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Scavenging beetles control the temporal response of soil communities to carrion decomposition

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Abstract

1. Carrion is a frequent but overlooked source of nutrients to the soil. The decomposition of carrion is accelerated by invertebrate scavengers, but the impact of the scavengers on below-ground biota and its functions is scarcely known.
2. We conducted a laboratory experiment to investigate the effects of the burying beetle *Nicrophorus vespilloides* on the soil community of a temperate broadleaved forest. We assembled microcosms from soil collected from an oak woodland and treated them with mouse *Mus musculus* carcasses and mating pairs of burying beetles (♀+♂) in a factorial design with control soils. We sampled independent replicates over time to investigate how the beetles affect soil microarthropods and microbial biomass (bacteria and fungi) in relation to soil pH and organic matter content.
3. The beetle treatment initially reduced the total microbial biomass and abundance of major groups of microarthropods relative to the control soil. At the same time, organic matter increased in the beetle treatment and then dropped to the pre-beetle level (i.e. soil baseline) at the end of the beetle breeding cycle (2 weeks). The rapid temporal changes in organic matter were mimicked by the relative abundances of the dominant microarthropod groups, with Oribatida relatively more abundant than Collembola and predaceous mites in the beetle treatment. The overall final effect of the beetle (relative to the laboratory control) on microarthropods was negative but the beetle kept these variables within the levels observed for freshly collected soil (baseline), while the final effect on pH was positive, and most likely driven by the surplus of nutrients from the carcass and biochemical changes triggered by the decomposition process.
4. In nature, scavenging invertebrates are widespread. Our study demonstrates that beetles breeding in carcasses regulate the dynamics of key components of the soil food web, including microbial biomass, changes in the relative abundances of dominant microarthropods and soil organic matter and pH. Given the abundance of these beetles in nature, the study implies that the distribution of these beetles is a key driver of variation in soil nutrient cycling in woodlands.

KEYWORDS
above-ground–below-ground linkages, burying beetles, carrion, fluctuations, microbes, organic matter, pulse nutrients, soil microarthropods

1 | INTRODUCTION

Terrestrial ecosystems consist of functionally coupled above-ground and below-ground ecological communities (Bardgett et al., 2005; Bardgett & Wardle, 2010; Van der Putten et al., 2001). Most of the research investigating above-ground–below-ground linkages has focused on plant–soil interactions because the bulk of soil organic matter consists of dead plant material and rhizodeposits (Coleman et al., 2004; Lehmann & Kleber, 2015) but in some terrestrial ecosystems, such as broadleaved forests, the carcasses of above-ground fauna, like micromammals and small passerines, arguably represent a constant input of organic matter (Barton et al., 2013, 2016; Carter et al., 2007). This ephemeral and unpredictable but pervasive and frequent occurrence of carrion in forest soil represents an important but not well-studied source of high-quality nutrients (low C:N ratio) entering the soil, in contrast to the relatively low quality but more evenly distributed plant detritus (De Deyn et al., 2008). The decomposition of carrion can also be seen as a short, intense pulse perturbation limited in space and time, representing an intermittent input of resources from above-ground to the below-ground communities, or 'islands of fertility' (Carter et al., 2007; Mondor et al., 2012).

Very little is known about the effects of carrion decomposition on below-ground communities although there are various bits of evidence that the effects are very important. When carrion is not directly consumed and removed by opportunistic saprophagous or necrophagous vertebrates (DeVault et al., 2011; Henrich et al., 2017; Young et al., 2014), they create islands of surplus nutrients, which are nearly always colonized by various invertebrate taxa. These invertebrates use carcasses as a food source and/or breeding substrate, accelerating the decomposition process (Barton & Evans, 2017; Blackith & Blackith, 1990; Trumbo et al., 2016; Yang, 2006). The scavenging activity might be vertebrate or invertebrate dominated, depending on the composition of the above-ground community and environmental factors such as latitude, landscape, seasonality or weather conditions (DeVault et al., 2011; Farwig et al., 2014; Parmenter & MacMahon, 2009; Turner et al., 2017). Scavenging activity might also be very limited, for example in certain oligotrophic environments or communities with extremely low diversity where inaccessibility to the carcass results in a slow decomposition process, as also shown in some experiments (Michaud & Moreau, 2017; Pechal et al., 2014).

When there are no scavengers, decomposition is mainly driven by fungi and bacteria, which results in the release of large amounts of gases and exudates leaching into the soil (Bornemissza, 1956; Metcalf et al., 2016). This could have long-lasting effects on the soil biochemistry (Barton et al., 2016; Benninger et al., 2008) and could in turn lead to changes in the functionality of the microbial community (Chimutsa et al., 2015; Olakanye et al., 2014; Pechal et al., 2013). Changes in microbial communities may propagate to soil animal communities directly in contact or adjacent to the carcass, and overall could eventually impact also the plant communities in the area (Barton et al., 2013; Bornemissza, 1956; Szelecz et al., 2016).

Various attempts have been made to describe the length and number of stages in the decomposition of vertebrate carcasses (Matuszewski et al., 2008; Payne, 1965). However, the number of stages and their relative duration are influenced by the same factors already described above for the overall decomposition process. Bornemissza (1956) recognized five different phases: initial decay (0–2 days), putrefaction (2–12 days), black putrefaction (12–20 days), butyric fermentation (20–40 days) and dry decay (40–450 days). In the presence of scavengers, each stage is accelerated in a manner directly proportional to abundance and diversity of the scavenging community (Farwig et al., 2014), which assembles following a predictable succession (Bornemissza, 1956; Zanetti et al., 2015). Scavenging invertebrates and the below-ground decomposer community are thus pivotal to the decomposition of carcasses and likely interact in the process, which is very much accelerated by many invertebrates, but especially insects.

