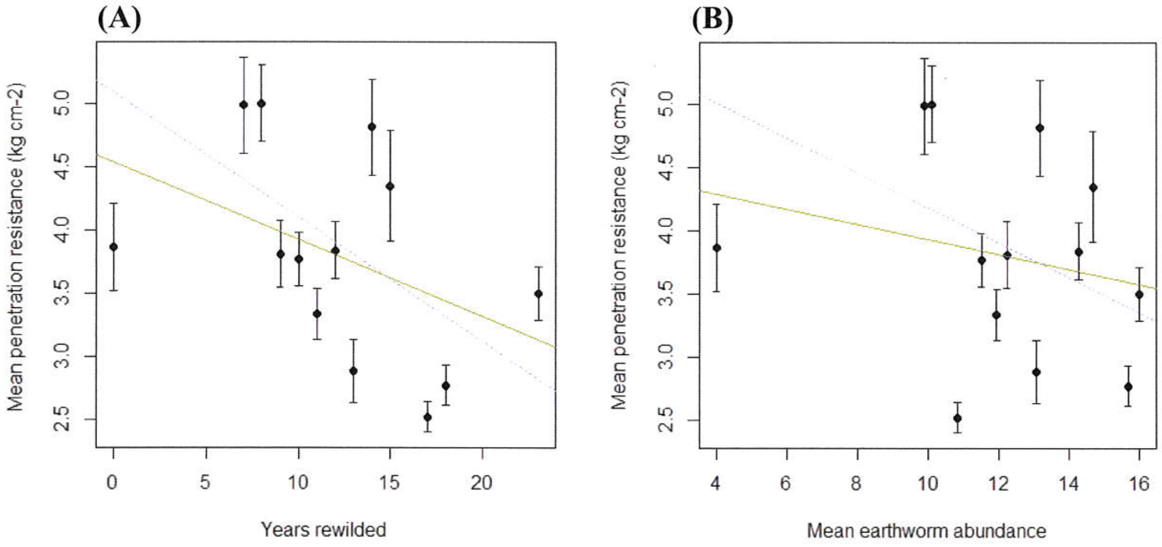

Figure 14: *Mean penetration resistance as a function of (A) years re-wilding, with control (green)* ($y = -0.06x + 4.5$), *without control (blue)* ($y = -0.09x + 5.1$) *and mean penetration resistance as a function of (B) earthworm abundance, with control (green)* ($y = -0.06x + 4.4$), *without control (blue)*($y = -0.14x + 5.6$).

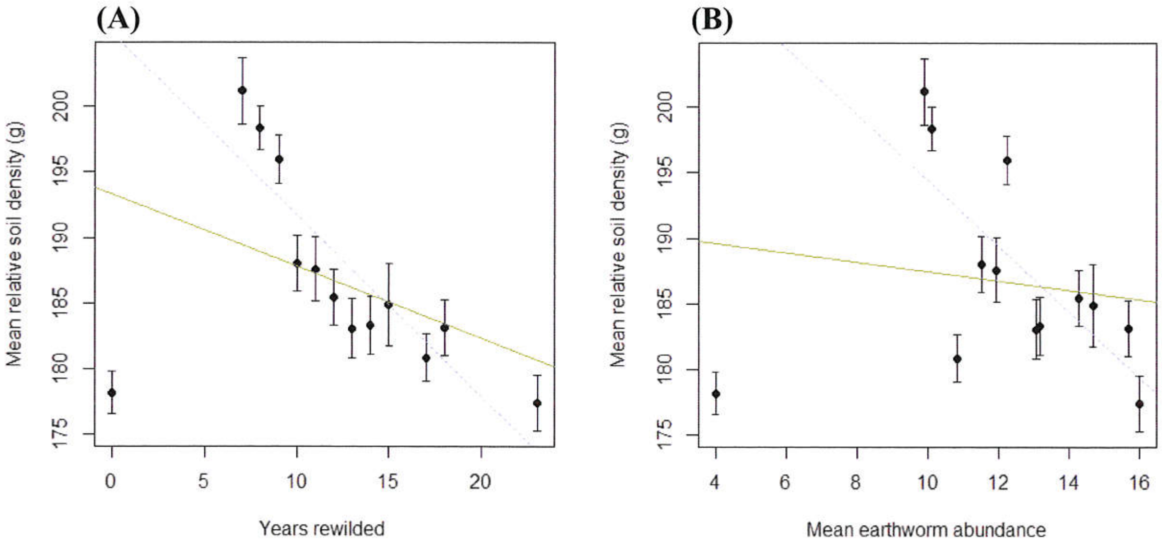

Figure 15: *Mean relative soil density as a function of (A) years re-wilding, with control (green)* ($y = -0.55x + 193.37$), *without control (blue)* ($y = -1.39x + 205.62$) *and mean relative soil density as a function of (B) earthworm abundance (green)* ($y = -0.36x + 191.05$), *without control (blue)*($y = -2.5x + 219.556$).

