communications
earth & environment

ARTICLE

https://doi.org/10.1038/s43247-023-01176-8 OPEN

# Restored lowland heathlands store substantially less carbon than undisturbed lowland heath

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The conversion of lowland heathland to agricultural land in Europe significantly depleted soil carbon stocks. Restoring heathlands has been proposed as a mechanism to sequester soil carbon. Here we compared soil carbon in (i) agricultural pasture; (ii) native heathland and (iii) restored heathland through acidification with elemental sulfur (sulphur). After 18 years of soil acidification, soil chemical properties (pH, extractable nutrients etc.), fauna and vegetation assemblage resembled that of native heathlands. However, native heathland was found to contain more than double the soil carbon stock of restored heath, with significantly higher contents of stable soil organic matter, and restored heath soil carbon was not significantly different to the control pasture. This result, combined with supporting findings of a comprehensive literature review, has ramifications for carbon-sequestration proposals, given the urgency required for climate mitigation tools.

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Lowland heath (below 300 m) is often characterised by nutrient poor, acidic soils, and an abundance of ericaceous plant species (such as heathers *Calluna vulgaris* and *Erica sp.*) and calcifugous species[1,2]. Lowland heath cover has reduced dramatically both in the UK, and across Europe, since the 19th century. Approximately 72% has been lost between 1830–1980 in England alone, largely as a result of land use change and subsequent optimization of heathland ecosystems for agricultural production[3,4]. Consequently, lowland heathland has been listed as a priority habitat in the UK Biodiversity Action Plan[5,6] and EU Habitats Directive 92/43/EEC (1992) due to the rare species it contains[7] and other ecosystem services heathlands provide. In 2009, the remaining ~58,000 ha of lowland heathland in the UK represents ~20% of the total global area of this habitat[8]. Therefore, in recent decades there has been particular interest in methods that revert improved agricultural land back to heathland systems[5]. Extensive lowland heath decline has also been observed in Denmark and the Netherlands and there are many examples of restoration on former heathland landscapes[9,10].

One of the challenges faced during the reversion of agricultural land back to a functioning heathland is a substantial reduction in nutrient availability[3,11–13]. Therefore, the successful establishment of heathland requires a reversal of the changes imposed on the soil by decades of fertilisation and liming[14–16]. Management techniques include topsoil removal, deep ploughing, planting of heather, site abandonment (natural regeneration) and sulfurous amendments to encourage establishment of ericaceous species[3,17–19].

In addition to the services heathlands provide as habitats to numerous rare and protected species, a recent EU Habitat Action Plan has recognised that carbon (C) storage is an increasingly important ecosystem service that could be provided by restored heathlands[20]. Which emphasises data collected in Dorset, SE England[21]. Ericaceous species such as *Calluna vulgaris*, which dominate in heathland systems, have been associated with litters that have high relative proportions of lipids and aliphatic biopolymers, which are more resistant to decomposition and accumulate in heathland soils[22]. Heathlands in England alone have been estimated to contain 29.8 Mt C[23], the majority of which resides in the soil (c. 98%). More recent estimations have suggested that heathland can contain 88–103 t C $ha^{-1}$ (ref. 2). The British Ecological Society have proposed that creating heathland from ex-arable land will result in increased carbon sequestration in soils[24]. Natural England have also suggested that creating heathland from arable lands could result in a net sequestration of carbon (−5.44 t $CO_2$-e $ha^{-1}$ $yr^{-1}$)[23]. However, it is recognised that further study in mineral soils in lowland heath would help to fill a significant evidence gap because current available data makes it difficult to extrapolate the impact of management on soil carbon stores[24].

A long-term study in Dorset, SE England, was established in 1999 to assess the efficacy of sulfurous amendments in promoting changes in soil chemistry and the resulting development of ericaceous floral assemblage on improved pasture[25]. During this study it was observed that the application of elemental sulfur significantly altered soil chemistry and the resulting plant community and soil fauna, when compared to a control treatment of current land use—improved pasture[25,26]. However, interestingly total soil carbon concentration was not significantly affected by the application of elemental sulfur compared to control-improved pasture[25]. This has led us to consider soil C dynamics in restored heathlands by studying the literature and our field sites in more detail. In order to gain a better understanding, it is important to go beyond bulk C and consider functional pools of C, or soil organic matter (SOM) fractions[27] and compare these to native heath in the same area.

The aim of our study was to examine the effects of restoring heathlands on accumulation and properties of soil carbon. Determining whether the reversion of agricultural land to their former heathland vegetation results in soil C accumulation in the restored heathland soil in a short to medium timeframe after reversion. We based our work on two hypotheses: (i) that total C contents and stocks will be enhanced in restored heathlands as recalcitrant litters accumulate; (ii) that these ericaceous litters will alter the nature of the soil carbon in the restored heathlands as determined by organic matter fractions, active carbon and C:N ratio. We used a well-characterised field experiment in Dorset[25] in which we investigated the distribution of carbon in different physical organic matter fractions alongside chemically extracted permanganate oxidisable carbon (POXC), which is indicative of active/labile carbon and a proxy of SOM stabilisation[28]. To the best of our knowledge this is the first physical organic matter fractionation or POXC to be conducted on native and restored heathland systems. A literature review of other studies that have measured bulk soil carbon in native and restored lowland heaths in Europe was also conducted in parallel to put our findings into wider context and benchmark against existing datasets. This will improve understanding of the mechanisms for carbon stabilisation and accumulation in lowland heathland soils.

## Results

**Vegetation community assemblage**. The restored heath, control pasture, and native heathland had a significantly different vegetation community from one another ($p < 0.01$ according to ANOSIM). This was a result of a higher percentage cover of mesotrophic species in the control pasture and a significantly higher percentage cover of acid/calcifugous grassland and heathlands species in the native heathland than the control pasture (Fig. 1). The restored heath had a greater predominance of intermediate species and acid and heath species (Fig. 1). The restored heath, in terms of acid and heath species cover, had no significant difference from the control pasture or native heathland treatments (Supplementary Fig. 1). However, native heathland had a significantly higher percentage cover of ericaceous species than the restored heath (Supplementary Fig. 1).

**Bulk Soil C and N**. Native heathland was significantly higher in total soil C, active C, total N, C:N ratio and organic C stock than the restored heath (Fig. 2, Supplementary Table 1). The proportion of SOC that was active C (POXC) was significantly lower in the native heathland than the restored heath (Fig. 2c). Furthermore, the restored heath bulk soil was not significantly different to the control pasture in any of the soil C or N parameters measured (Fig. 2).

There was a significant positive correlation between the percentage cover of plant species classified as characteristic of acid/ calcifugous grassland and heathlands according to the National Vegetation Classification, or NVC, (listed in Fig. 1 legend), and bulk soil C, active C, organic C stock and C:N ratio (Table 1). Conversely, there was a significant negative correlation between acid and heath species cover and the proportion of soil organic carbon attributed to by active carbon. This was also the case for ericaceous species cover (Table 1).