Scavenging insects can be generic (e.g. ants and various beetle families) and opportunistic necrophages (e.g. flesh flies) but others are more specialized and reliant on finding a carcass as a food source for their broods. Of these, particularly interesting and well-studied are the burying beetles (or carrion beetles) of the family Silphidae, with some species obliged to find, secure and bury a small vertebrate carcass to complete their life cycle (Eggert & Muller, 1997; Pukowski, 1933). The species *Nicrophorus vespilloides*, which we used here, is commonly found in open forests throughout Europe and the wider Palearctic, and has been used for decades as a model species for laboratory experiments or field observations on behavioural ecology, immunology and forensic studies because of its adaptability to laboratory conditions (microcosms) and its relatively fast reproductive cycle (Dekeirsschieter et al., 2011). In <2 weeks, a pair of breeding adults and their brood can completely consume the carcass of a small mammal or bird until only fragments of the skin, bones, hairs or feathers are left. They exert parental care, and both adults and larvae smear the carcass and the surroundings with secretions that prevent bacterial and fungal colonization by soil saprophytes via a combination of antimicrobial activity (Arce et al., 2012, 2013; Cotter & Kilner, 2010; Degenkolb et al., 2011; Reavey et al., 2014; Shukla, Plata, et al., 2018; Shukla, Vogel, et al., 2018; Trumbo, 2016), and via the seeding of the carcass with gut-derived microbes that outcompete soil-derived saprophytes (Duarte et al., 2017, 2018; Shukla, Plata, et al., 2018; Shukla, Vogel, et al., 2018; Vogel et al., 2017), and reduce competition with flies and other necrophagous species

(Cotter & Kilner, 2010; Degenkolb et al., 2011; Reavey et al., 2014; Shukla, Plata, et al., 2018; Trumbo, 2016).

In either slow or accelerated decomposition, there is a considerable amount of organic matter being released into the soil, which represents a substantial increase in nitrogen, phosphorous and other nutrients for the soil ecosystem and the associated plant community (Barton et al., 2016; Parmenter & MacMahon, 2009). Such significant input of nutrients, exudates and antimicrobial chemicals is bound to affect the surrounding soil and its biota, but studies are lacking. For example, the effects of carrion decomposition on the dynamics of soil animal communities have often been overlooked or poorly investigated, even more in the presence of scavenging macroinvertebrates such as carrion beetles. Within the soil food web, microarthropods and nematodes represent the most abundant invertebrates in nearly all soil communities (Coleman et al., 2004). They display high diversity levels and are important regulators of soil food webs as they exert direct control on microbial biomass (Lussenhop, 1992).

Given the link between soil biota and nutrients, and the existing knowledge on the process of carcass decomposition, we here started from the general hypothesis that a carcass decomposition event determines a sudden pulse of high-quality nutrients (Woelber-Kastner et al., 2021) that causes a bottom-up perturbation of the soil food web. Two very recent studies have looked at the effects of *Nicrophorus* carcass use on soil chemistry *after* carcass decomposition (Hoback et al., 2020; Woelber-Kastner et al., 2021). Hoback et al. (2020) found that the presence of a carcass decreased soil pH and increased salts and nitrates in the soil, with *Nicrophorus marginatus* having additional positive effects on the latter two measures. Woelber-Kastner et al. (2021) found that carcass decomposition increased labile C, dissolved organic N and C, but decreased soil pH and microbial C:N ratios. The presence or absence of the related species, *Nicrophorus orbicollis*, on the carcass resulted in no measurable difference in these soil parameters. However, neither study considered the effects of the beetles on soil macrobiota, or looked at changes in any measures *during* the process of carcass decomposition.

In this study we report the results from a controlled laboratory experiment in which we hypothesized that changes in the soil community (microarthropods and microbes) caused by the carcass will be controlled by the breeding activity of burying beetles during the process of carcass decomposition/consumption. Burying beetles should accelerate the velocity of the decomposition process and affect the biochemistry of the soil with the production of antimicrobial compounds that specifically target soil saprophytes (Cotter & Kilner, 2010; Cotter et al., 2013; Duarte et al., 2017, 2018; Shukla, Plata, et al., 2018; Shukla, Vogel, et al., 2018). Given the antimicrobial compounds should inhibit bacteria and fungi, we also expected a reduction of microbial biomass when the beetle is present and an increase in microbial biomass in the carcass only treatment. We expected these changes to cascade to soil microarthropods and we also expected changes in pH and organic matter caused by the carcass and the beetle. More generally, we hypothesized that changes in the soil (biotic and abiotic) will vary over time as a function of the key steps in the breeding cycle of beetle (see Figure 1 for a graphical summary of key hypotheses and findings).

2 | MATERIALS AND METHODS

2.1 | *Nicrophorus vespilloides*

The colony was founded in February 2011 from an outbred colony maintained in the Zoology department at the University of Cambridge. Adult beetles were maintained individually in small plastic boxes containing moist compost. Beetles were fed twice weekly with minced beef and maintained at 20°C under a 16:8 light:dark cycle. During breeding, unrelated males and females were selected and placed as a pair in a breeding container (17 × 12 × 6 cm), one third filled with moist compost, provided with a newly defrosted mouse carcass obtained from a pet food supplier (Livefoods Direct) and placed in a cupboard to simulate underground conditions.

Approximately 8 days after the parents were paired, larvae dispersed from the consumed carcass and were weighed, counted and placed individually in compartments of 25 cell Petri dishes, with different Petri dishes used for each family. The containers were topped up with moist compost and the larvae left to pupate. Eclosion occurs around 20 days following dispersal, after which the beetles were set up in their individual containers and were either used as colony beetles or used in later experiments.

