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A role for liming as a conservation intervention? Earthworm abundance is associated with higher soil pH and foraging activity of a threatened shorebird in upland grasslands

Running title: Conservation benefits of liming

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Abstract

The relationship between farmland bird populations and agricultural intensification has been well studied. However, the impact of variation in soil conditions and soil management is an exception, especially in upland (sub-alpine) farming systems. In this study, we examined the relationships between liming history, soil pH and patterns of foraging by Northern Lapwing, *Vanellus vanellus*, chicks in order to test the potential utility of soil amendment as a conservation intervention for shorebirds nesting in agricultural grasslands. Limed fields had higher soil pH than unlimed fields, and soil pH declined with the number of years since a field was last limed. The most important predictor of total earthworm abundance was soil organic matter with very few earthworms in peats of very high organic matter content. However, there was a marked additive effect of soil pH with earthworms more than twice as abundant at high (pH = 6.0) as at the low (pH = 3.5) extremes of soil pH recorded in the study. Specifically, at Lapwing chick foraging locations, the density of *Allolobophora chlorotica*, an acid-intolerant species of earthworm found just below the surface of the soil, was significantly higher than at randomly selected locations. These results suggest that liming helped to maintain breeding habitat quality for Lapwings and other species dependent on earthworms. This is of conservation significance in upland agricultural grasslands in the UK, where there has been a long-term reduction in agricultural lime use since the mid-20th century. Field-scale trials of liming would be valuable to test whether targetted amendment of soil pH in agriculturally improved grasslands could retain an important role in conservation management for shorebirds in upland landscapes where geology, high rainfall, and leaching tend to acidify soils over time.

Key words: agriculture, grassland, lime, earthworm, lapwing, *Vanellus*, soil pH

1 Introduction

Agricultural intensification has been implicated in widespread declines in biodiversity, with negative effects of agricultural change on birds in Europe particularly well documented (Robinson & Sutherland, 2002, Newton, 2004, Wretenberg *et al.*, 2007, Wilson *et al.*, 2009). Intensification has resulted in a simplification of the farmed landscape associated with reduced habitat heterogeneity and availability of nesting opportunities and food sources for many farmland birds (Benton *et al.*, 2003, Tscharntke *et al.*, 2005).

One aspect of agricultural change which has received relatively little attention in relation to farmland bird declines is soil management in upland (sub-alpine) grassland systems, and especially the amendment of soil pH. This is surprising because soil invertebrates provide important food resources for a wide range of farmland-feeding birds including shorebirds, thrushes, starlings and corvids (Tucker, 1992, Wilson *et al.*, 2009), and the diversity and abundance of many of these invertebrate groups are pH-sensitive (Edwards & Bohlen, 1996, Cole *et al.*, 2006).

Soil pH is reduced by agricultural processes such as cropping and the use of nitrogenous fertilisers, but also naturally through leaching of calcium and other base cations from the soil and has been further lowered in some areas by anthropogenic atmospheric acid deposition (Rowell & Wild, 1985). Natural leaching of calcium is faster in areas with higher rainfall, especially where acidic underlying geology and peat formation result in low buffering capacity. These conditions describe agriculturally marginal, upland grasslands over much of the UK. Such landscapes are now an internationally important stronghold for populations of breeding shorebirds of several species (e.g. Eurasian Curlew, *Numenius arquata*; Brown *et al.*, 2015). Yet even in these environments, they are declining rapidly (Balmer *et al.*, 2013, Brown *et al.*, 2015) having already suffered catastrophic declines in lowland agricultural systems (Wilson *et al.,* 2005, Lawicki *et al.*, 2011).

The effects of soil acidification are widely counteracted through agricultural liming to raise soil pH (MAFF, 1969, Wilkinson, 1998, Spaey *et al.*, 2012). In the UK, agricultural lime sales peaked in the 1950s and '60s under a Government subsidy which persisted into the 1970s (Figure 1), but have since declined steadily to pre-subsidy levels. Low soil pH and declines in pH occurred between the 1970s and 2001, particularly in western and northern areas that are dominated by livestock farms in higher altitude, higher rainfall environments (Baxter *et al.,* 2006). By 2007, there was some evidence that this trend was being reversed, perhaps due to the declining impacts of acid deposition from industrial pollution (Emmett *et al.* 2010).

Earthworms comprise around 75% of soil fauna biomass in temperate grasslands (Bardgett & Cook, 1998), play a key role in maintaining soil fertility and constitute a prey resource for a number of birds that are associated with farmland, including shorebirds, gulls and corvids (Barnard & Thompson 1985, Wilson *et al.*, 2009). Earthworms are sensitive to soil pH and very few earthworms occur in soils below pH 4.3 (Edwards & Bohlen, 1996). Because lime is applied as a surface dressing, it has a greater effect on epigeic and endogeic (surface and near-surface dwelling) than anecic (burrowing) earthworm species, with reported increases in earthworm abundance following liming being mainly in epigeic species (Deleport & Tillier, 1999, Bishop, 2003, Potthoff *et al.*, 2008). Accordingly, Brandsma (2004) identified an increase in field use by both Northern Lapwings *Vanellus vanellus* (henceforth 'Lapwings') and Black-tailed Godwits *Limosa limosa* following increases in earthworm abundance that occurred after liming.