**Total C in physical organic matter fractions**. The larger total C content in the bulk soil of the native heathland was principally attributed to a significantly higher mass of C in the litter fraction and the small macroaggregate fraction (Fig. 3, Supplementary Table 2). The restored heath contained significantly less carbon than the native heathland in the microaggregate fraction, despite there being no significant difference between the control and the

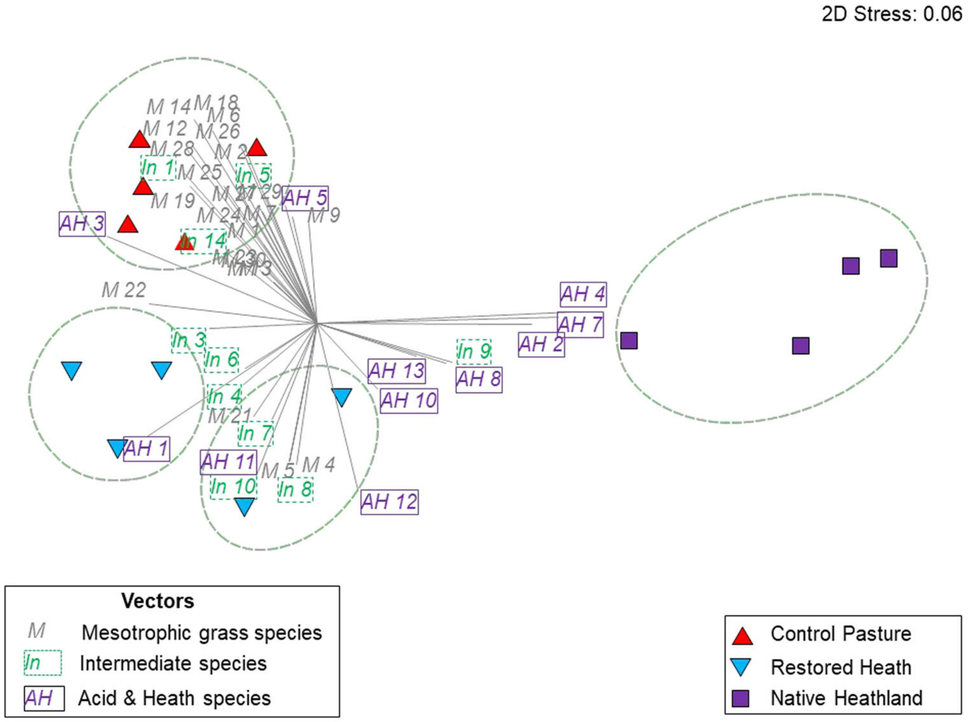


**Fig. 1 Vegetation communities in restored heath, control pasture and native heathland.** Nonmetric multidimensional scaling of vegetation community on restored heath, control pasture and native heathland. Based on Bray-Curtis resemblance matrix. Dashed lines encircle plots that have ≥50% similarity. Species vectors key: AH 1 - *Agrostis capillaris;* AH 2 - *Agrostis curtisii;* AH 3 - *Anthoxanthum odoratum;* AH 4 - *Calluna vulgaris;* AH 5 - *Cerastium glomeratum;* AH 6 - *Cirsium vulgare;* AH 7 - *Erica cinerea;* AH 8 - *Erica tetralix;* AH 9 - *Juncus inflexus;* AH 10 - *Molinia caerulea;* AH 11 - *Polygala serpyllifolia;* AH 12 - *Ulex europaeus;* AH 13 - *Ulex minor;* In 1 - *Cynosurus cristatus;* In 2 - *Epilobium spp.;* In 3 - *Holcus lanatus;* In 4 - *Juncus effusus;* In 5 - *Lotus corniculatus;* In 6 - *Lotus uliginosus;* In 7 - *Luzula campestris/multiflora;* In 8 - *Potentilla erecta;* In 9 - *Pteridium aquilinum;* In 10 - *Rumex acetosella;* In 11 - *Sonchus oleraceous;* In 12 - *Stellaria graminea;* In 13 - *Urtica dioica;* In 14 - *Veronica officinalis;* M 1 - *Achillea millefolium*; M 2 - *Bellis perennis*; M 3 - *Bromus mollis*; M 4 - *Capsella bursa-pastoris*; M 5 - *Centaurium erythraea*; M 6 - *Cerastium fontanum*; M 7 - *Cirsium arvense*; M 8 - *Cirsium palustre*; M 9 - *Crepis capillaris*; M 10 - *Dactylis glomerata*; M 11 - *Elymus repens*; M 12 - *Festuca rubra*; M 13 - *Geranium mole*; M 14 - *Hypochoeris radicata*; M 15 - *Leontodon autumnalis*; M 16 - *Lolium perenne*; M 17 - *Phleum pratense*; M 18 - *Plantago lanceolata*; M 19 - *Poa pratensis*; M 20 - *Poa trivialis*; M 21 - *Ranunculus bulbosus*; M 22 - *Ranunculus repens*; M 23 - *Rubus fructicosus*; M 24 - *Senecio jacobaea*; M 25 - *Taraxacum officinale agg.*; M 26 - *Trifolium dubium*; M 27 - *Trifolium pratense*; M 28 - *Trifolium repens*; M 29 - *Vicia sativa*; M 30 - *Vulpia bromoides*.

native heathland. There was no significant difference in the silt and clay fraction in any of the treatments.

After dispersal of the aggregate fractions (small macroaggregates and microaggregates) there was no significant difference in the carbon associated with the intra-aggregate silt and clay fractions (sMa s + c or mi s + c) (Fig. 4, Supplementary Table 2). There was, however, a significantly higher concentration of intra-aggregate particulate organic matter (sMa POM and mi POM) in the native heathland than the restored heath. There was no significant difference between the control pasture and the native heathland in total carbon in intra-microaggregate particulate organic matter (mi POM).

There was a significant positive correlation between the percentage cover of acid/calcifugous grassland and heathland plant species and the mass of carbon in four physical SOM fractions. Including the litter fraction, small macroaggregates, microaggregates and intra-microaggregate particulate organic matter (Table 1). There was no significant correlation between acid/calcifugous and heath plant species cover and the silt and clay sized fractions (within aggregates or outside of aggregates). There was also no significant correlation between ericaceous species cover and the silt and clay sized fractions (within aggregates or outside of aggregates).

**C:N ratio of organic matter fractions**. All fractions, except for intra-microaggregate silt and clay (mi s + c), had a significantly higher C:N ratio in the native heathland than the control and restored heath (Table 2). There was no significant difference in C:N ratio between the control pasture and restored heath in any of the fractions.

**Active C in aggregate fractions**. The native heathland contained a significantly lower proportion of organic carbon as active carbon than the control pasture, in both small macroaggregates and microaggregates (Table 3). The restored heath was not significantly different to either the control pasture or the native heathland in terms of the proportion of active C in either the small macroaggregates or microaggregates.

**Calluna vulgaris tissue C:N**. *Calluna vulgaris* above-ground tissue samples collected from the restored heath had a significantly lower carbon content and C:N ratio than the native heathland (Fig. 5).