2.2 | Soil sampling and microcosm assemblage

Microcosms were assembled in the laboratory to test the effects of carrion decomposition on soil communities with and without *Nicrophorus vespilloides*, and over the duration of the breeding cycle of the beetle. Soil samples for the experiment were collected from a native oak woodland in Northern Ireland (Breen Oak Wood, Armoy). *N. vespilloides* has been recorded from several locations close to Breen oak wood in the past and are likely to be present but the site has not, to our knowledge, been surveyed for carrion beetles. The sampling location was chosen according to accessibility, level of disturbance and previous surveys of the study area. This mature open woodland, a National Nature Reserve surrounded by larch, spruce and pine plantations, is dominated by an ancient population of oak trees *Quercus robur* and *Quercus petraea*, with an understorey of sparsely distributed hawthorns and hollies, and a thick undergrowth of mainly carpeting Great woodrush *Luzula sylvatica* in places. It is easily accessible but scarcely frequented by the public. Previous surveys of the area had shown the presence of a highly diversified below-ground communities and abundant soil microarthropods communities (e.g. Magilton et al., 2019).

Soil samples were randomly collected, within an area of forest of approximately 4000 m^2, with the use of soil corers of 10 cm in diameter, to a depth of 10 cm. To facilitate the insertion of the soil corer into the soil, excessive vegetation and leaf litter were removed.

In the laboratory, the soil samples were gently mixed together to avoid excessive physical disturbance of the fauna while obtaining a relatively homogenized substrate, which was then used to assemble 75 microcosms, built in lidded transparent plastic boxes of approximately 17 × 12 × 6 cm in size. Five microcosms were extracted immediately to have an instantaneous, snapshot baseline representing the soil community as sampled from the field and assembled in the laboratory. This baseline was not replicated over time in the field, under the assumption that, over the short-term interval of the experiment, natural temporal variance would be comparable to the variance observed between replicates in the laboratory. This assumption is supported by what observed in the laboratory control soil. The other 60 microcosms were left to equilibrate with the conditions of the laboratory for a week, after which 20 microcosms were left as controls with soil only, 20 contained the carcass only treatment (soil and a dead mouse) and 20 contained the carcass + beetle treatment, that is soil, a dead mouse and a mating pair of *N. vespilloides*. In the beetle treatment, a pair of beetles was introduced in each microcosm, one male and one female. The pair would mate and use the provided carcass for breeding and raise their brood (Figure 1a).

2.3 | Microcosms sampling and analysis

At the start of the experiment, the microcosms were placed and kept in the dark at a temperature of 20°C. During the experiment, five microcosms per treatment were harvested at each of four points in time (T1, T2, T3 and T4). Sampling was not repeated on the same microcosm to avoid repeated measurements and physical disturbance of the experimental units, and also to achieve full replication of the time by treatment combinations for a full factorial design. The four points in time were chosen to map on to the key four stages of the beetles' reproductive cycle on the carcass (see also figure 1 in Cotter et al., 2013, which shows the production of antimicrobials by the beetle as a function of time). At the start of the experiment, the beetles begin preparing and burying the carcass, they mate and the female lays the eggs in soil around the carcass; at day 3, chosen as the first sampling time T1, the beetles' eggs begin to hatch and the parents provide care for the larvae by feeding them chewed and partially digested food. At this time, larvae also already begin to feed on the carcass. This is the time when antimicrobial production starts to peak (figure 1 in Cotter et al., 2013). At day 6, the second sampling time (T2), the larvae continue to feed on the carcass by themselves and parents reduce their production of antimicrobial secretions; by day 10, our third sampling time (T3), adults have been removed (day 8), the carcass has been consumed more or less completely and the larvae have started to disperse around the microcosm; after a further week, at day 17 (fourth sampling time T4), the larvae are well into the pupal stage, buried and scattered across the microcosm.

At harvest, carcass and beetles (adults, larvae, pupae, depending on sampling time) were removed, and a subsample of 5–10 g of soil was collected from directly underneath the carcass for the extraction and quantification of the phospholipid fatty acids (PLFAs) of bacteria and fungi (see below). During the collection of the subsample, care was taken not to physically disturb the rest of the soil microcosm, which was put in Berlese-Tullgren extractor funnels for a total of 7 days to extract microarthropods (eventually preserved in 75% ethanol solution). Air-dried soil was used, after being ground and sieved through a