In this study we use upland agricultural grassland with a known liming history to test the impact of lime use on prey resources and foraging habitat use by Lapwings, for whom earthworms are an important component of the diet, including during chick development (Beintema *et al.,* 1991, Sheldon, 2002). Specifically we addressed the following questions:

1) How long does the positive effect of liming on soil pH last?
2) How is earthworm abundance related to soil pH, soil moisture and soil organic matter?
3) Do locations selected by foraging Lapwing chicks have a higher abundance of epigeic or endogeic earthworms than randomly selected locations?

2 Methods

2.1 Study area

The study took place from 2009 – 2011 on upland grassland in central Scotland (56° 4'40.06"N 4° 0'45.00"'W), covering three livestock farms (Townhead, Muirpark and Lochend) and a total area of 685 ha. The underlying geology is basalt, overlain by glacial tills, and peat. The average annual precipitation within the area is 1020 mm. The three farms all produce beef cattle and sheep and range from 140 m to 340 m above sea level. Field types in marginal agricultural areas such as this are split into two types; 'in-bye' (enclosed fields used for either arable or sown grass production), and 'out-bye' (semi-natural grass and dwarf shrub 'moorland' vegetation cover used for rough grazing only (Gray 1996).

2.2 Soil pH and earthworm sampling

Soil properties and earthworm abundance were assessed in 19 fields which had undergone differing numbers of lime application within the preceding 10 years (Table 1). Around 50ha of the in-bye land at Townhead had been used to grow a brassica fodder crop in the preceding ten years (McCallum, 2012). This provided a contrast between fields that had undergone fodder crop management and had received two or three lime applications (5 tonnes ha^{-1} $annum^{-1}$, applied as a surface dressing of calcium carbonate dust) in the preceding 10 years, and fields that had not undergone this cropping management, and had received either no or just one lime application during this period. Because liming occurred at the time of fodder crop management and this was rotated round fields, the number of years since the last lime application varied between fields. In-bye fields at the other two study farms had not experienced fodder crop management. Those at Muirpark had received no lime during the preceding 10 years, whereas fields at Lochend had received one or two lime applications. Out-bye fields had received no lime within the preceding 10 years.

Soil cores (10cm depth x 10.5 cm diameter) were collected from nine random locations (generated using the sampling tool extension, Finnen & Menza, 2007, within ArcGIS 9.2) within each field between 19 April and 11 May, and were used to measure soil pH, soil organic matter and earthworm abundance. For fields with high variability in earthworm abundance between the samples, an additional five samples were collected. Two soil moisture measurements were taken in the field within 15cm of each soil core. In 2009 this was done with a theta probe (ML2, Delta-T Devices, Cambridge, England) and in 2010 with a soil moisture metre (HH2 moisture metre, SM200 moisture sensor, Delta-T Devices, Cambridge, England).

Soil was air-dried for a minimum of two weeks then sieved to < 2 mm prior to carrying out soil analysis. Soil pH was measured using a digital pH meter (pH209, Hanna Instruments, Woonsocket, Rhode Island, USA), calibrated using buffers of pH 7 and pH 4. Soil pH was tested on 10 g of air dried, sieved soil, mixed with 25 ml distilled water, once the solution had been left to settle for a minimum of 10 minutes. Soil organic matter was calculated as the percentage of weight lost by burning sieved soil in a furnace at 425^{o}C overnight (i.e weight loss on ignition). The soil was prepared by drying at 105°C for a minimum of four hours and then weighed both before and after burning.

Earthworms were sampled using the same cores used to assess soil properties, with soil cores hand sorted in the laboratory within four days of collection (Edwards & Bohlen, 1996, Laidlaw, 2008). To avoid double counting of broken earthworms, only those with heads were counted. Earthworms were identified to species level (Sims & Gerard, 1985), with the exception of juveniles of either *Lumbricus* species or *Apporrectodea caliginosa* and *A. rosea*, which were assigned to one of these two groups based on colour, prostomium shape and spacing of chaetae.

2.3 Field observations of foraging Lapwing chicks

To test whether chick foraging location (hereafter termed chick location) was related to earthworm abundance, 19 lapwing chicks (10 in 2010, 9 in 2011) from separate broods were fitted with Pip3Ag376 backpack mounted radio-tags (Biotrack Ltd, Dorset, UK). All chicks within a brood were also ringed using British Trust for Ornithology metal rings, above the knee. Coloured insulating tape was used on the ring to provide each brood with a temporary unique colour marker. Radio-tagged chicks were re-captured at approximately weekly intervals in order that tags that were beginning to come loose could be re-glued.