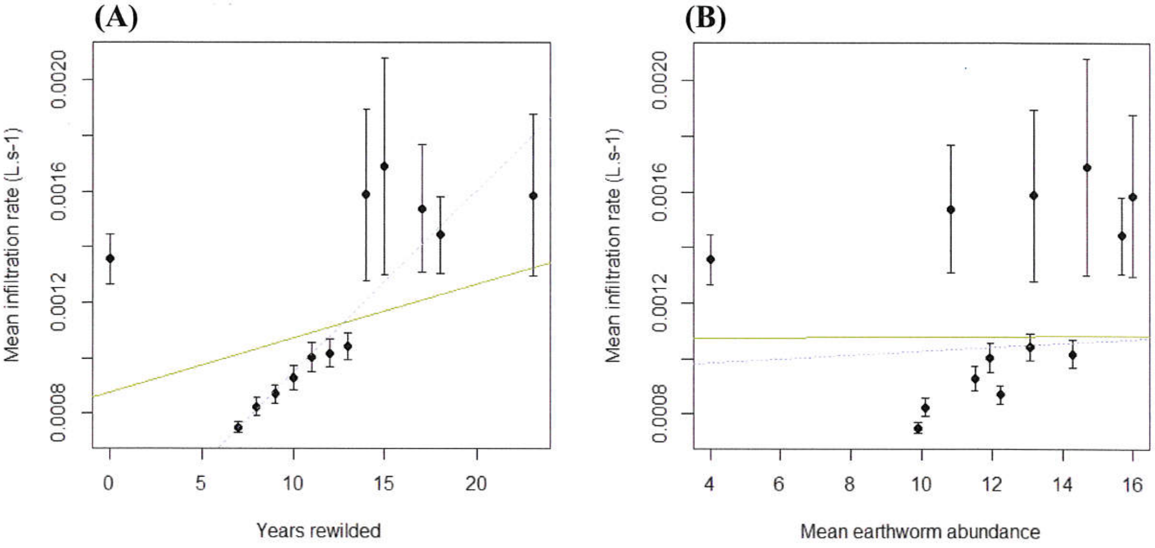

***Figure 16**: Mean infiltration rate as a function of (A) years re-wilding, with control (green) ($y = -1.9545e^{-0.7}x + 8.772e^{-0.4}$), without control (blue) ($y = -0.00007x + 0.00029$) and mean infiltration rate as a function of (B) earthworm abundance (green) ($y = -4.916e^{-0.7}x + 1.071e^{-0.4}$), without control (blue)($y = -7.242e^{-0.6}x + 9.552e^{-0.4}$*

Discussion

The results show statistically significant positive correlations of both earthworm abundance and species diversity with the length of time fields had been in the re-wilding project. It is worth noting that correlation does not imply causation (MacNally, 2002). Many confounding variables were not recorded for logistical and economic reasons (see limitations section below) however those deemed most likely to have confounded the observed correlations are discussed below. These circumstances make the drawing of meaningful inferences and conclusions a fluid exercise, strongly influenced by the choice of boundaries and assumptions.

Sampling was stratified in order to minimise the effects of temporal variation and there was a significant change in weather patterns throughout the sampling period, from cold and wet at the start, to hot and dry towards the end. Temperature is known to affect the earthworms' metabolic rate and is of primary importance in determining their abundance and diversity, thus it is rather unsurprising that the results show air temperature positively correlated with both.

Re-wilding in the Southern block of the Knepp Castle Estate manages ecological succession in a passive manner (Navarro & Pereira, 2012). By definition, this has led to a complete removal of anthropocentric soil disturbance (scarification) and biomass removal (harvesting). This has had direct and indirect effects on earthworm composition and could be the variables contributing to the results observed in this study (Chan, 2001). Uncertainties in the specific ways these effects may have interacted make it difficult to tease them apart using linear regression models (Raich & Tufekgcioglu, 2000).

One direct effect scarification has on earthworms is the mortality caused by its machinery, so reduced scarification is naturally associated with lower mortality and an increase in earthworm abundance over time. Earthworms feature in the diet of many organisms so an indirect effect of no scarification is reduced exposure to predators (Curry, 2004).

Another indirect effect of no scarification is that more nutrients from undisturbed leaf litter are available to earthworms when the carbon-rich litter at the soil surface remains separated from mineralised nitrogen below and fungal-based decomposition systems dominate. When this separation is lost through scarification, bacterial communities thrive which leads to higher decomposition rates and nutrient loss (Holland & Coleman, 1987). The availability of this organic matter is a major factor in determining earthworm abundance (Curry, 2004).

