Beneficial links for the control of aphids: the effects of compost applications on predators and prey

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Summary

1. Polyphagous predators, such as spiders and beetles, perform a fundamental ecosystem service as regulators of agricultural pests, particularly aphids. They are most effective when they colonize the crop before the pest has reached its exponential growth phase. However, this is also when predators find themselves in a state of near-starvation.

2. Predator numbers can be enhanced by applications of different types of organic matter, but the mechanism is not clearly understood. One hypothesis is that compost applied to the field may introduce a new detrital food chain to maintain predators until the pest arrives, but this may also be detrimental to effective pest control, fostering a surplus of alternative prey and causing a switch away from the pest. To elucidate these possible outcomes, we report on the use of within-field compost applications on aphids and their predators, presenting 4 years of field-scale manipulations.

3. We found both direct *and* indirect links between compost, aphids and predators. In years when compost-treated plots had significantly higher numbers of predators, aphids were in significantly lower numbers than in plots without compost. Conversely, when there was a lack of response by predators, aphid numbers showed similar trends in all treatments.

4. In all years, alternative prey responded strongly to compost application and did not fluctuate at the level shown by predators, suggesting that these two prey groups were decoupled. Instead, the predicted positive feedback of compost on predators numbers was either weak or absent.

5. *Synthesis and applications.* The effect of compost on aphids clearly requires further practical refinement if it is to provide constant pest suppression, making it difficult to provide specific management recommendations at this stage. In the short term, compost application may not always confer immediate benefits in terms of pest control alone but this must be set against other better known benefits (moisture retention, nutrients). In the long term, experiments measuring the full trophic pathway are needed to unravel the effects of organic matter type, application time and the siting of compost relative to the crop in order to optimise pest suppression potential.

Key-words: apparent competition, conservation biological control, detrital subsidy, integrated pest management, prey switching, *Sitobion avenae*, trophic cascades, winter wheat

Introduction

In Western Europe, *Sitobion avenae* (F.), the grain aphid, is one of the most harmful cereal aphids, reducing yields when outbreaks exceed the economic injury threshold (Wratten

1975). Fortunately, the population dynamics are such that there is a characteristically slow build-up of the population in May and early June (Larsson 2005) when polyphagous predators could provide control (Landis, Wratten & Gurr 2000; Symondson, Sunderland & Greenstone 2002a). Biocontrol by polyphagous predators is most successful when the predators arrive early, before the aphid population shows exponential growth (Landis *et al.* 2000; Symondson *et al.*

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2002a; Harwood, Sunderland & Symondson 2004). However, at this time, a polyphagous predator may be under some considerable food stress due to a lack of within-field prey abundance or diversity (Bilde & Toft 1998; Toft & Bilde 2002; Mayntz *et al.* 2005).

Under such circumstances, increasing importance is placed on methods of 'conservation biological control' to provide effective pest suppression (Landis *et al.* 2000). These habitat manipulations take many forms (Bianchi, Booij & Tscharntke 2006), including wildflower strips or margins which provide pollen and nectar for flying predators and a moist understorey for ground predators (e.g. Rebek, Sadof & Hanks 2005). Other non-flowering within-field habitat manipulations can have positive conservation biological control effects, such as compost applications to boost and maintain predator numbers that then facilitate effective and sustained top-down pest control (Symondson *et al.* 2002a,b; Gurr, Wratten & Luna 2003).

Compost introduces a detrital food chain into the crop which Settle *et al.* (1996) argued was vital in supporting generalist predators higher up the food chain. Indeed, various types of organic matter have been shown to have a positive impact on numbers of polyphagous predators, including carabid beetles (Purvis & Curry 1984; Helenius *et al.* 1995; Halaj & Wise 2002), staphylinid beetles (e.g. Pietraszko & De Clerq 1982; Rämert 1996) and spiders (e.g. Riechert & Bishop 1990; Rypstra *et al.* 1999; Wise *et al.* 1999; Halaj & Wise 2002). In part, this is because organic matter introduces energy into the system which detritivores, an alternative food source for predators, are able to exploit (Scheu 2001). These detritivores either feed directly on the mulch or manure or consume the associated fungi, bacteria and other microbes that grow on it (Pimentel & Warneke 1989). Consequently, as the fungi and microbes flourish, so do the detritivores which usually increase significantly in number (e.g. Scholte & Lootsma 1998; Axelsen & Kristensen 2000; Halaj & Wise 2002).