**Literature review - European lowland heath soil C**. A total of forty-nine soil C contents and twenty soil C stocks were extracted from thirty-one papers, the majority of which were reported from native lowland heathlands (Supplementary Table 3). Most papers reported single values for a specific location, in one of five countries: The Netherlands; England; Belgium; Germany; and Denmark (Supplementary Fig. 2). Two papers reported a mean for several locations across England and Wales[29] and Southern

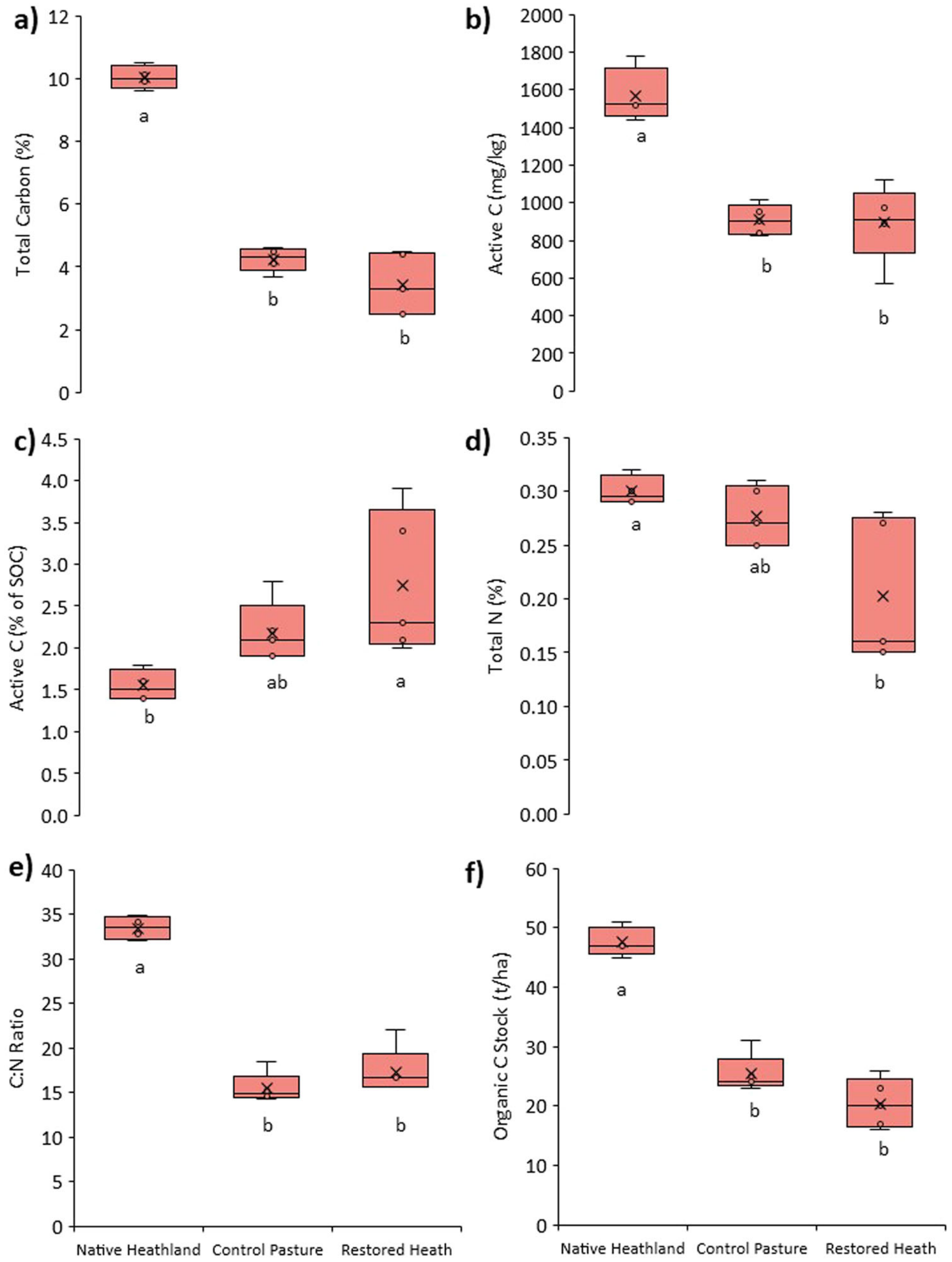


**Fig. 2 Bulk Soil Carbon in restored heath, control pasture and native heathland.** Soil carbon in bulk soil samples of native heathland ($n = 4$), control pasture ($n = 5$) and restored heath ($n = 5$): **a** total soil C; **b** active C; **c** active carbon as a proportion of total organic carbon; **d** total nitrogen; **e** carbon:nitrogen ratio; **f** organic C stock in the top 5 cm of soil. Treatments that are labelled with the same lower-case letter are not significantly different according to one-way ANOVA and Tukey's post hoc testing ($p > 0.05$). Model outputs can be found Supplementary Table 1. Lower and upper box boundaries represent the 25th and 75th percentiles, respectively. The line inside box represents the median. The upper and lower whiskers represent the maximum and minimum value (which is not an outlier), respectively. Mean values are represented by an X. Dots within the box represent individual values.

England[30], but do not report values for each of the individual locations.

Soil C content reported in the literature was generally higher in the native lowland heath sites (Fig. 6a) compared to heathland that has been converted to agriculture (Cohen's d 1.99 ± 0.96, Supplementary Table 4) or restored heath that was previously agricultural land (Cohen's *d* 2.87 ± 0.70, Supplementary Table 4). Restored heath also has lower reported carbon stocks in the literature compared to native lowland heath (Fig. 6b), but differences were less prominent than observed in soil C contents, possibly due to there being fewer records of soil C stocks reported in the literature. Methods of restoration included sulfurous amendments, topsoil removal, deep ploughing, planting heather and leaving the site abandoned for natural succession (Supplementary Table 1). C contents were reduced in systems that used topsoil removal as a restoration technique compared to other options such as sulfurous amendments or leaving the site abandoned (Supplementary Fig. 3)

## Discussion

It has been proposed that we should restore heathlands to increase soil carbon stocks[24]. However, despite being comparable to native heathland in a number of abiotic and biotic parameters[25,26,31], we observed that restored heath contained less

**Table 1 Relationships between soil carbon and vegetation cover.**

| Soil C characteristic | Acid/Calcifugous Grassland and Heath (AH) species cover (%) | Ericaceous species cover (%) |
|---|---|---|
| Bulk soil | | |
| Total C (%) | 0.670** | 0.857*** |
| Active C (mg/kg) | 0.733** | 0.669** |
| Active C (% of SOC) | −0.538* | −0.770*** |
| Total N (%) | 0.298 | 0.437 |
| C:N | 0.748*** | 0.818*** |
| Organic C stock (t/ha) | 0.658** | 0.891*** |
| Total C in fraction (mg C/g soil) | | |
| Litter | 0.805*** | 0.859*** |
| Small macroaggregates (sMa) | 0.625* | 0.630* |
| Microaggregates (mi) | 0.528* | 0.613* |
| Silt and clay (s + c) | −0.015 | −0.032 |
| Intra-small macroaggregate particulate organic (sMa POM) | 0.482 | 0.623* |
| Intra-small macroaggregate silt and clay (sMa s + c) | 0.453 | 0.397 |
| Intra-microaggregate particulate organic matter (mi POM) | 0.579* | 0.884*** |
| Intra-microaggregate silt and clay (mi s + c) | 0.099 | −0.061 |

Correlation coefficients of bulk soil C characteristics and total C in physical organic matter fractions against the percentage cover of plant species classified as acid/calcifugous grassland and heath species according to the NVC or ericaceous species. Spearman Rank correlation coefficient $^{*}p \leq 0.05$ $^{**}p \leq 0.01$ $^{***}p \leq 0.001$. $n = 14$.

than half the soil C content (and stock) than the native heathland, both in our field site and in the average soil C contents reported in the literature. Suggesting that current heathland restoration techniques are failing to restore a heathland that quickly increases soil C stocks. This has implications for land management suggestions that heathland restoration can sequester carbon. This is particularly so as heathland soil C may also become less stable under future climatic conditions[32]. In addition, it has been suggested that soil carbon practises may be maladaptive if it results in a loss of revenue or yield[33], as would be typically the case with a land use change away from agriculture to heathland. Furthermore, conservation of lowland heath often results in the removal of trees, or disruption of vegetation succession, limiting the potential for carbon storage above-ground[34]. It is important to ensure that damage to soil is minimised during habitat restoration[19], this is further highlighted in our literature review where C contents were reduced in systems that used topsoil removal as a restoration technique compared to other management strategies. Finally, the fact that after 18 years the restored heath treatment did not present a significant difference to control pasture in any of the carbon parameters measured raises concern given the urgency of climate mitigation needs.