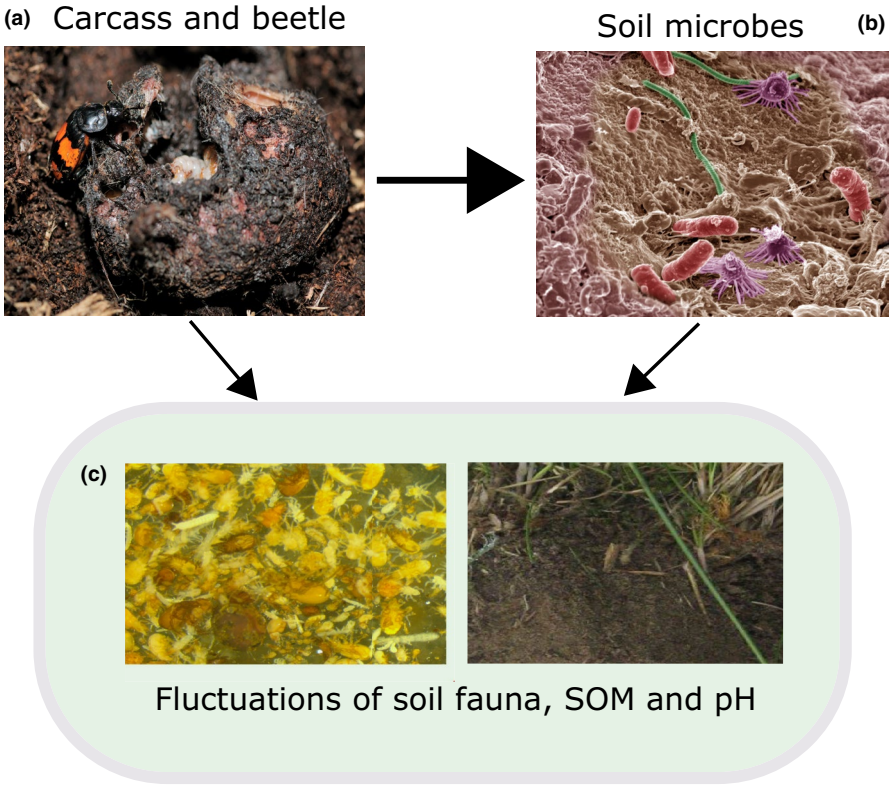

FIGURE 1 Graphical abstract of the paper: burying beetles alter the dynamics of carcass decomposition with their scavenging activity and production of antimicrobial compounds. We hypothesized that these beetle activities will affect soil microbes (b) directly (thick arrows connecting panels a and b) and also fauna and general soil parameters (c) either directly (narrow arrow connecting panel a to panel c) or via microbes (narrow arrow connecting panel b to panel c), or both. Our experiments strongly support this hypothesis, showing that changes in soil microbes, fauna, pH and organic matter vary over time as a function of the key steps in the breeding cycle of beetle. Photograph credits: (a) Oliver Krueger; (b) Courtesy of Pacific Northwest National Laboratory and Alice Dohnalkova/PNNL (CC licence); (c) Marco Ilardi

0.5-mm mesh size, to measure soil pH and to quantify organic matter content by loss on ignition (in muffle furnace at 500°C for at least 5 hr, until the sample stopped losing weight). The animals were sorted, identified and counted with the use of stereo-microscopes; microarthropods were identified as oribatid mites, Mesostigmata predaceous mites, Prostigmata and other mites (grouped together given the very low densities) and collembolans. All other arthropods were identified at the order or higher level (and were present at very low densities compared to the other ones). Occasional worms and molluscs were also recorded but not considered in the analysed data here. For a list of all identified taxa and their average abundances across all samples and treatments, see Table S4.

To estimate the impact of the treatment on microbial biomass and bacterial-fungal ratios, we lyophilized 5 g of soil from the subsamples of each microcosm, and used this to extract lipids according to Frostegård et al. (1991). Lipids were fractioned into neutral lipids, glycolipids and polar lipids on a silica acid column (Bond Elut, Varian Inc.) via successive elution with chloroform, acetone and methanol. We focused on the methanol fraction, which contains the phospholipids, and subjected this to mild alkaline methanolysis to transform the PLFAs into free fatty acid methyl esters, which we then identified and quantified on a gas chromatograph with a flame ionization detector and a 50-m HP5 capillary column. The sum of the PLFAs i15:0, a15:0, i16:0, 10Me16:0, i17:0, a17:0, cy17:0, 10Me17:0, 10Me18:0 and cy19:0 was used as an indicator of bacterial biomass while the PLFA 18:2ω6 was used as an indicator of saprotrophic fungi (Birgander et al., 2014; Å. Frostegård et al., 1991; A. Frostegård & Bååth, 1996).

2.4 | Statistical analysis

We visualized data using mean and standard errors, scatter and correlation plots and multivariate ordinations. Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.mw6m905wr (Caruso et al., 2021). The univariate responses of organic matter, pH, microbial lipid biomass and the abundance of microarthropods were analysed using a linear model based on the two-way fully factorial design with factor Time (four levels: T1, T2, T3 and T4) and Treatment (control, mouse only and mouse + beetle). The fully replicated design allows us testing for the main and interaction effects. The model was fitted using generalized least squares to explicitly account for heterogeneity of variance between times and treatments (Zuur et al., 2009), and thus relaxing the classical assumption of homogeneity of variance required by standard ANOVA without increasing type 1 error (false positive). Multivariate patterns in the distribution of animal communities were analysed using principal coordinate analysis (PCoA) on the Hellinger-transformed abundance data (Legendre & Gallagher, 2001; Legendre & Legendre, 1998). Permutational multivariate analysis of variance (PERMANOVA) was used to test the community ordination results (Anderson, 2001; McArdle & Anderson, 2001). Analyses were performed in R using the packages NLME and VEGAN (Oksanen et al., 2007; Pinheiro et al., 2021).

3 | RESULTS

3.1 | Microbial biomass, pH and organic matter

Microbial PLFA biomass ranged from approximately 18 to 186 nmol/g dry soil, which is a typical range for micro and mesocosm experiments (e.g. Hestrin et al., 2019). Bacteria dominated the system, with the fungal to bacterial ratio ranging from 0.014 to 0.25. Total microbial biomass was significantly inhibited by the presence of the beetle at T1 and T2 (when the production of antimicrobial exudates by the beetles is the highest) but also clearly recovered at time T3 and T4, which returned to the levels observed in soil and with the mouse carcass (Figure 2a, see Table S1 for full statistical model, including effect sizes) but higher than the baseline of freshly collected soil. Both in the mouse only and the beetle microcosms, pH increased over time relative to the control but with an interaction pattern in the beetle treatment that resembles the pattern observed in microbial biomass (Figure 2b, Table S2 for full statistical model). Organic matter showed a strong time by treatment interaction driven by the beetle (Figure 2c); in T1, T2 and T3, organic matter peaked in the beetle treatment while slightly increasing over time in the carcass treatment and remaining basically constant in the control. At T4, however, the effect of the beetle disappeared, and the beetle and carcass treatment converged to a mean value lower than that of the control (see Table S3 for full statistical model) but in line with the field baseline. All T4 values (control and treatments) were indeed within the baseline organic matter values, while both pH and microbial biomass were shifted by treatment to values clearly much higher than the original baseline. The fungal to bacterial ratio, instead, showed neither pattern over time, nor by treatment (Figure 2d), although at T1 the ratio is shifted to the advantage of fungi in treatments and control relative to the baseline, an effect that even if significant lasted for a very short time.