There are also some serious concerns about introducing alternative prey via compost because higher numbers of alternative prey may not necessarily benefit agriculture directly. A switch away from the target pest to alternative prey could lead to pest populations no lower than would be found in the absence of predators (Symondson *et al.* 2006). In these circumstances, prey switching may suggest 'apparent competition' between two prey species that have a shared polyphagous predator (e.g. Müller & Godfray 1997, 1999; van Veen, Morris & Godfray 2006). The effects of polyphagous predators have been argued to be diffuse, spreading from a source habitat (i.e. within-field habitat manipulation such as a compost strip) into the cropped environment (Müller & Godfray 1997, 1999), and thus very relevant to any within-field habitat manipulation. On the other hand, diffuse sources of alternative prey may foster (through aggregation and reproduction) higher densities of predators, leading to reductions in aphid numbers. Whatever the outcome, many polyphagous predators in the cropped environment that are also major predators of aphids (Symondson *et al.* 2002a) have in addition strong trophic connections with flora and fauna

that are found in large numbers in compost. For example, large carabid beetles feed on worms (Symondson *et al.* 2000); some staphylinid beetles demonstrate a strong tendency towards mycophagy (Dennis, Wratten & Sotherton 1991) and spiders locate their webs where collembola are abundant (Harwood *et al.* 2004).

In this study, we report on the findings of 4 years of research on manipulations in winter wheat and test the effects of compost applications on numbers of predators and alternative prey. This will address the extent to which organic matter provides a beneficial trophic link that indirectly enhances control of cereal aphids.

Methods

All experiments were conducted in winter wheat crops between 2000–2005 at the Warwick HRI experimental farm, Wellesbourne, Warwickshire, UK (52°12·18′N, 1°36·00′W). The experiments used compost and were either in mesocosms (2000–2002) or on a field scale (2005). Mesocosm experiments were small-scale field experiments and were concerned with the assessment of fauna collected within, or on top of, the compost using a destructive sampling technique. The field-scale experiment in 2005 examined the supposed percolation of 'within-treatment' biodiversity from compost into the surrounding cereal crop as determined by pitfall traps and quadrats placed adjacent to the experimental plots. These trapping methods were complemented with direct assessments of crop yield and aphid numbers.

2000–2002 FIELD-BASED SMALL-SCALE MESOCOSM EXPERIMENTS

Experimental design

In all 3 years, spent mushroom compost was applied to half of the plots to a depth of about 6 cm between 3–10 April, the remaining plots acting as uncomposted controls. In 2000, 160 mini-plots were used (30×35 cm, 4 m apart) which were then scaled-up in size to a smaller number (20 per year) of larger plots (4×4 m, 8 m apart) in 2001 and 2002 (see Fig. S1a,b, Supplementary material). In 2000, a split-plot design was used: five blocks in each of two fields. Each block contained 16 systematically arranged plots evenly split between the compost and control treatments, with invertebrates collected from each plot over five separate weeks (sub-plot treatment). The experiments in 2001 and 2002 were arranged in an array of 20 plots (arranged as five columns and four rows) with 10 plots for each of the two treatments (compost, control) allocated systematically in a 'chequer-board' pattern.

Collection of invertebrates from the field

In all years, we used a destructive sampling method to examine the effects on major groups of invertebrates. In 2000, plastic bowls ($30 \times 35 \times 12$ cm deep) representing 'mesocosms' were dug into the mini-plots on the 10 April (one bowl plot⁻¹) and either filled with soil (control mini-plots) or given a 6-cm bottom layer of soil then filled to the brim with spent mushroom compost (compost-treated mini-plots) and set level with the soil surface. From 10 April until 31 May the mesocosms were colonized by invertebrates in the field until they were lifted, sealed inside ventilated polythene bags in the field, then removed to a laboratory for processing. The bowls were

housed at 18 °C 18 L: 6D and their contents were carefully hand-sorted and extracted into alcohol. A modified version of the 2000 destructive sampling procedure was used in 2001 and 2002 when eight and four larger plastic mesocosms ($38 \times 15 \times 10.5$ cm deep) per plot were used respectively (see Fig. S1a,b).