We based our work on two hypotheses, the first of which was that total C contents and stocks will be enhanced in restored heathlands as recalcitrant litter accumulates. Ericaceous species such as *Calluna vulgaris* are characterized by long-lived leaves, low in N and high in phenolics, and a lignified woody stem, resulting in more recalcitrant litter than species associated with mesotrophic grassland[35]. This accounts for the significant positive correlations between the ericaceous plant species, and bulk soil C, organic C stock and C:N ratio. An increase in ericaceous plant species was also associated with a decrease in the proportion of SOC that was active C. This provides further evidence that an increase in ericaceous species results in an accumulation of recalcitrant litters and is the determining factor in increasing soil carbon stocks. This is in concordance with studies that found that carbon storage increased with ericaceous plant cover during restoration of a degraded upland heathland[36,37]. This suggests that in order to quickly sequester carbon in heathland restoration projects ericaceous species cover should be increased to a high percentage.

The association between ericaceous species and plant litter recalcitrance may account for the fact that our restored heath contained less soil C than native heathland. Although there was a shift in vegetation community in the restored heath to one that was significantly different to the control pasture, the community was largely dominated by intermediate species and remained significantly different to the native heathland community, with a significantly lower percentage cover of ericaceous species. it is likely that ericaceous species cover has not been able to develop as quickly due to residual rock phosphate from former agricultural use of the site[25]. Legacy nutrients from former agricultural land use is a known barrier in heathland restoration[3]. Removal of topsoil, and the organic matter contained within, can result in the indiscriminate removal of soil nutrients[38]. Therefore, topsoil removal as a management strategy could lead to conditions that are favourable for ericaceous species. However, results in the literature suggest that topsoil removal, leads to lower soil carbon stock than other management strategies, likely a result of removal of organic matter. This presents a challenge for heathland restoration and carbon sequestration. If legacy nutrients in topsoil are allowed to remain, then ericaceous species cover cannot develop to a percentage high enough to increase soil carbon stocks through input of ericaceous litter. If the topsoil is removed to reduce the nutrient content to allow ericaceous species to establish, there will be an initial carbon cost in the removal or organic matter in the topsoil. Either way, the soil C sequestration potential of heathland restoration is likely to be a lengthy process.

The lower C:N in the plant tissue of *Calluna vulgaris* on the restored heath suggests that this biomass was not as resistant to decomposition as the *Calluna vulgaris* on the native heathland. This is further reflected by the fact that the proportion of soil organic C that was active C, in the bulk soil, was significantly lower in the native heath than the restored heath. This could be a result of the *Calluna vulgaris* being less mature on the restored heath. For example, it has been observed that plant tissue carbohydrates, which are largely labile, decrease with age in *Calluna vulgaris*[39]. In addition, a greater contribution of woody stems to plant litter production, rather than less lignified part of the plant (e.g. leaves) can take decades[40]

Native heathland was also found to have a higher C:N ratio in the bulk soil and fractions compared to the restored heath. This is

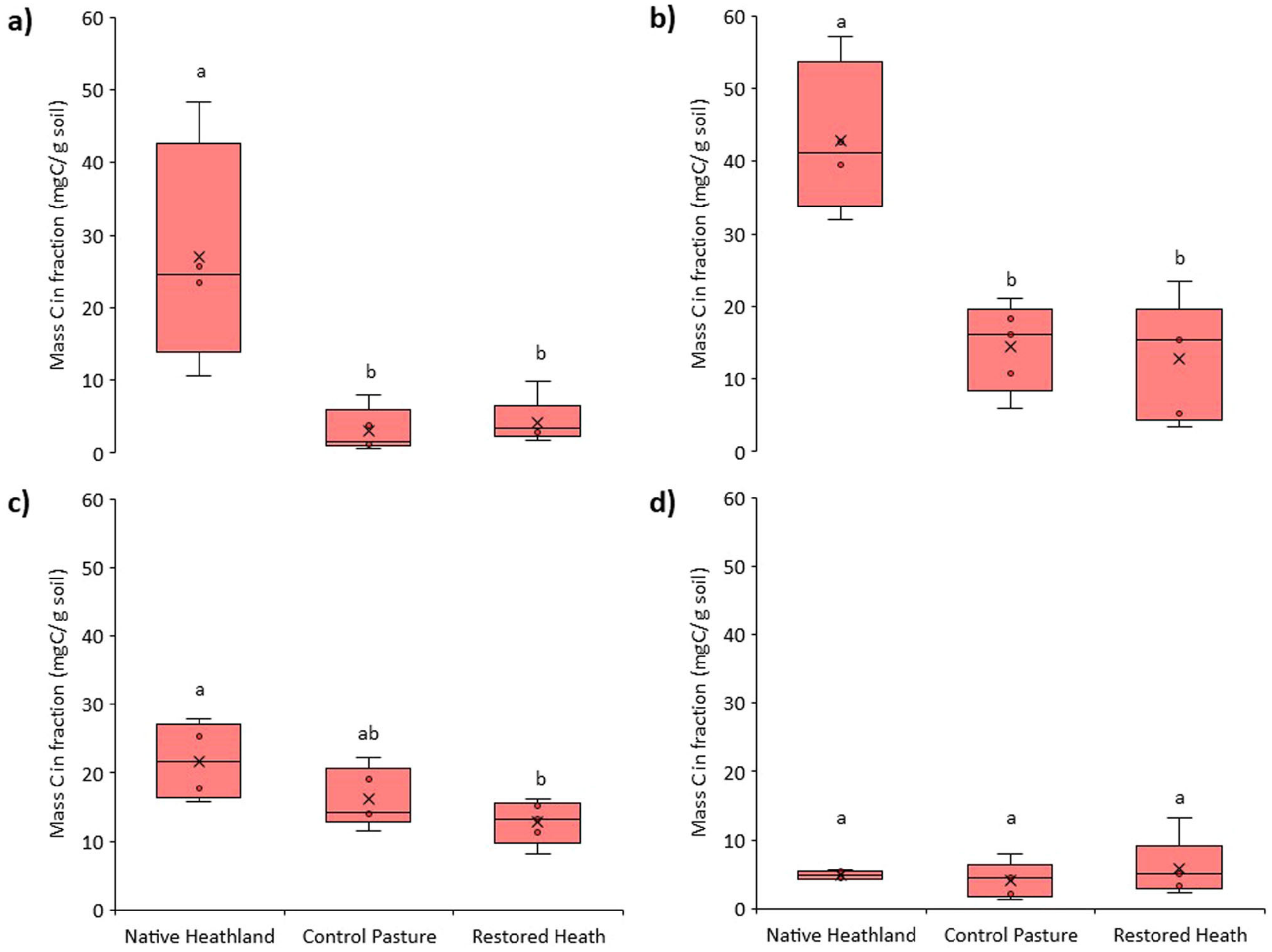


**Fig. 3 Carbon in physical organic matter fractions in restored heath, control pasture and native heathland.** Total carbon in physical organic matter fractions of native heathland ($n = 4$), control pasture ($n = 5$) and restored heath ($n = 5$). Fractions are **a** litter; **b** small macroaggregates (sMa); **c** microaggregates (mi); and **d** silt and clay (s + c) size fractions. Treatments that are labelled with the same lower-case letter for a particular fraction are not significantly different according to one-way ANOVA and Tukey's post hoc testing ($p > 0.05$). Model outputs can be found Supplementary Table 2. Lower and upper box boundaries represent the 25th and 75th percentiles, respectively. The line inside box represents the median. The upper and lower whiskers represent the maximum and minimum value (which is not an outlier), respectively. Mean values are represented by an X. Dots within the box represent individual values.

in concordance with Vos et al.[41] who observed that historical heathland sites had a higher C:N ratio than historical cropland and grassland sites. Degradation of organic matter with a high C:N ratio, has been shown to be limited by the relative lack of N in the early stages of decomposition[42–44].