Harvesting leads to the removal of floral biomass which has been shown to have negative indirect effects on earthworm abundance. The absence of harvesting means floral communities that would otherwise have been inhibited or removed under agricultural management were given the opportunity to grow, reproduce and shed leaf litter. This has meant that plant-derived organic matter and minerals have a chance to accumulate on the soil surface (Anderson et al, 1984). These standing stocks of organic matter act as a physical barrier which maintains a stable microclimate for soil-dwelling organisms (Raich & Tufekgcioglu, 2000; Curry, 2004; Wilson et al, 2012).

Increased vegetation cover in fields that had been in the re-wilding project the longest could have benefited earthworm communities by providing them with shelter and thus protection from predation.

Considering that earthworms consume plant-derived organic matter, the aforementioned build-up of leaf litter from above ground plants provides a rich resource which could well contribute to their abundance. It is known that the removal of surface residues can be detrimental, leading to a decline in numbers and in some cases, local extinction of populations (Snyder & Hendrix, 2008). Consequently, it seems likely that the accumulation of surface residues over time contributed to the positive correlation observed between earthworm abundance and the length of time fields had been in the re-wilding project (Edwards & Lofty, 1977).

This is supported by the fact that surface residues were not present in the control fields, which could explain why they held the lowest diversity and abundance of earthworms. It is also worth noting that agricultural practices used on the control fields are likely to have had a direct effect on earthworm abundance, for example, direct mortality of earthworms caused by machinery (e.g. tillage).

Moreover, the fact that floral diversity within landscapes under naturalistic grazing are likely to change in idiosyncratic ways (Kirby, 2009) may have led to the provision of a more heterogeneous resource (Smith et al, 2008a). Both *A. rosea and* A.caliginosa were among the five most common earthworm species collected throughout this study. Different species of earthworm prefer certain types of litter over others. Hendriksen (1990) showed that *A. rosea* had a preference for litter samples of *Alnus glutinosa* (*A. glutinosa*) and *A.caliginosa* preferred litter samples *Fraxinus excelsior* (*F. excelsior*). It seems possible that increased heterogeneity in terms of food supply may have improved the soils capacity to support a greater variety of earthworm species. This could partly account for the statistically significant positive correlation observed between earthworm diversity and the length of time fields had been in the re-wilding project.

Both increased supply and heterogeneity of organic matter may have been contributing factors to the correlations observed between years re-wilding and the abundance of both endogeic and epigeic earthworm species (*Figure 9 and 10*). This is primarily because both ecological groups heavily rely on the presence of plant-derived organic matter (Lavelle et al, 2004). This falls in line with Smith et al, (2008a) who carried an experiment to investigate the effect of different management practices (spring cut, herbicide application and scarification) and seed mixes on the biodiversity, conservation and functional value of arable field margins on soil macrofauna. They found that the epigeic earthworm L.castaneus had very low densities in scarified plots, due to their requirement for surface residues (Smith et al, 2008a). Although the relationship between years re-wilding and anecic species was not found to be statistically significant, the general trend shown in *Figure 11* may be indicative of a time-lag in their response to increased organic matter availability on the soil surface (Hedlund et al, 2003).

As with earthworm composition, the absence of scarification and harvesting may have had direct and indirect effects on the soil characteristics recorded. It is worth noting that the variables contributing to the correlations observed are inter-related and dynamically dependent. Such variables include; abundance and diversity of both flora and fauna, past management history and climatic conditions - none of which were within the scope of this investigation.

The regression analysis results (*Table 2*) show three statistically significant negative correlations between

- Years re-wilding and soil moisture content
- Earthworm abundance and soil moisture content
- Years re-wilding and top soil shear torsion

According to Raich & Tufekgcioglu (2000) vegetation cover alters soil moisture content. Similarly, Marlatt, (1961) showed vegetation cover plays an essential role in processes that reduce soil moisture content through evapotranspiration. Thus there is a possibility that variations in soil moisture content observed in this study were partly affected by vegetation cover, which itself is likely to be higher in the fields that had been in the re-wilding project the longest.

However, the fact that both earthworm abundance and years re-wilded were correlated with soil moisture content, as well as between themselves could indicate that these three variables were themselves linked. Earthworms may have influenced soil moisture content directly as a result of the effects of their burrowing, casting and feeding activities (Edwards, 2004) or indirectly through their interactions with other organisms such as plants and microbial communities (Schmidt & Curry, 1999; Brown et al, 2011; Brown & Doube, 2004). If this is the case, it may also be possible that the degree to which earthworm abundance modulated soil moisture content was itself influenced positively by the length of time fields had been in the re-wilding project (*Figure 3 and 4*). This could give rise to a feedback loop in which the initial deposition of organic matter after the first year of restoration positively influences earthworm abundance, which in turn stimulates floral growth and thus leads to an increase in organic matter for the earthworms to feed upon. This is an example of interdependency of variables discussed above.