Chick locations were estimated using triangulation by taking the bearing of the strongest signal from the chick's radio-tag (using a Sika receiver and three-element flexible Yagi antennae – Biotrack Ltd, Dorset, UK) from a minimum of three locations in succession (White & Garrot, 1990, Kenward, 2001). Estimated chick locations and the associated error ellipses (50% confidence) were calculated using Lenth's maximum likelihood estimator (White & Garrot, 1990), using Location of a Signal 4.0.3.7 (Ecological Software Solutions LLC, 2010). Error ellipses incorporated antenna error, which was established from a number of test triangulations carried out at the study site (standard deviation 11.5). Chicks were located by triangulation every one to three days. In addition to triangulated locations (22 locations), some radio-tagged chicks were sighted using direction of the strongest signal to guide where to look for the chick (9 observations). Fields were also searched visually (with a telescope) for non radio-tagged chicks, using clues from adult behaviour to concentrate on areas in which chicks were likely to be located (8 observations). Visual searches for chicks were carried out no more than once per day for each field. Where chick location was estimated by triangulation, chick foraging was not confirmed as it was not possible to see chicks. Lapwing chicks spend most of the time either foraging or being brooded (Beintema & Visser, 1989) so it was likely that chicks would be located in areas where they were foraging.

At each chick location four soil cores were collected, and four randomly located soil cores were also taken from the same field. Soil moisture and earthworm abundance were measured as described above.

2.4 Data analysis

2.4.1. The relationship between soil properties and liming history

To determine whether liming had the agriculturally desired impacts on soil pH, we tested the relationship between soil pH and whether or not a field had received lime in the preceding 10 years, using a linear mixed effects model (LMM). This model included data from 12 fields across the three farms, but excluded seven fields which had received either no or one lime application during the preceding 10 years, but could not be formally assigned as ‘limed’ or ‘unlimed’ in the preceding decade. An additional LMM was run using in-bye fields at Townhead only (n = 13), comparing those that had two or three lime applications (i.e. had been subjected to the fodder crop management regime) with those that had received one or none, as a binary fixed factor. In both models, the response variable, pH, was measured at the soil core scale, with field identity included as a random (grouping) factor within the model, and year included as a fixed effect. The first model also included farm as a fixed effect. These models were also run using percentage soil organic matter as the response variable to test whether this differed between the treatment groups. Finally, a third LMM was implemented including only fields that had been limed two or three times within the preceding 10 years. This model tested whether soil pH was related to the number of years (covariate) since the last lime application, and was also implemented with soil core as the replicate (n = 58) and field (n = 6) fitted as a random effect.

2.4.2. The relationship between soil properties and earthworm abundance

GLMMs were used to test the relationship between earthworm abundance and soil properties. The response variable, total earthworm abundance (and, in separate models the abundance of the three most numerous species or groups of earthworms: *Aporrectodea rosea / caliginosa*, *Allolobophora chlorotica* and *Lumbricus* spp.), was measured on the soil core scale, with field identity included as a random factor. The explanatory variables were soil pH, soil organic matter and soil moisture, and their quadratic terms were also included because earthworms are not tolerant of extreme soil conditions (Edwards & Bohlen, 1996). Explanatory variables were checked for collinearity prior to analysis, and because no correlations exceeded 0.5, collinearity was not considered to compromise inference. Farm and year were also included as fixed effects. These models used data from all 19 fields assessed across the three farms.

2.4.3. Differences between chick and random locations

GLMMs were used to test whether earthworm abundance differed between chick foraging locations and random locations, whilst accounting for soil moisture. Mean earthworm abundance was calculated from the four soil cores collected at a chick location. However, because the four random cores were collected from separate locations, data from these were not pooled. Total earthworm abundance and the abundance of *A. chlorotica* (the individual species with the biggest overall difference between foraging and random locations in the raw data) were each modelled as the response variable with location (chick foraging or random) and soil moisture as predictor variables. Sample identity (chick foraging and the four random locations) nested within chick identity was included as a random factor to account for non-independence of samples (i.e. each chick location is spatially associated with random locations within the same field) and repeated sampling involving the same chick. Because triangulation error meant that associated errors for chick locations were variable, the inverse of the area of the error ellipse was included as a case weight (Crawley, 2007) within the GLMMs, with weights calculated using the formula:

$$(1/\text{Area}_i) / \Sigma\ (1/\ \text{Area})$$

where Area_i is the area of the 50% confidence ellipse for the individual triangulated chick location, and Σ (1/ Area) is the sum of 1/Area for all triangulated chick locations. Direct observations of chick locations and random locations were given a case weight of 1.

All statistical analyses were performed with R version 2.15.0 (R Development Core Team 2012). All LMMs and GLMMs were conducted using glmmPQL from the MASS package (Venables & Ripley, 2002). Covariates were standardised prior to analysis (Schielzeth, 2010).

Models where the response variable was a count were implemented with Poisson errors and log link and were corrected for over-dispersion. Models where the response variable was a percentage were implemented with binomial error structure and logit link. For all other models Gaussian error structure and identity link, were specified. Model residuals were checked graphically for normality and homogeneity of variance (Zuur *et al.*, 2007). Minimum adequate models were obtained using stepwise backwards selection, retaining all variables that were significant at the 5% level and fixed factors that accounted for the study design. Model fit was assessed by calculating pseudo r^2 (from now on referred to as r^2), the square of the correlation between the predicted values and the observed data (Zuur *et al.*, 2009).