SOM is both a substrate for, and a product of soil microorganisms[45]. Shifts in soil community composition (e.g. bacteria: fungi ratio) and activity due to environmental stressors can therefore have significant consequences for carbon cycling[46,47]. Therefore, the fact that previous work on the site demonstrated that belowground biology in the restored heath was not yet comparable to that of the native heathland[31] may have implications for the soil carbon in our field study. In addition, on average, belowground inputs from roots are stabilised as SOM with more than five times the efficiency than aboveground inputs from litter[48]. Previous work conducted on the site found that there was no significant difference in belowground biomass between the restored heath and the control pasture[26]. This, therefore, may also have implications for SOM stabilisation in the restored heath.

It is vital that the importance of soil carbon pools within restoration is acknowledged[49]. Therefore our second hypothesis was that ericaceous litters will alter the nature of the soil carbon in the restored heathlands as determined by physical organic matter fractions. The higher carbon content in native heathland soils were largely attributed to a higher proportion of carbon contained within the litter fraction of the native heathland compared to the control pasture or restored heath. This litter fraction carbon was significantly positively correlated with ericaceous species.

Due to the fact that litter is not associated with mineral surfaces or aggregates, it is more likely that the stability of litter in soils is determined by its molecular structure, or intrinsic recalcitrance, rendering it unavailable to microbial degradation[50]. Soil organic matter rich in aliphatics have been linked to input of lipids, long chain aliphatics and sterols from heathland vegetation, along with the low soil pH and microbial activity observed under heathland[22,51]. Aliphatic C, often associated with waxes from the cuticles of leaves, are thought to be resistant to decay in soils[52,53]. It has been previously concluded that organic matter in historical heathland sites was resistant to decomposition[41,54], resulting in a thick recalcitrant organic layer often referred to as mor humus[55]. Moreover, historical heathland sites have been found to contain a higher proportion of bulk C in the light

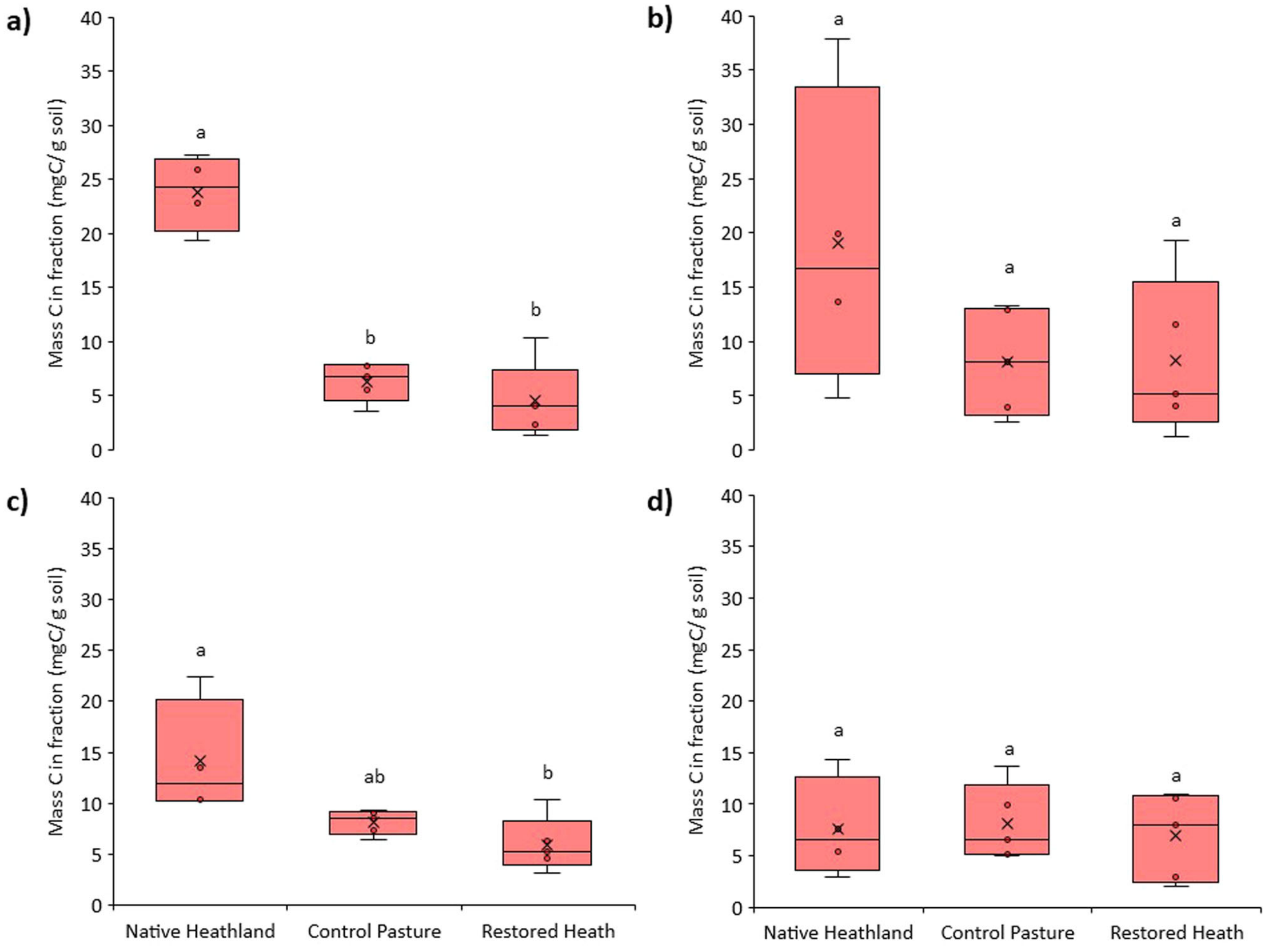


**Fig. 4 Carbon in intra-aggregate fractions in restored heath, control pasture and native heathland.** Total carbon in small macro- and micro-aggregate fractions of native heathland ($n = 4$), control pasture ($n = 5$) and restored heath ($n = 5$). Total C in (**a**) intra-aggregate particulate organic matter in small macroaggregates (sMa POM); intra-aggregate silt and clay (sMa s + c) in small macroaggregates; **c** intra-aggregate particulate organic matter in microaggregates (mi POM); and **d** intra-aggregate silt and clay (mi s + c) in microaggregates. Treatments that are labelled with the same lower case letter for a particular fraction are not significantly different according to one-way ANOVA and Tukey's post hoc testing ($p > 0.05$). Model outputs can be found in Supplementary Table 2. Lower and upper box boundaries represent the 25th and 75th percentiles, respectively. The line inside box represents the median. The upper and lower whiskers represent the maximum and minimum value (which is not an outlier), respectively. Mean values are represented by an X. Dots within the box represent individual values.