The interaction between years re-wilding and earthworm abundance may have also affected the topsoil shear torsion (*Figure 13*). However, the absence of a significant correlation between top soil shear torsion and earthworm abundance suggests this may not be the case. This is somewhat surprising given that many studies have found earthworm burrowing and casting activities lead to a significant reduction in the compaction of the soil surface (Blanchart et al, 1999; Lavelle et al, 2004). Edwards & Bohlen (1996) explain that the recovery of many terrestrial ecosystems which have suffered from compaction is related to earthworm abundance.

It should be noted that the absence of a significant negative correlation between soil shear torsion and earthworm abundance does not imply that they are not related. It may be the case that the effect earthworm abundance had on top soil shear torsion was influenced by another variable, such as compaction from free roaming Long Horn cattle and Fallow deer. It is worth pointing out the lack of significance could also be due to the experimental design (see limitations section).

As can be seen from *Table 2* the correlations between earthworm abundance and most of the soil characteristics were insignificant. These results are surprising given the body of literature which has highlighted and quantified the effects earthworm communities have on soil structure and functioning throughout a range of terrestrial ecosystems (Kretzschmar, 2004; Shipitalo et al, 2004;). This leads one to question whether these well-established correlations are being masked or distorted by confounding variables that lay outside of the studies' boundaries.

Thus, the results indicate an opportunity for research able to account for these confounding variables to reveal the causal links between re-wilding, earthworm community composition and their provision of soil ecosystem services, by either measuring their effects or excluding them through experimental design.

LIMITATIONS

Carrying out research in a Gestalt system, such as a re-wilded landscape, requires the selection of arbitrary reference points (variables) to form a background against which patterns may be seen. In this paper, these were the number of replicates and the data collected in each replicate.

The limitations in the design of this research are a consequence of the variables selected, within any constraints that were present. Variables remain which had been considered and not selected for measurement or whose existence may not be known. These are the limitations and they are briefly explored below:

- A major limitation in this investigation was the fixed number of spatial replicates available for study (n=3). Consequently, only weak inferences could be made from the data collected. Knepp is unique in having a chrono-sequence of re-wilding and due to the socio-economic context strongly influencing land use, there are severely limited opportunities elsewhere for this type of investigation.
- Another major limitation in this study was the six year gap at the beginning of the chrono-sequence. This meant that the immediate responses to the re-wilding project were not recorded. Thus a very interesting and informative section of the profile of re-wilding was not available. Further research needs to be conducted to fill this void. Going forwards, at the moment land is put in a re-wilding project, measurements need to be taken of selected variables and a standardised method applied, to assess the condition of the land in order to establish a baseline. This should be followed by period assessments and evaluations at appropriate intervals to track changes over time. In this study, the ideal would have been to have conducted the research over the last 23 years on the same fields to tracked changes through the chronosequence.
- Field management histories varied. For example, all fields had been treated with fertilisers, herbicides, fungicides and insecticides in differing amount in different years. This introduced an unknown number of variables that could have confounded the correlations observed.
- A fixed volume of soil was taken to be capable of indicating earthworm abundance and diversity from the ground beneath. The same volume of soil was sampled across various fields, with a view to compare measurements. This relies on the unverified assumption that the way in which this volume is a proxy for abundance and diversity in one sample, can be applied to all samples.

- This study assumed that the mustard solution used to sample earthworms below the pit affected every earthworm species to the same degree. Moreover, there were several instances when the mustard solution was not fully absorbed by the soil. This made the uniform sampling of earthworms difficult and also meant that soil water infiltration rates could not be calculated in the time available.

CONCLUSIONS

Taken together, the results suggest that the re-wilding project at Knepp has had a positive effect on the abundance and species diversity of earthworm communities, which in turn has positively influenced processes that are directly related to the provision of vital soil ecosystem services. The results also show how complex and non-linear some variables can be, underlining how important it is to design an experiment to take this into account.

This suggests that agri-environemnt schemes, namely HLS, through the application of naturalistic grazing and disturbance regimes, have the ability to support the restoration of ecological functions and processes within degraded agricultural landscapes.

With further study to identify and quantify the interactions between a greater number of variables, it may become possible to discern any causal relationships between re-wilding, the abundance and diversity of earthworms and their provision of soil ecosystem services. Undoubtedly this is would be valuable information when making future policy decision about land-use.

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