3. Results

3.1 The relationship between soil properties and liming history

Between individual samples, soil pH ranged from pH 3.5 to 6.0. On average pH was highest in fields at Lochend where fields had received 1 or 2 lime applications in the preceding 10 years, and lowest for out-bye fields at Townhead (and in-bye fields at Muirpark) where no liming had occurred within the preceding 10 years (Table 1). Soil organic matter ranged from 5 to 90%, on average being lowest in fields at Townhead that had been limed two or three times in the preceding 10 years and highest on fields at Muirpark Farm which had received no lime within the preceding 10 years.

Soil pH was significantly higher (by 0.8 pH units) in soil that had been limed than that which had not in the preceding 10 years (Table 2, Figure 2a). However, soil organic matter was significantly lower in limed soil compared to un-limed soil (Table 2, Figure 2b), indicating that differences in pH were the result of intrinsic differences in soil properties combined with differences in liming history. Soil pH was higher (0.3 pH units) in soil that had been limed two or three times within the preceding 10 years, in comparison to 0 or 1 times (Table 2, Figure 2c). Soil organic matter was not significantly different between these two groups (Table 2, Figure 2d), indicating that differences in soil pH on agriculturally improved ‘in-bye’ land were probably due to liming rather than difference in the nature of the soil. Soil pH declined by around 0.07 pH units with every year since liming ($t = -2.4$, $p = 0.022$, $n=58$; $r^2 = 0.50$; Figure 3).

3.2 The relationship between soil properties and earthworm abundance

Across the three farms and the two years of the study, 516 earthworms were collected of which 75% were *Apporectodea caliginosa /rosea*, 9% were *A. chlorotica*, and 8% were *Lumbricus* spp. (Appendix A).

There was weak evidence of an increase in total earthworm abundance with soil pH, and a decline at high levels of soil organic matter (i.e. in the context of this study, peat-rich soils), but there was no relationship with soil moisture (Table 3, Figure 4a & b). The model predicted earthworm density of close to 390 earthworms m^{-2} (in the top 10 cm of soil) at pH 6.0, in comparison to just 190 earthworms m^{-2} at pH 4.0. Differences with change in soil organic matter were even greater with close to 650 earthworms per m^{-2} predicted at 10% soil organic matter, in comparison to just 25 earthworms per m^{-2} in very peaty conditions at 90% soil organic matter ($r^2 = 0.31$).

Apporectodea caliginosa / rosea exhibited a weak quadratic relationship with soil pH and declined with increasing soil organic matter (Table 3, Figure 4c & d). Abundance peaked at around 250 earthworms m^{-2} at pH 5.4, over 3 times as many as occurred at pH 4.0 (70 earthworms m^{-2}). Again the change with increasing soil organic matter was more substantial, with close to 540 earthworms m^{-2} predicted at 10% organic matter in comparison to just 10 earthworms m^{-2} at 80% organic matter ($r^2 = 0.27$).

Allolobophora chlorotica abundance also had a quadratic relationship with soil pH, but this relationship was stronger and abundance of this species was not correlated with soil organic matter, and weakly with soil moisture (Table 3, Figure 4e). Abundance peaked at around pH 5.2 at a predicted density of around 40 earthworms m^{-2}, and this species was not found below pH 4.5 ($r^2 = 0.39$).

Lumbricus spp. abundance was not related to soil pH or soil moisture but declined with increasing soil organic matter (Table 3, Figure 4f), although we note that the r^2 for this model was very low at 0.14.

3.3 Differences between chick and random locations?

A total of 263 earthworms was found across 39 chick foraging locations that occurred within 13 fields at the study site, with 189 in total at random locations. The most abundant earthworm species group across both chick and random locations was *A. caliginosa* / *A. rosea* (57% of total), with *A. chlorotica* accounting for 21%, and *Lumbricus* spp. 13%. Total earthworm abundance was not related to chick foraging location, but was higher when soil moisture was higher (r^2 = 0.40; Table 4). The abundance of *A. chlorotica* was significantly higher at chick foraging locations than random locations, with the model predicting over twice as many *A. chlorotica* at chick foraging compared to random locations (39 earthworms m^{-2} at chick foraging locations, compared to 15 earthworms m^{-2} at random locations; Figure 5). *Allolobophora chlorotica* was also significantly more abundant when soil moisture was higher (r^2 = 0.27).