**Table 2 C:N ratio of physical organic matter fractions.**

| | Mean C:N ratio of fraction ± standard error | | |
|---|---|---|---|
| | **Native Heathland ($n = 4$)** | **Control Pasture ($n = 5$)** | **Restored Heath ($n = 5$)** |
| Litter | 33.49 ± 0.72a | 19.12 ± 1.40b | 20.45 ± 1.33b |
| Small macroaggregates (sMa) | 34.44 ± 0.54a | 13.90 ± 0.70b | 15.85 ± 1.39b |
| Microaggregates (mi) | 34.54 ± 1.06a | 15.01 ± 1.10b | 17.47 ± 1.17b |
| Silt and clay (s + c) | 31.25 ± 1.39a | 16.50 ± 0.82b | 18.76 ± 1.59b |
| Intra-small macroaggregate particulate organic (sMa POM) | 34.21 ± 0.47a | 12.59 ± 0.96b | 12.73 ± 1.99b |
| Intra-small macroaggregate silt and clay (sMa s + c) | 33.08 ± 3.35a | 15.94 ± 0.91b | 19.83 ± 1.71b |
| Intra-microaggregate particulate organic matter (mi POM) | 33.97 ± 1.55a | 13.83 ± 1.14b | 15.22 ± 0.74b |
| Intra-microaggregate silt and clay (mi s + c) | 36.45 ± 2.24a | 16.79 ± 1.19a | 29.19 ± 11.61a |

Treatments that share the same lower case letter suffix for a particular fraction are not significantly different according to one-way ANOVA and Tukey's post hoc testing ($p > 0.05$).

particulate organic matter fraction than sites used as cropland in the same period[41]. The chemistry of free particulate organic matter within the soil often resembles that of plant litter input to the soil with some partial decomposition and microbial by-products[56].

In our study site we found there was also significantly higher C in the small macroaggregate and microaggregate size fractions of that native heathland than the restored heath. In addition, these aggregate size classes were also found to have a lower proportion of soil organic C attributed to active C. This suggests that the

**Table 3 Active carbon in small macroaggregates as a percentage of organic carbon.**

| | Mean Active C in fraction (% of SOC) ± standard error | |
|---|---|---|
| | **Small macroaggregates (sMa)** | **Microaggregates (mi)** |
| Native Heathland ($n = 4$) | 1.23 ± 0.08b | 1.21 ± 0.05b |
| Control Pasture ($n = 5$) | 2.97 ± 0.45a | 2.47 ± 0.35a |
| Restored Heath ($n = 5$) | 2.77 ± 0.54ab | 2.22 ± 0.22ab |

Treatments that share the same lower case letter suffix for a particular fraction are not significantly different according to one-way ANOVA and Tukey's post hoc testing ($p > 0.05$).

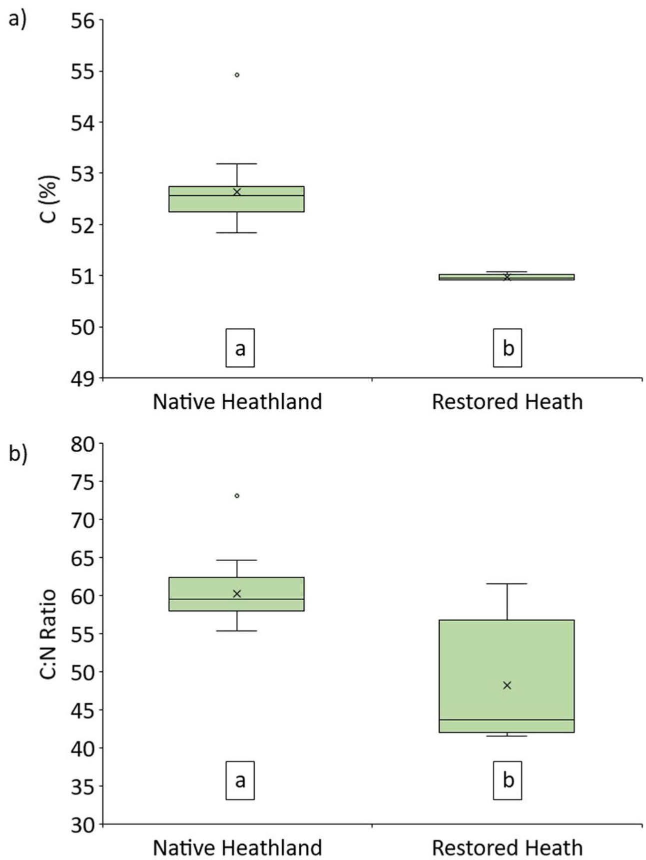


**Fig. 5 Carbon in heather growing in restored heath and native heathland.** Carbon in *Calluna vulgaris* above-ground tissue samples in native heathland ($n = 18$) and restored heath ($n = 5$). Treatments that are labelled with the same lower case letter are not significantly different according to Kruskal–Wallis ($p > 0.05$). Lower and upper box boundaries represent the 25th and 75th percentiles, respectively. The line inside box represents the median, and the upper and lower whiskers represent the maximum and minimum value (which is not an outlier), respectively. Mean values are represented by an X. Dots outside the box represent outliers.

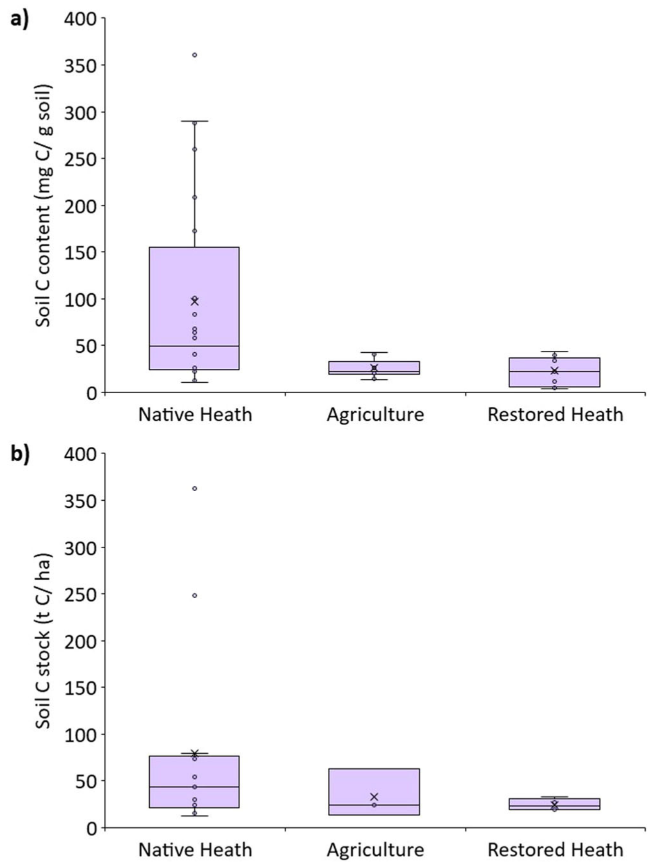


**Fig. 6 Soil carbon in European lowland heath according to different land uses.** Values reported in the literature for (**a**) soil carbon content in native heathland ($n = 24$), heathland converted to agriculture ($n = 14$) and restored heath previously under agricultural use ($n = 11$); **b** soil carbon stocks in native heathland ($n = 13$), heathland converted to agriculture ($n = 3$) and restored heath previously under agricultural use ($n = 4$). Lower and upper box boundaries represent the 25th and 75th percentiles, respectively. The line inside box represents the median. The upper and lower whiskers represent the maximum and minimum value (which is not an outlier), respectively. Mean values are represented by an X. Dots within the box and whiskers represent individual values, dots outside the box represent outliers.

organic matter held in the aggregates of native heathland is more stable, potentially as a result of both physical occlusion within the aggregate and intrinsic recalcitrance. However, logistical considerations meant that the physical organic matter fractionation method used in this research did not include a density separation step. This means that is not possible to distinguish between intra-aggregate organic matter and free particulate organic matter of the same aggregate size class[57].