Aphid count

In each year, tillers were searched weekly (16 June–14 July 2000; 13 June–10 July 2001; 5 June–9 July 2002) for the presence of aphids. In 2000, the counts were from 50 tillers across five equivalently treated plots (one plot block^{-1}), whilst in the other years, 50 tillers were searched per plot across all plots. The counts from tillers were summed to give a total aphid count per plot (set of plots). Two replicates per field, per treatment per date were taken in 2000, increasing to 10 replicates per treatment per date in 2001 and 2002. In the latter years, each of the 10 replicates gave a measure of the aphid population per plot, but in 2000, each count was taken across the blocks within each field and pooled because of the constraints of plot size.

Statistical analysis of mesocosm experiments

We divided the invertebrates into two groups: 'predators' (linyphiid spiders, lycosid spiders, pergamasid mites, carabid beetles, staphylinid beetles, predatory beetle larvae, centipedes, heteropteran bugs, others) and 'potential prey' (slugs, mites, millipedes, Arthropleona springtails, Symphypleona springtails, herbivorous beetles and their larvae, flies, fly larvae, aphids, thrips, bugs and others) and analysed the counts in each group as response variables in two discrete and separate ANOVA tests. In 2000, data were analysed as a split-plot ANOVA for the main effects of treatment and date, and the interaction between these factors. The block structure specified a nesting of date within plot, and plot within field. In both 2001 and 2002, data were analysed taking account of the row–column spatial arrangement of plots, including date as a sub-plot factor, and to test for the main effects of treatment and date, and the interaction between these factors. Data were transformed [$\log(x + 1)$ or square root($x + 0.5$)] to satisfy the assumptions of homogeneity of variances and the normal distribution of residuals. All analyses were done using GENSTAT (ninth edition, VSN International Ltd, UK). Back-transformed means from [$\log(x + 1)$ or square root($x + 0.5$)] transformations with 95% confidence intervals (CI) are given for main effects of compost.

The total aphid counts were analysed using a log-linear model [a generalized linear model (GLM) assuming a Poisson error distribution and logarithm link function]. In all analyses, the dispersion parameter was estimated from the data, indicating a level of over-dispersion. Analyses allowed for differences due to the fields and plots (2000) or the rows, columns and plots (2001, 2002), and assessed for the main effects of both treatment and date, and the treatment-by-date interaction. The importance of model terms was assessed by comparing the deviance ratios for each term with the appropriate *F*-distribution (an approximate test), with predictions of mean fitted counts calculated from the fitted models.

2005 FIELD-SCALE EXPERIMENT

Experimental design

At the centre of a 12·8-ha winter wheat field (var. Hereward), a randomised complete block design was imposed on a 200×80 m area of the crop (see Figure S1c, Supplementary material). Six

blocks measuring 20×40 m and separated by 10 m in both longitude and latitude, were divided into three 20×10 m plots which were randomly assigned two compost treatments and an untreated control. Each plot was separated from other plots within each block by a 5-m strip. The compost treatments comprised of 56 tonnes of equally mixed mushroom and green waste compost, arranged in two types of strip (single or double) that extended across the width of each plot (i.e. 10 m) at a rate of 0·15 tonnes wet weight m^{-2}. This rate provided for a thick layer of compost on top of the soil. 'Single' strips of compost measured 3 m in breadth, whilst 'double' strips were arranged as two strips each of 1·5 m breadth separated by 3 m. These treatments allowed a test of whether habitat pattern had implications for aphid predation rates, given that the compost occupied the same area but was differently distributed. The control plot contained a winter wheat crop but with no compost treatment. The field of winter wheat underwent normal management, but no insecticides were used.