4. Discussion

In the UK, agricultural lime use has declined by over 70% in the past 50 years. We found higher soil pH in fields that had received more lime applications in the preceding decade and a decline in soil pH with the number of years since a field had last been limed. This supports the hypothesis that a reduction in lime use may have contributed to declining soil pH in upland grassland areas. Total earthworm abundance was strongly related to soil organic matter with very few earthworms in soils with high organic content. In this environment, this means very peaty soils, where the high soil moisture, low soil pH and poor quality of organic matter combine to make conditions generally unsuitable for earthworms (Edwards & Bohlen, 1996). In addition, total earthworm abundance increased with increasing soil pH and earthworm densities were very low in soils below pH 4.5 which accounted for almost 20% of our samples. *Allolobophora chlorotica* exhibited the strongest relationship with soil pH of the three earthworm groups tested and was the only one for which soil organic matter content was unimportant. This species of earthworm was over twice as abundant (after correcting for soil moisture) at Lapwing chick foraging locations than random locations. In this study, most liming was associated with establishment of a fodder crop which involved shallow cultivation. Given that cultivation is known to reduce earthworm densities (Curry *et al*., 2002), this suggests that the beneficial impacts of liming were more than sufficient to outweigh any initial cultivation impact. Overall, our results suggest that the long-term reduction in lime use in upland grassland areas could have led to a decline in earthworm abundance, due to lower soil pH, therefore reducing foraging opportunities for Lapwing chicks and other shorebird species that occur within this habitat and are dependent upon earthworms as a key prey item.

Substantial declines in shorebirds in Europe are primarily due to poor breeding productivity, with reproductive success insufficient to replace losses due to adult mortality (Roodbergen *et al*., 2012). Whilst predation is a key limiting factor, poor chick growth in sub-optimal habitats is likely to contribute to poorer chick survival in these environments (Kentie *et al*., 2013). Lapwing chick condition is positively associated with the number of earthworm chaetae within their faeces, indicating the importance of this prey type in Lapwing chick development (Sheldon, 2002). The low densities of earthworms in soils with high organic matter and / or low soil pH within this study, suggest that these soil conditions may result in poor foraging opportunities for breeding shorebirds and thus limit the numbers and breeding success of these species in these areas. This is further supported by a Scotland-wide study which showed an additive effect of soil conditions on breeding Lapwing densities such that densities were highest when soil pH was relatively high and organic matter relatively low (McCallum *et al.,* 2015); in other words soils which we find here to support high earthworm densities.

Allolobophora chlorotica was only found in soils between pH 4.7 and 5.7, towards the upper end of soil pH in this study. This species is intolerant of acidic soil conditions (Satchell, 1955) and has previously been shown to respond positively to liming (Bishop, 2003). Lapwing chick foraging location was associated with *A. chlorotica* density suggesting that this may be a favoured prey resource. *Allolobophora chlorotica* is generally found in the upper 5 cm of soil amongst the grass roots (Gerard, 1967), which is also where Lapwing chicks find food resources (Benteima *et al.,* 1991). *Apporectodea caliginosa* and *rosea*, the most abundant species group within this study may be lower in the soil profile (within the top 10 cm; Gerard, 1967) and consequently may not be as accessible to Lapwing chicks. Soil conditions suitable for *A. chlorotica* occurred more frequently in fields that had undergone liming at least once within the past 10 years indicating that liming could increase this species abundance and therefore prey resources for breeding Lapwings.

4.1 Conclusions

Our results highlight the importance of lime use in maintaining soil pH in upland grassland areas. Declining soil pH associated with a reduction in lime use on agricultural grasslands is likely to have led to declines in earthworm abundance and reduced foraging habitat quality for birds reliant on earthworms as prey, especially where underlying geology has poor buffering capacity and rainfall levels are high enough to reduce soil pH through leaching. We found that Lapwing chick foraging location was associated with higher densities of one particular earthworm species, *A. chlorotica,* which only occurred within a narrow range of soil pH, and further work to identify if this earthworm species contributes more substantially to Lapwing chick diet than others would be valuable.

We suggest that field scale trials of lime use within upland grassland agricultural areas would be useful to test whether liming could be used as a conservation measure for farmland birds where earthworms constitute a major component of their diet. Application of agricultural lime does lead to some carbon dioxide emissions from soil, although these emissions may be lower than assumed by modelling studies (West & McBride, 2005, Biasi *et al*., 2008) and this, along with quarrying and transport of lime, mean that use of agricultural liming as a bird conservation intervention in upland areas would need to be carefully targetted. This would entail a focus on existing sown and agricultural improved grasslands of low biodiversity interest that are topographically suited to settlement by breeding shorebirds (McCallum *et al*., 2015), and where soil pH has fallen below that recommended for agricultural grass production.

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Tables

Table 1 Mean ± standard error of field soil pH (raw data) for each farm showing fields grouped by history of liming.

Farm	Field Type	Lime applications in preceding 10 years	No. of fields	Mean soil pH	Mean soil organic matter (%)
Townhead	In-bye	2 or 3	6	5.1 ± 0.10	21 ± 3
Townhead	In-bye	0 or 1	7	5.0 ± 0.10	30 ± 2
Townhead	Out-bye	0	2	4.5 ± 0.33	33 ± 3
Muirpark	In-bye	0	2	4.6 ± 0.003	37 ± 1
Lochend	In-bye	1 or 2	2	5.3 ± 0.16	26 ± 5

Table 2 Statistical summary for LMMs testing the relationship between liming history and soil pH for Lime Model 1 (comparison of limed fields v non-limed fields) and Lime Model 2 (comparison of fields receiving 2/3 lime applications within the past 10 years to those that received 0/1). The same models were repeated using soil organic matter as the response variable to test whether this differed between the two pairs of treatment groups, and the statistical summaries are also presented here. The sample size for Lime Model 1 was 138 across 12 fields, and for Lime Model 2 was 115 across 13 fields.