Particulate organic matter often comprises a large proportion of total C and is considered one of the more sensitive C fractions to changes in management[58]. Fast turnover times, therefore, suggest that this a labile fraction of the SOM in soils, providing a large proportion of the nutrients required by plants[58–60]. However, in our study, native heathland soils contain high contents of stable (not active) soil C, even though they also contain a high amount of particulate organic matter (in the aggregate size fraction and as low density particulate organic matter we have defined as litter). These findings are supported by a study conducted by Vos et al.[41] which concluded that particulate organic matter fractions in historical heathland soils might not be directly linked to higher turnover rates and lower stability.

While our research has focussed on the surficial soil increment (0–5 cm), the vast majority of papers focused on the top 15 cm (see Supplementary Table 3). Direct comparisons between different studies is also complicated by the different sampling depths (see Supplementary Table 3). We therefore recommend a more extensive survey of lowland heaths, taken at consistent depths, including subsoil, to generate a more holistic assessment of C storage in native and restored heath. It is important to recognise that soil carbon storage at depth is a valuable carbon sink that has not been extensively investigated[52,61,62].

Direct statistical comparisons of the data obtained from the literature was not always possible due to the range of locations, restoration methods, ages of sites, and methods for carbon analysis. In addition, soil carbon contents are not reported as standard in literature discussing heathland restoration and management. We therefore suggest that future studies should measure and report soil carbon, as this information is vital for future policy.

## Conclusions

It has been proposed that creating heathland from ex-arable land will result in increased carbon sequestration in soils. However, after 18 years the restored heath treatment bulk soil was not significantly different to the control pasture in any of the soil C or N parameters measured. This has significant implications for policy. A lower acid/ calcifugous plant species cover and C:N ratio of *Calluna vulgaris* plant tissue in the restored heath compared to the native heathland resulted in a lower soil C content which highlights that establishing a mature ericaceous vegetation community is key to increasing soil C in restored heathlands. This is further evidenced by the large proportion of soil C in the native heathland being present in the particulate organic matter and litter fractions.

## Methods

**Site description**. We compared three environments: (i) native heathland; (ii) control pasture—heathland that has been converted to agriculture; and (iii) restored heath—former native heathlands that have been restored. Detailed descriptions of the field experiment can be found in Diaz et al.[63]; Green et al.[11], and Tibbett et al.[25]. Briefly, experimental plots were established in 1999 on the Isle of Purbeck, Dorset, UK (50.657425°N, −2.067085°W). The plots were on agricultural pasture of a single farm (Newline Farm), established during the 1950s and 1960s by the gradual improvement of acidic heathland soil through the addition of rock phosphate, manure and chalk marl. The restored heath treatment consisted of five replicate 50 × 50 m plots of improved agricultural pasture that were treated with 2000 kg $ha^{-1}$ of elemental sulfur in May 2000 as an acidifying agent, with an additional 1600 kg $ha^{-1}$ in 2001. The control pasture treatment consists of five replicates of 50 × 50 m plots that received no amendments. In addition, four replicate sites representative of native heathland, were selected in the nearby Middlebere Heath to benchmark against the restored heathlands plots.

**Soil sampling**. Eighteen years after the initial elemental sulfur application soil samples were collected using a gauge auger at 0–5 cm (after removal of the litter layer). Samples representative of each experimental plot were taken by sampling 25 points in a “W” configuration from each plot that were combined and thoroughly mixed to create one sample.

**Organic matter physical fractionation**. Figure 7 is a schematic of the physical organic matter fractionation regime used, which is adapted from the method described in Rolando et al.[64]. Briefly, 100 g of air-dried soil was soaked in deionised water for 5 min. Following this, the soil was poured onto a 250 µm sieve. The sieve was gently shaken vertically (30 × 3 cm strokes $min^{-1}$ for 2 min) under water, any floating material after this initial wet sieving was siphoned off into a pre-weighed aluminium tray and classified as litter. All material >250 µm, that was not floating, was washed off the sieve into a pre-weighed aluminium sieve and classified as the small macroaggregates (sMa) size class. Material that passed through the sieve was transferred to a 53 µm sieve and the wet sieving procedure was repeated. Any material >53 µm was classified as the microaggregates (mi) size class and material <53 µm was classified as the silt and clay (s + c) size class.

A 10 g subsample of each aggregate size class fractions (sMa and mi) was dispersed in 30 ml of 5% sodium hexametaphosphate (NaHMP) and shaken for 15 h at 180 r $min^{-1}$ on a reciprocal shaker. The resulting soil slurry was then passed through a 53um sieve and rinsed several times with deionised water. Material >53 µm was classed as intra-aggregate particulate organic matter (sMa POM/ mi POM). Material <53 µm was classified as the intra-aggregate silt and clay (sMa s + c/mi s + c). All fractions were oven dried at 60 °C. The total C recovery in fractions was 95.34% ± 3.14

**C and N analysis**. Fractions and bulk whole soil samples were analysed by NRM Laboratories (Bracknell, UK). Total carbon and nitrogen were analysed by combustion. The dried ground soil samples were combusted in pure $O_2$ at 1200 °C, the resultant gas mixture was led through a splitter where the $CO_2$ content was measured using an infrared (IR) detector. Organic and inorganic carbon were also measured through combustion. However, soil inorganic carbon, for all samples analysed, was below the detection limit (<0.1%). As a result, total C and organic C are the same value for all samples (bulk soil and fractions).

The dried, ground soil samples were acidified with orthophosphoric acid and sparged at 150 °C. The available $CO_2$ from the carbonates in the sample were led through a carrier gas to an IR detector which determined the amount of inorganic carbon present in the sample. Organic carbon was then ascertained by the difference between total and inorganic carbon. Active carbon was determined using a potassium permanganate oxidisable carbon (POXC) method. Dried, ground soil samples were mixed with permanganate for a fixed period. The absorbance of the supernatant was then measured by spectrometer with the amount of C oxidised acting as a function of the quantity of permanganate reduced, thereby giving the active/labile form of C. Due to the small mass of some fractions obtained, active carbon analysis was not conducted on the litter and silt and clay fractions. Bulk density of whole bulk soils was determined through the disturbed method, prepared dried soil (2 mm sieved) was weighed to determine the kg/l. This, along with an estimation of stoniness and sample depth, made calculation of organic carbon stock possible.

**Plant community survey and sampling**. As the primary source of fresh organic matter inputs, vegetation on each site was surveyed 18 years after the initial application of elemental sulfur amendments. The percentage cover of all plant species was recorded in ten randomly located 2 m × 2 m quadrats in each plot. Plant species were then classified as either: (i) characteristic of acid/calcifugous grassland and heathlands (*AH*); (ii) characteristic of mesotrophic grassland (*M*); or (iii) intermediate species which can occur in both mesotrophic and acid grasslands (*In*). Classifications were according to the National Vegetation Classification[65,66]. Ericaceous species were also identified separately for further analysis.