Collection of invertebrates from the field

Ground-active predators were trapped live in large dry pitfall traps (Sankey™ terracotta plastic flower pots 36 cm diameter × 23 cm depth) a third filled with clay granules (hydroleca™) to discourage interactions between predators during containment. The traps were dug into the soil with the lip level with the ground (see Figure S1c for experimental design and trap locations.) To prevent aphids raining into the trap, 40 cm diameter lids were suspended ~3 cm above ground level. Collected specimens were placed within a vial chilled in a cold box in the field then frozen at –80 °C. Each plot was allocated one trap which ran for 24 h every fortnight during the growth and decline phases of the aphid population. There were four collection dates between 25 May and 5 July 2005, giving a total of 72 observations.

Two quadrats (0.5×0.5 m) per plot were used to provide density estimates of predators unlikely to be found in the pitfall traps in any numbers. Quadrat sampling (every fortnight in dry conditions) began on 24 May and ended on 4 July during the main period of aphid infestation (for a plan view of quadrats, see Figure S1c). In both the single and double compost strip treatments, quadrats were placed at distances of 1 m and 6 m from the outside edge of the compost strips respectively, but in the control they were randomly placed. These two nested quadrats were kept separate for later intraplot distance-based analysis. Specimens were placed within a vial chilled in a cold box then frozen at –80 °C, as described above.

Aphid counts

The size of the aphid population was estimated weekly over a 12-week period (from 2 May to 18 July) based on total numbers from four randomly selected wheat tillers per plot. All aphids were frozen at –80 °C. Although *S. avenae* represented the great majority of aphids, other species occurred including *Rhopalosiphum padi* (L.) and *Metopolophium dirhodum* (Walker).

Yield and Collembola measurements

For yield data, the experiment was considered a strip-plot (a.k.a. criss-cross) design with six replicate blocks. Yield samples were taken at three positions (0 m, 1 m and 6 m away from compost strips) relative to the edge of each plot. The number of ears per quadrat (0·25 m^2) were counted from which five ears were removed

(one from the middle, four from the corners). The grain from these ears were separated, dried overnight in an oven and weighed (dw). Data were then scaled to represent yield as kg dw m^{-1}. Yield samples were kept apart for later intraplot distance-based analysis.

Collembola were collected using a 330-cm^3 core that was inserted into the soil either in the compost strip or 6 m away in the winter wheat crop relative to the edge of the strip in each of the 18 plots. These yielded a total of 36 soil cores from which the Collembola were extracted concurrently in a bank of Tullgren funnels. These two nested cores were kept apart for later intraplot distance-based analysis.

Statistical analysis of field data

All data apart from yield were transformed [log(x + 1) or square root (x + 0·5)] prior to analysis of variance. Complementary statistical models were assumed for the different data sets: a strip-plot design for the yield data, a split-plot design for the quadrats and collembolan data (allowing for both distance and date effects within plot) and a randomized complete block design for the aphid and pitfall trap data. All analyses were performed using GENSTAT. Back-transformed means from [log(x + 1) or square root(x + 0·5)] transformations with 95% CI are given in the text where appropriate.

Results

2000–2002 FIELD-BASED SMALL-SCALE MESOCOSM EXPERIMENTS

In all years, the presence of compost had a significant positive effect on the numbers of both predators and potential prey. For the destructive sampling carried out in 2000 (n = 2419 predators; n = 4590 potential prey) (Table 1), mean numbers were significantly higher in the compost treatment compared with those for the untreated control (predators $F_{1,27}$ = 368·48, $P \leq 0·001$; potential prey $F_{1,27}$ = 123·83, $P \leq 0·001$). A treatment-by-date interaction was also detected (predators $F_{3,108}$ = 6·80, $P \leq 0·001$; potential prey $F_{3,108}$ = 7·10, $P \leq 0·001$), caused by the relatively high numbers within both treatments in June compared to those for the July and September samples.

In 2001, the compost treatment produced significantly higher numbers of both predators (n = 24 198 individuals; $F_{1,11}$ = 279·79, $P \leq 0·001$) and potential prey (n = 120 869 individuals; $F_{1,11}$ = 111·20, $P \leq 0·001$) compared with the untreated control. As in 2000, an effect of date was detectable, although generally it was not as strong because of the comparatively shorter sampling season (predators $F_{2,36}$ = 13·67, $P \leq 0·001$, potential prey $F_{2,36}$ = 5·77, $P = 0·007$). This had implications for the treatment-by-date interactions, which were weaker than in 2000, but still significant for both predators and potential prey ($F_{2,36}$ = 7·09, $P = 0·003$, $F_{2,36}$ = 7·81, $P = 0·002$, respectively).