	Soil pH			Soil Organic Matter		
	DF	F	p-value	DF	F	p-value
Lime Model 1						
Lime	1	50.2	0.0001	1	9.6	0.015
Year	1	32.2	<0.0001	1	2.05	0.15
Farm	2	1.1	0.39	2	1.76	0.23
Lime Model 2						
Lime	1	10.5	0.008	1	2.29	0.16
Year	1	35.9	<0.0001	1	3.38	0.07

Table 3 Statistical summary for GLMMs testing the relationship between (i) total earthworm, (ii) *Apporectodea caliginosa / rosea,* (iii) *Allolobophora chlorotica* and (iv) *Lumbricus* spp. abundance and soil properties, showing the minimum adequate model. Sample size was 190 soil cores across 19 fields.

	DF	Parameter estimate ± SE	Statistic	p-value
	Total earthworm			
Soil pH	1	0.21 ± 0.11	t = 2.0	0.051
Soil organic matter	1	-0.55 ± 0.12	t = -4.5	<0.0001
Farm	2	-	F = 0.18	0.83
Year	1	-	F = 1.8	0.18
	Apporectodea caliginosa / rosea			
Soil pH	1	0.29± 0.12	t = 2.38	0.018
Soil pH^2	1	-1.17 ± 0.08	t = -1.88	0.061
Soil organic matter	1	-0.67 ± 0.13	t = -5.12	<0.0001
Farm	2	-	F = 1.08	0.36
Year	1	-	F = 2.09	0.15
	Allolobophora chlorotica			
Soil pH	1	1.33± 0.39	t = 3.44	0.0007
Soil pH^2	1	-1.77 ± 0.43	t = -4.16	0.0001
Soil moisture	1	0.47 ± 0.24	t = 1.94	0.054
Farm	2	-	F = 0	1
Year	1	-	F = 0.25	0.61
	***Lumbricus* spp.**			
Soil organic matter	1	-0.65 ± 0.25	t = -2.63	0.0093
Farm	2	-	F = 0.17	0.84
Year	1	-	F = 0.26	0.61

Table 4 Statistical summary for GLMMs testing whether earthworm abundance (total and *A. chlorotica*) differed with foraging location (chick compared to random location) and soil moisture; minimum adequate models are presented. The sample size was 195 soil cores, accounted for by 39 sample groups (including 1 chick location with 4 cores and 4 random locations with 1 core), for 22 chicks.

	DF	Parameter estimate ± SE	t	p-value
	Total earthworm			
Soil moisture	1	0.26 ± 0.11	2.31	0.0223
	Allolobophora chlorotica			
Foraging location (CvR)	1	0.89 ± 0.30	3.01	0.0031
Soil moisture	1	0.62 ± 0.19	3.33	0.0011

Figures

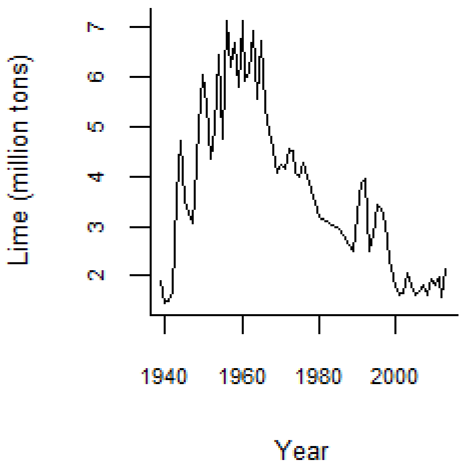

Figure 1 The quantity of lime sold in Great Britain for agricultural purposes, annually since 1939: data sources: 1939 – 1976, Agricultural Lime Producers Council (1977), 1980 – 1989, Wilkinson (1998), 1990 – 2000, Hillier *et al.* (2003), 2001 – 2013, Bide *et al.* (2015).