3.2 | Microarthropod community

We counted and identified a total of 56,393 arthropods. Of these, the vast majority (54,639) were either mites (45,195) or collembolans (9,444). Other relatively abundant taxa included the larvae of Diptera and Coleoptera, Pseudoscorpions, Myriapoda (especially Diplopoda and some Pauropoda) and Thysanoptera. Overall, the taxonomic composition was as expected for woodland soils, with the presence of Pseudoscorpions and Pauropoda indicating a well-established forest fauna (Dindal, 1990), which could be maintained over the course of the experiment despite the artificial assembly imposed by laboratory conditions. Average values (arithmetic mean) of all the taxa found in the experiments are reported in Table S4. Multivariate ordination (PCoA of Hellinger-transformed data) of the community table was dominated by collembolans, and oribatid and predaceous mites (Figure 3). The community was highly structured, with the first two axes of the ordination accounting for 76% of the total variance. This is mostly due to the overdominance of three

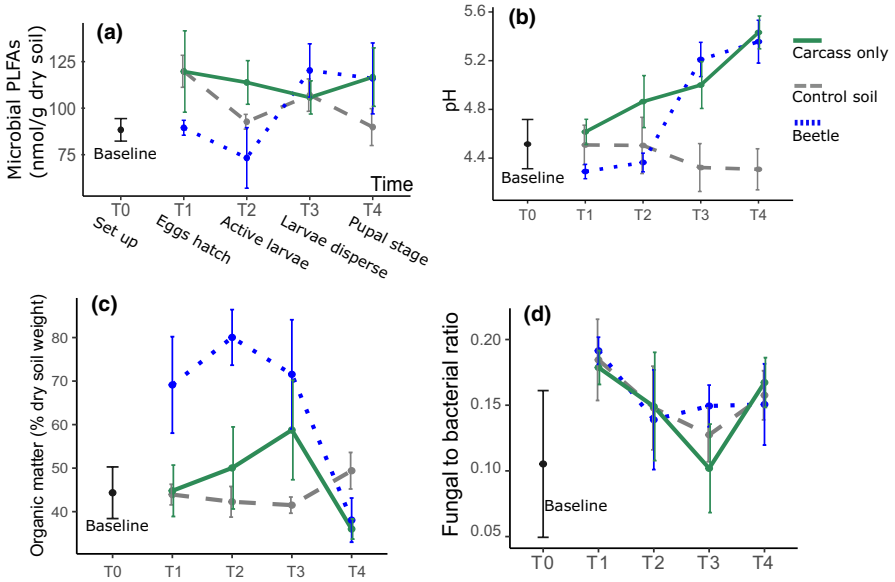

FIGURE 2 Mean ± 1 *SE* of (a) total microbial PLFAs (an estimate of microbial biomass), (b) soil pH, (c) organic matter and (d) fungal:bacterial ratio. The main effects of the factor sampling Time (*x*-axis; four levels: T1, T2, T3 and T4) and Treatment (colours and line type, four levels: baseline, control, carcass only and beetle) and their interaction were tested using a linear model fitted with generalized least square, which allowed us modelling heterogeneity of variance (see variable size of standard errors). The baseline consisted of five independent replicates of soil freshly collected and processed just before the experiment started. The beetle treatment is a mouse carcass with an actively breeding pair of *Nicrophorus vespilloides*. Control is just soil (no carcass, no beetle). Full results of the linear models for the total PLFAs, soil pH and organic matter are available in Tables S1–S3. The linear model for the fungal to bacterial ratio returned fully negative results (data not shown). For pH and organic matter, we observed very high *F*-values with *p*-values < 0.001 for the Time × Treatment interaction terms (Tables S2 and S3). Effect sizes showed that effects were particularly strong for the beetle treatment. For total PLFAs, the interaction term $F_{6,46} = 2.13$ with a *p*-value = 0.07 and the effect sizes showed that the interaction term was much higher and statistically significant for the beetle treatment only (Table S1B)

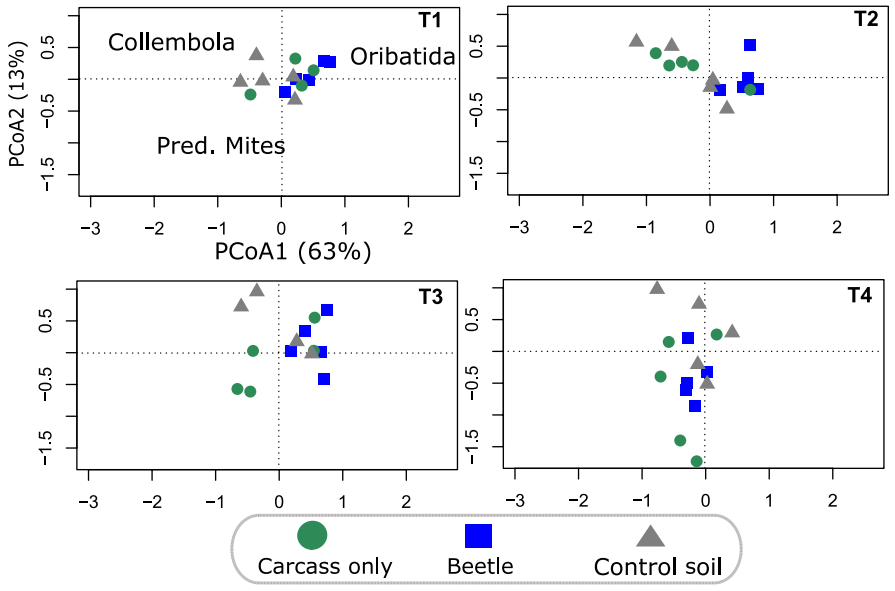

FIGURE 3 Principal coordinate analysis (PCoA) of Hellinger-transformed microarthropod abundance data. The same ordination was split into four panels to better visualize the position of samples across the four sampling times T1, T2, T3 and T4. Every point in the graphs represents the community of a single microcosm, with the colours/symbols representing the three main treatments (control, beetle, carcass only). The baseline soil was also included in the ordination, and the data points all fell tightly around the centre of the ordination plot. These points are not plotted here to improve the clarity of the representation. The beetle samples mostly gravitated on the right side of the first axis compared to the control and the carcass only samples but this effect disappears at T4. As these four panels are exactly the same ordination (but with data split by sampling time), the axis labels and the taxa labels are reported only in the top left panel (T1)