In each of the native heathland sites 4–5 above-ground samples of *Calluna vulgaris* were collected. Five samples were also

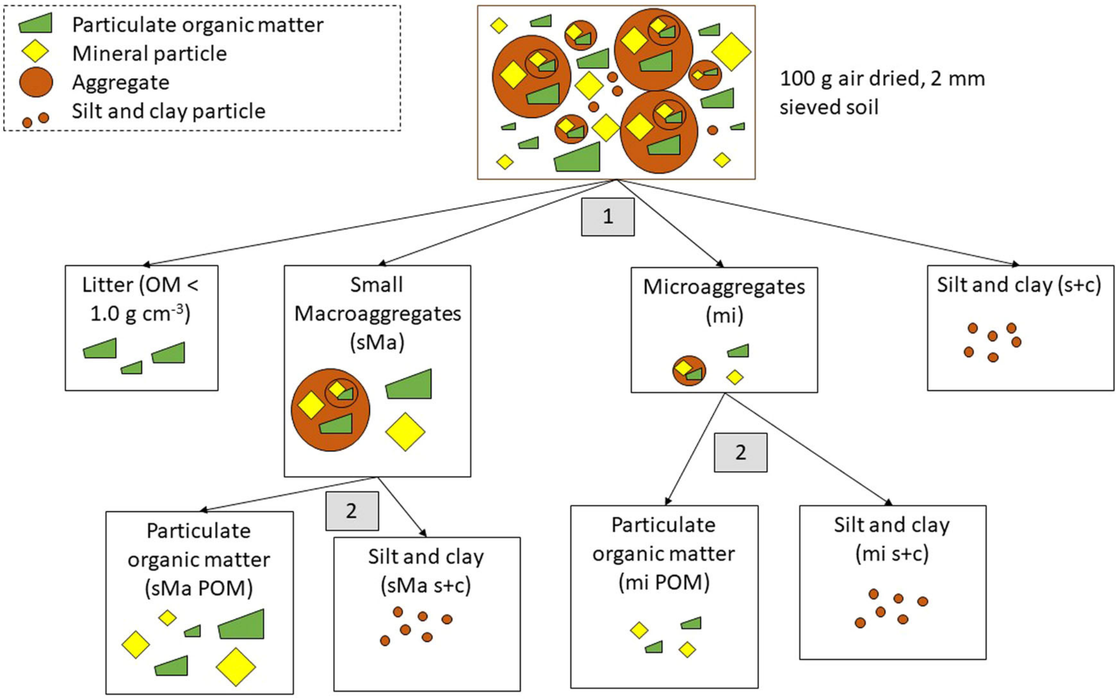


**Fig. 7 Schematic for physical soil organic matter fractionation.** Protocol with (1) wet sieving and (2) dispersion of aggregates.

collected from the restored heath plot that had the highest percentage cover of *C. vulgaris*. These samples were analysed for total C and N, expressed as C:N ratio.

**Statistics**. The effect of treatment (restored heath, control pasture, native heathland) on a single carbon or nitrogen variable, was assessed with the use of a one-way ANOVA and Tukey's post hoc testing. The relationship between percentage cover of plant species characteristic of acid/ calcifugous grassland and heathlands and a single carbon or nitrogen variable was assessed using Spearman Rank correlation coefficients. This was also conducted for ericaceous species only. Particular emphasis was given to these species as they are the dominant species of native heathland and therefore target species for restoration. These analyses used Minitab Version 20, after being tested for normality and homogeneity of variances with a Levene's test. Multivariate analysis on vegetation community was performed using nonmetric multidimensional scaling (nMDS), cluster analysis, and analysis of similarity (ANOSIM), using Primer Version 6. An nMDS of plant community was conducted using a Bray Curtis resemblance matrix based on the square root of plant species' abundance, with 1000 restarts and one-way ANOSIM, with treatment as a factor was conducted with 1000 permutations.

**Literature review**. A literature review which focused on lowland heath in Europe was conducted. A series of searches were conducted on Web of Science (28 December 2021) using terms that included, but not limited to: heath* AND soil carbon; heath* AND soil organic matter; heath* restoration; and heath* reconstruction. A total of 136 papers were returned in one or more of these searches. Papers were discounted if they were from upland heaths, peat moorland, outside of Europe or did not report soil carbon, loss on ignition or organic matter content. This resulted in a total of thirty-one papers that were found to report soil carbon or soil organic matter contents of native heathlands, heathland that has been converted to agriculture, or heathlands that have been restored from agricultural use. A full list of the references can be found in Supplementary Table 3. It should be noted that by taking this approach we eliminate the possibility of grey literature being included.

If a paper reported several concentrations for the same location and land use, a mean of the samples was calculated for a single record in the database. If the paper reported several concentrations for different locations, or land uses/management strategies, they were kept as separate records in the database. All soil C contents were converted into mg C $g^{-1}$ soil before they were entered into the database, and soil C stocks were converted into t $ha^{-1}$. Papers rarely reported the bulk density of the soil, so it was not possible to convert between soil C contents and soil C stocks, so we reviewed these data separately (contents and stocks). Organic matter (or loss on ignition) contents or stocks were converted to soil C contents or stocks using the conversion factor of 0.55 for soil organic matter to soil C[67].

There were five papers[3,25,30,68,69] that reported soil C contents (inc. standard deviations/errors and *n*) for all three environments (native heathland, heathland that has been converted to agriculture, and former native heathlands that have been restored). For these five papers, it was possible to calculate a Cohen's *d* effect size[70], comparing native heathland to heathland that has been converted to agriculture, and heathlands that have been restored from agricultural use.

**Reporting summary**. Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

## Data availability

Supporting data is available here: https://doi.org/10.5281/zenodo.10184907[71]

Received: 7 September 2023; Accepted: 8 December 2023;
Published online: 05 January 2024

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## Acknowledgements
The authors would like to thank the National Trust for the use of the field site and their support, along with Martin Smith and the late Rob Haslam for their invaluable contribution to setting up the field sites. We would also like to thank Joseph Tibbett and Tammy Edmonds-Tibbett for their assistance during field sampling. This project was part of the RECARE project (http://www.recare-project.eu/), which received funding from the European Union's Seventh Framework Programme for research, technological development and demonstration under grant agreement no 603498. This project also received funding from the University of Reading Undergraduate Research Opportunities Programme (UROP) for AH-H and MBs time.


## Author contributions
S.D.: Conceptualisation, Supervision, Data curation, Formal analysis, Investigation, Visualisation, Methodology, Writing—Original draft, Writing—review and editing, Funding acquisition. A.H.-H.: Data curation, Formal analysis, Investigation, Writing—review and editing. M.B.: Data curation, Formal analysis, Investigation, Writing—review and editing. A.D.: Conceptualisation, Methodology, Supervision, Investigation, Funding acquisition, Writing—review and editing. M.T.: Conceptualisation, Methodology, Supervision, Investigation, Funding acquisition, Writing—review and editing.

## Competing interests
The authors declare no competing interests.

## Additional information
**Supplementary information** The online version contains supplementary material available at https://doi.org/10.1038/s43247-023-01176-8.

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**Peer review information** *Communications Earth & Environment* thanks Hao Tang and Joost J. Vogels for their contribution to the peer review of this work. Primary Handling Editors: Clare Davis. A peer review file is available.

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