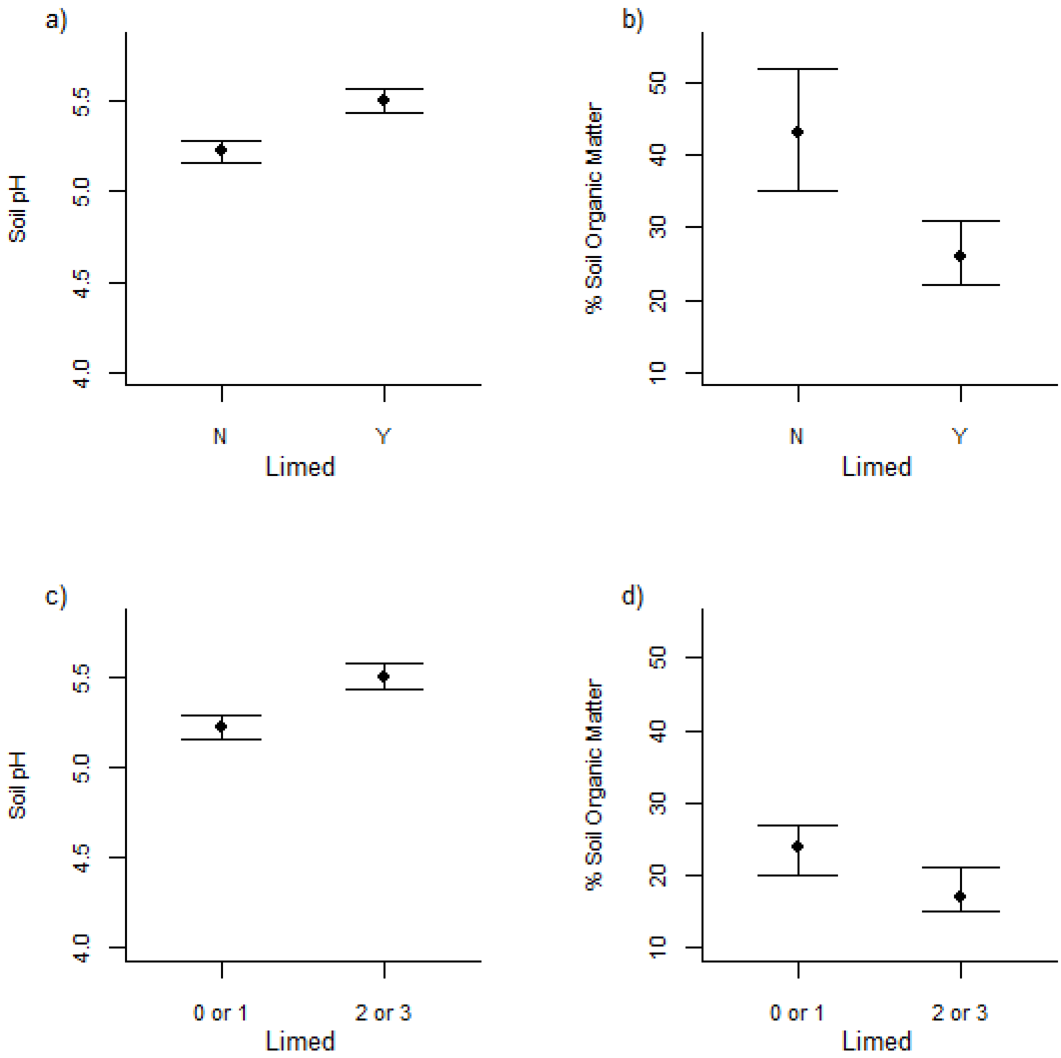

Figure 2a) Modelled values of soil pH ± standard errors in fields (n=12) which had been limed compared to those that had not, within the preceding 10 years, b) Modelled values of percentage soil organic matter ± standard errors in fields (n=12) which had been limed compared to those that had not, within the preceding 10 years, c) Modelled values of soil pH ± standard errors in fields (n=13; Townhead only) which had undergone 2 or 3 lime applications in the preceding 10 years, compared to those that had undergone 0 or 1, d) Modelled values of percentage soil organic matter ± standard errors in fields (n=13; Townhead only) which had undergone 2 or 3 lime applications in the preceding 10 years, compared to those that had undergone 0 or 1.

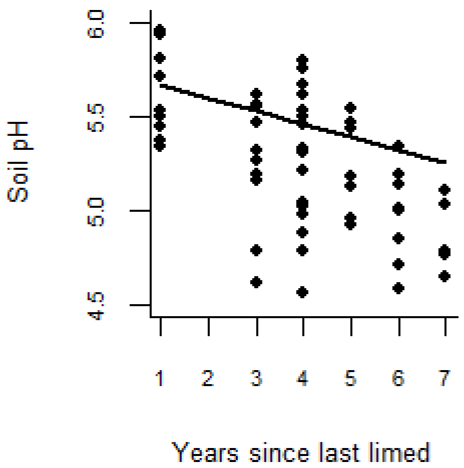

Figure 3 Modelled decline in soil pH with number of years since last lime application compared to the raw data of soil pH (solid circles) verses number of years since last limed. Each point represents one soil core (n = 58 from six fields).