taxonomic groups. Axis 1 (63%) is a contrast between oribatid mites (positive loading on the axis) and collembolans and predaceous mites (negative loading on the axis). Axis 2 (13%) is a contrast between collembolans and predaceous mites. When splitting the data points of the same ordination by sampling times (Figure 3), it is clear that the beetle treatment mostly gravitated on the positive side of axis 1, especially at T2 and T3. The baseline data points fell on the origin of the PCoA (not shown in Figure 3), and the mouse and soil treatment mostly gravitated on the negative side of axis 1. At T4, however, all samples display minimal variation along axis 1 and mostly dispersed around axis 2. Thus, overall, the relative abundance of Oribatida increased in the beetle treatment at T1, T2 and T3. This pattern is very similar to what observed for organic matter, which is very evident when plotting mean and standard error of the first axis of the ordination (compare Figure 4d with Figure 2c and see Table S5 for full statistical model).

Given the multivariate patterns were dominated by the abundance of three taxa, we further analysed these three taxa on their own (Figure 4a–c; Tables S6–S8). Collembolans (Figure 4b) were clearly inhibited by the beetles, with a minimal but significant recovery at the end of the experiment. Predaceous mites (Figure 4c), who mostly feed on collembolans, followed a similar pattern. Oribatids (Figure 4a), instead, consistently decreased over time in the beetle treatment while increasing over time in the soil only treatments and remaining stable in the carcass only treatment after an initial sharp drop between T1 and T2.

Finally, to further illustrate how the experimental treatments affected overall correlations between all the measured variables, we constructed bivariate correlation plots for the microarthropod groups, microbial PLFAs, pH and organic matter (Figure 5). These plots show in one glance how the beetle treatment and the carcass only treatment affected many of the bivariate correlations between the three major microarthropod groups, but also between abiotic variables (pH and SOM), microbes and between abiotic variables, microbes and the microarthropods. The most evident effects are increased correlation between microarthropod groups in the beetle treatment, and the inversion of the sign in the correlation between total microbial PLFAs (a proxy for microbial biomass), the abundance of mites and total organic matter. The correlation plot also shows that the beetle treatment generated a positive correlation between microbial biomass and pH while the carcass only treatment generated a negative correlation between these two variables. In the control soil, there was no clear correlation between these two variables.

4 | DISCUSSION

The easily observable, major impact of the necrophagous beetle *N. vespilloides* is the acceleration of the decomposition process of the carcass. The decomposition of a carcass is hypothesized to create a sudden pulse of nutrients such as N and P to the soil but the presence of the beetle alters this input of nutrients, with impacts on soil biota (Figure 1). During breeding, the production of antimicrobial secretions by *N. vespilloides* adults peaks shortly after larvae hatch (Cotter et al., 2013). When larvae feed autonomously, antimicrobial production by adults falls and in about 10 days the carcass is completely decomposed and the larvae have entered the pupal stage. The timing of all these processes is very predictable and our sampling of the experimental units was tailored around this timing, which helped us demonstrate that the breeding activity of *N. vespilloides* had a profound effect on the temporal dynamics of the soil community, and that these effects correlated with changes in soil organic matter and pH. The beetle secretions, which prevent bacterial and fungal colonization of the carcass by soil saprophytes (Duarte et al., 2017, 2018; Shukla, Plata, et al., 2018; Shukla, Vogel, et al., 2018; Vogel et al., 2017), are known to show increasing antibacterial activity between our sampling T1 and T2, that is between day 3 and 6 of the cycle (Cotter et al., 2013). Our data demonstrate that this is the

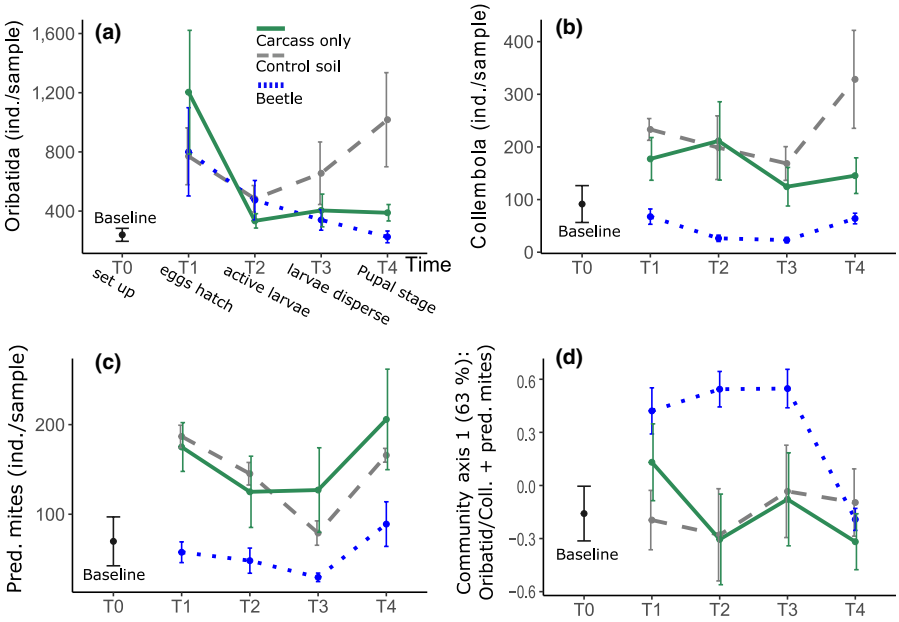

FIGURE 4 As Figure 2 but for (a) Oribatid mites, (b) collembola, (c) predaceous mites and (d) the first axis of the ordination in Figure 3. The linear model output for these data are available in the Supporting Information with the effect sizes, ANOVA *F*- and *p*-values (Tables S5–S8). The interaction term of the first ordination axis (d) had $F_{6,46} = 2.76$ (*p*-value < 0.05), while the interaction term for the single taxa (a–c) was not significant. The main effects of both time and treatment were highly significant (*p*-value < 0.01) for all the four variables