The 2002 results generally mirrored those found in the previous years with compost significantly augmenting both the numbers of predators (n = 352 individuals; $F_{1,11}$ = 8·68, $P = 0·001$) and the numbers of potential prey (n = 14 842 individuals; $F_{1,11}$ = 18·15, $P = 0·001$). The effect of date was more variable: July had the highest numbers for potential prey ($F_{1,11}$ = 11·72, $P = 0·003$; treatment-by-date interaction

Table 1. Back-transformed means and 95% confidence intervals from the 2000–2002 experiments. Only the main treatment effect of compost compared to the control is given

Year	Treatment	Means and 95% confidence intervals	Potential prey	Predators
2000	Compost	Mean	41·86	26·53
		+95% CI	52·11	29·96
		–95% CI	32·73	23·31
	Control	Mean	3·46	1·95
		+95% CI	4·55	2·46
		–95% CI	2·52	1·50
2001	Compost	Mean	2708·38	586·76
		+95% CI	3554·88	717·42
		–95% CI	2063·46	479·91
	Control	Mean	474·74	100·85
		+95% CI	621·51	125·02
		–95% CI	362·64	81·35
2002	Compost	Mean	433·00	13·76
		+95% CI	629·98	18·49
		–95% CI	297·61	10·24
	Control	Mean	127·77	2·25
		+95% CI	166·91	2·85
		–95% CI	97·81	1·78

$F_{1,18}$ = 6·72, $P = 0·023$), but differences between months were not significant for numbers of predators ($F_{1,11}$ = 3·76, $P = 0·068$; treatment-by-date interaction $F_{1,18}$ = 3·31, $P = 0·085$).

We expected a significant interaction between date and aphid numbers, as populations experienced exponential growth. We do not present these data unless there was a treatment-by-date interaction, indicating that the treatment effect changed over time. In both 2000 and 2001, there were more aphids in the untreated control plots (that contained significantly smaller numbers of natural enemies) than in the compost-treated plots. In 2000, differences between treatments were strong (Fig. 1A; log-linear GLM $F_{1,24}$ = 27·60, $P \leq 0·001$), although there was variation in responses between the two fields (log-linear GLM: $F_{1,24}$ = 22·25, $P \leq 0·001$). Treatment differences were smaller in 2001 (Fig. 1B), but reduced plot-to-plot variances meant that these differences were still significant (log-linear GLM $F_{1,81}$ = 61·7, $P \leq 0·001$). In 2002, the difference between the compost treatment and the untreated control was not significant (log-linear GLM $F_{1,219}$ = 0·55, $P = 0·459$) (Fig. 1C).