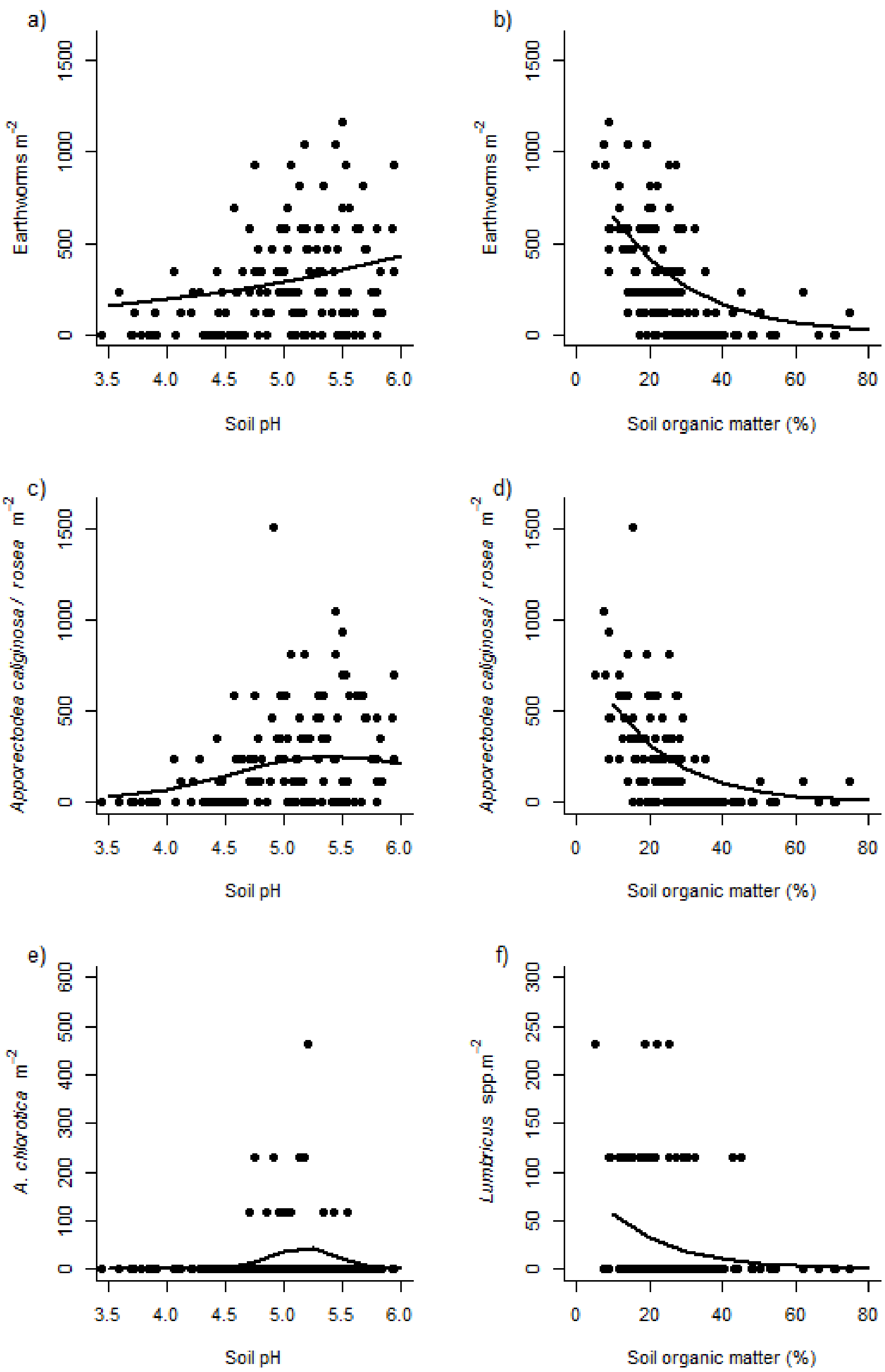

Figure 4 The relationship between a) total earthworm abundance and soil pH, b) total earthworm abundance and soil organic matter, c) *Apporectodea caliginosa / rosea* abundance and soil pH d) *Apporectodea caliginosa / rosea* abundance and soil organic matter, e) *Allolobophora chlorotica* and soil pH and f) *Lumbricus* spp. And soil organic matter, showing the predicted earthworm abundance with varying soil pH or organic matter generated from GLMMs, with raw data represented by closed circles. Each point represents the number of worms in a single core multiplied up to per m^2 value to enable direct comparisons to other studies.

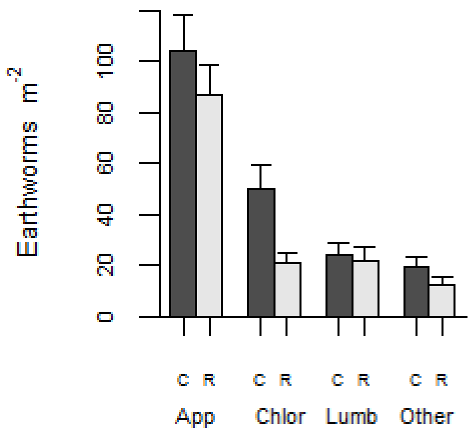

Figure 5 Mean earthworm density, and standard error, at chick (C) compared to random (R) locations, showing the 3 main species groups *Apporectodea caliginosa / rosea* (App), *Allolobophora chlorotica* (Chlor), *Lumbricus* spp. (Lumb), and all other species (other). Densities to a depth of 10 cm.