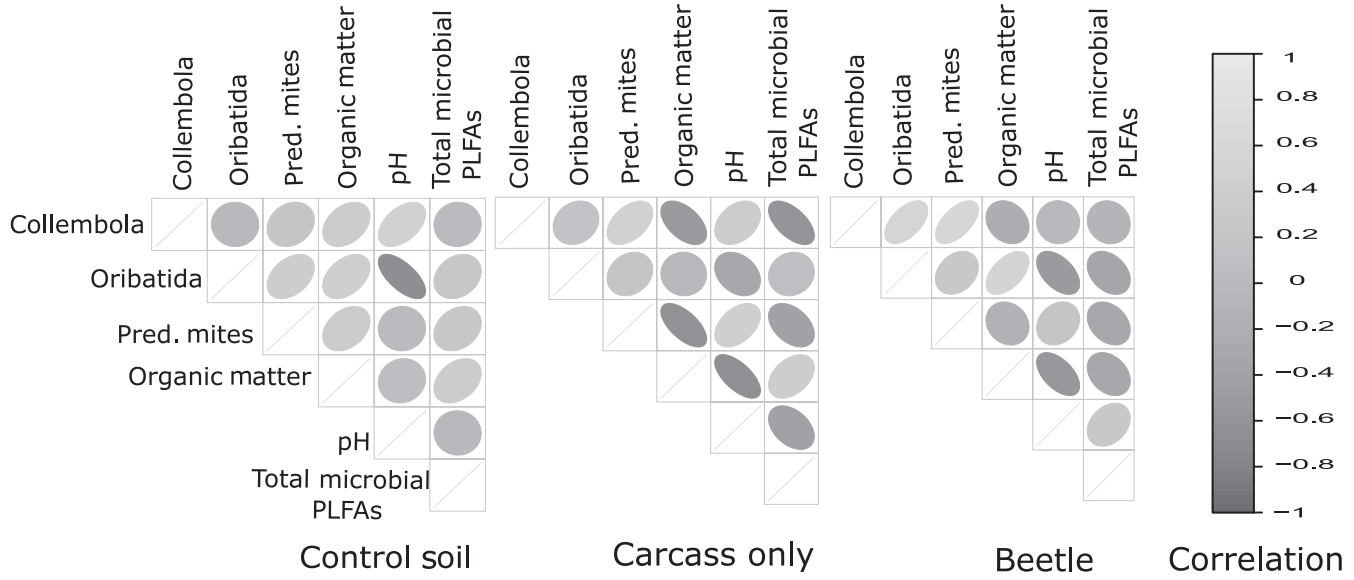

FIGURE 5 Bivariate correlation plots between the three major soil animal groups, soil properties (organic matter and pH) and microbial total PLFAs (a proxy for microbial biomass). The orientation of the ellipsoid and the intensity of grey together with the width of the ellipsoid indicate the sign and strength of the correlation respectively; dark grey and negative slope in a relatively thinner ellipsoid represent strong negative correlation (see, e.g. the row Oribatida and column pH in the control soil), while light grey and positive slope and a relatively thinner ellipsoid represent strong, positive correlation (see, e.g. the row Oribatida and column Organic matter in the beetle treatment). Correlations were calculated across the 20 replicates for control, carcass only and beetle treatment, and they thus compound all the temporal variability displayed over the duration of the experiment

time when soil microbial communities were mostly inhibited by the beetle while after T3 (day 10), when the adults have gone, microbial biomass returned to the level of the control and the carcass only treatment. In fact, microbes seemed to increase relative to the baseline provided by the freshly collected soil and the control soil. The change observed in microbes was reflected in the microarthropod communities, especially collembolans, which are microbivores (Potapov et al., 2016) but also in predatory mites, which consist of many species that mostly, although often not exclusively, feed on collembolans (Dindal, 1990; Walter & Proctor, 1999). The reduction of collembolans in the beetle treatment could be not only due both to the negative effects on microbes, their food, but also due to the secretions of the beetle. We have currently no data to assess which effect might be more important but it is clear that there is an effect. Predaceous mites are most likely negatively affected by the beetle indirectly due to the negative effects of the beetle on collembolans, the main prey of many of the predaceous mites found in the samples.

The changes observed in collembolans and predaceous mites contrast with the response of oribatid mites, which increased in the beetle treatment relative to the collembolans although oribatid mites overall also decreased in abundance over the course of the experiment in the beetle treatment. Oribatid mites include many fungal feeder species but also various species that feed on range of items, spanning various trophic levels (Maraun et al., 2011; Schaefer & Caruso, 2019), and so the group overall may be less directly affected by the beetle. When looking at the overall multivariate pattern of the microarthropod community, the clearest effect of the beetle was on the very similar pattern displayed by the variation of organic matter and the major gradient in community structure of the fauna, which accounted for more than two third of community variance. This gradient can be summarized by the ratio between oribatid mites, on the one hand, and collembolans and predaceous mites on the other hand. Organic matter and the first axis of the community ordination (i.e. the relative abundances between the three major microarthropod groups) both increased in T1, T2 and T3 to drop off at T4 to the control level. This was parallel to the inhibition of microbial biomass in T1 and T2. Although a fully mechanistic description of the relationship that link all these variables is not possible, the beetle clearly drove all these patterns and we know that beetles produce antimicrobial secretions at T1 and T2 (Cotter et al., 2013). The inhibition of microbial biomass at T1 and T2 thus strongly suggests that all the other patterns are driven by the changes that the beetle induces in the microbial communities, and that cascades on pH, organic matter and the abundances of soil microarthropods. We thus propose that it is very likely that all the other components of the soil food web that we did not measure (e.g. nematodes and protists) were equally affected, which can be tested in future experiments.

Our results support our general theory that burying beetles, in regulating the timing of the decomposition events, control the temporal variation of the soil food webs and affect critical soil properties such as organic matter and pH over time. In this process, the beetle changed the timing of the effects that the carcass alone has on soil biota, pH and organic matter. Also, carcass and beetle significantly increased pH by almost one unit at the end of the experiment relative to the control and baseline soil, and also caused a transitory change in the relative abundance of soil microarthropod groups until the larvae dispersed. These two changes can cascade on microbial community composition given the role of pH in controlling microbial

populations and the fact the different soil fauna groups feed differentially on different microbes (Potapov et al., 2016; Schaefer & Caruso, 2019). At an ecosystem level, it is also important to consider what did not change at the end of the experiment in the presence of the beetle. The beetle first reduced the mean biomass of microbes (bacteria and fungi) and changed the relative abundances of dominant microarthropods, at least relative to the carcass only treatment. But, eventually, the beetle and carcass treatment resulted in a relatively modest and highly variable increase in microbial biomass and no net change in the density of the three major arthropod groups. Instead, in the carcass only treatment, Collembola and predaceous mites, which mostly although not exclusively feed on them, resulted in increased populations relative to the soil baseline. Also, while the decomposition process of the carcass is basically completed at the end of the beetle breeding cycle, the carcass only treatment decomposition was much slower as has been noted previously (Metcalf et al., 2016).

In natural woodlands, small mammal populations are large and represent a continuous input of carcasses to the floor. Given the effects of the beetle on the velocity of the decomposition process, soil biota and abiotic properties, we speculate that the spatial and temporal distribution of the beetle and of carcasses scattered across woodland floors contributes to both the timing of the input of nutrients to soil from mammal populations and the cycling of these nutrients through soil biota. An important future direction of research is thus the quantification of this ecosystem-level impact of the beetle and the relative importance of burying beetles and other scavengers such as flies.

On the surface, our results appear to contrast with the recent studies on the North American congeners, *Nicrophorus orbicollis* and *Nicrophorus marginatus*, which either did not find any effects of the beetles on soil chemistry (Woelber-Kastner et al., 2021), or found effects on salts and nitrates only (Hoback et al., 2020). However, both studies concentrated on the period *after* carcass decomposition, which relates to our T4 (17 days here, 18 days in the study by Hoback et al. (2020) and 21 days in the study by Woelber-Kastner et al. (2021)). Importantly, we show large and rapid effects of beetles on pH, microbial biomass and soil biota, but most of these effects are transient, with most measures back to 'normal' by the end of the experiment. Therefore, given the differences in the soil types and methodologies, our results are remarkably consistent with these two studies. Where Woelber-Kaster et al. (2021) and this study used acidic woodland soils, both showed an *increase* in pH during carcass composition. Hoback et al. (2020) used highly alkaline soil from a sandpit and found that carcass decomposition *decreased* pH, suggesting that microbial breakdown of a carcass, in the presence of absence of beetles tends to move soil to a more neutral pH.

Woelber-Kaster et al. (2021) found no effects of beetles on soil dissolved organic carbon, and indeed, we only found large differences in soil organic matter between beetle and carrion only treatments in the early stages of beetle-induced carrion decomposition (up to day 6). In both carrion only and beetle treatments, organic matter had returned to baseline levels by day 17 in our study, whereas they were still elevated in both treatments in the Woelber-Kaster study. This is likely due to the fact that we measured all soil organic matter by ignition, while Woelber-Kaster focused on dissolved organic matter but the differences may also be due the different soils and beetle species used. The differences could also be due to slower decomposition in the field, such that the 21-day time period in the Woelber-Kaster study mapped more closely to our T3, where the carrion and beetle treatments were indistinguishable from each other. In any case, high levels of organic matter or C were observed compared to the controls at the end of the experiment. The microbial biomass reported here and in the Woelber-Kaster study is comparable. They found slightly higher fungal to bacterial ratios (0.2–0.26 at day 21 vs. 0.15–1.17 at day 17) but, as here, found no effects of the carcass or the beetle on those ratios. This confluence in findings across three studies, using three different burying beetle species suggests that their activity is comparable across species and locations.

Previous research has shown that burying beetles are widespread across the northern Palaearctic region, and have been shown to sequester up to 75% of small vertebrate carcasses during their active period (spring to late summer) in woodland (e.g. Trumbo, 2016). We showed that the decomposition of small vertebrate carcasses, especially in woodland, affects the temporal dynamics of key groups of soil biota, which are central to nutrient cycling. We thus propose that the combined system 'beetle-carcass-soil biota' is an overlooked but central part of nutrient cycling in woodlands. This system thus deserves much more attention, especially for future field studies that should also include plants.

5 | CONCLUSIONS

Our study shows that the burying beetle *N. vespilloides* is a strong, short-term regulator of the temporal dynamics of soil biota and their response to vertebrate carcasses. We also show the potential for these ecological dynamics to alter the biochemistry and microbiology of soil. Soil biology and biochemistry is central to above-ground vegetation dynamics, and we thus propose that future studies should investigate the relationships between the temporal and spatial heterogeneity of burying beetle activity and plants in the field. Future studies will have to unveil the direct and indirect pathways that link the activity of scavenging beetles to the dynamics of soil, and quantify the relative importance of the beetle-carcass-soil interaction in plant community dynamics and the functioning of woodland ecosystems.

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AUTHORS' CONTRIBUTIONS

T.C., S.C.C. and M.O.I. conceived the study; M.O.I. and S.C.C. set up and maintained the experiment; M.O.I. harvested and processed soil fauna and soil; M.O.I., E.C.H. and G.R. quantified microbial PLFAs; T.C. and M.O.I. analysed the data; T.C. and M.O.I. led the writing with contributions from all the other authors.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.mw6m905wr (Caruso et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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