2005 FIELD-SCALE EXPERIMENT

The compost treatments showed significant effects on wheat yields (as kg dw m^{-1}) when compared to the untreated control and averaged across distance and strip number ($F_{1,10}$ = 11·56, $P = 0·004$). Yields were significantly greater adjacent to the edge of the strip (zero distance) than they were at either 1 m or 6 m away when averaged across compost treatment [$F_{1,10}$ = 13·73, $P = 0·029$; zero distance mean = 7·58 (+95% CI = 8·23, –95% CI = 6·93); aggregated 1 m and 6 m mean = 5·53 (+95% CI = 5·98, –95% CI = 5·08)]. There was
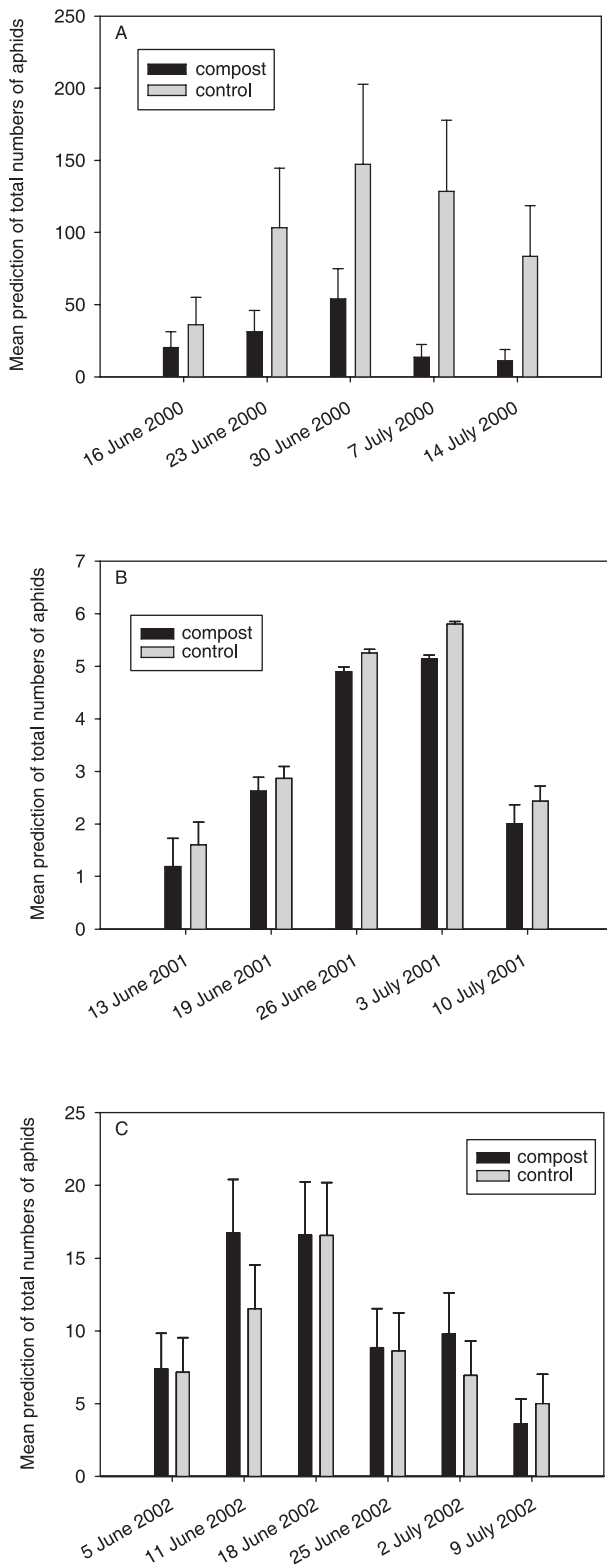
Fig. 1. Results of log-linear GLM analyses, showing the predicted means (and standard errors) of the total numbers of aphids in years 2000 (A), 2001 (B) and 2002 (C). (A) Results of log-linear GLM analysis, showing the predicted means (and standard errors) of total numbers of aphids. (B) Results of log-linear GLM analysis, showing the predicted means (and standard errors) of total numbers of aphids. (C) Results of log-linear GLM analysis, showing the predicted means (and standard errors) of total numbers of aphids.

a significant interaction ($F_{1,20} = 23 \cdot 09$, $P \leq 0 \cdot 001$) between the effect of including compost and the distance from the edge of the plot, since the effect of distance was not detectable in the control, but strongly evident in the compost strip treatments.

Although there were fewer aphids per tiller in the compost treatments compared to the untreated control when averaged over the season, this difference was not significant ($F_{2,89} = 0 \cdot 469$, $P = 0 \cdot 282$). There was no effect of habitat arrangement (double strips vs. single strip) on numbers of collembola ($F_{1,5} = 0 \cdot 295$, $P = 0 \cdot 227$), but both compost treatments show the same effect of distance, with significantly more collembola recorded in the compost strips compared to 6 m away [$F_{1,10} = 3 \cdot 977$, $P \leq 0 \cdot 001$; compost mean = 89·63 (+95% CI = 127·11, –95% CI = 63·20); 6 m mean = 13·75 (+95% CI = 21·72, –95% CI = 8·70)] , while as expected, there was little difference in the untreated controls.

Overall, pitfall trap data did not show significant differences of activity–density between treatments [$F_{2,53} = 0 \cdot 453$, $P = 0 \cdot 605$; control mean = 1·23 (+95% CI = 2·23, –95% CI = 0·53); double strip mean = 1·54 (+95% CI = 2·05, –95% CI = 1·10); single strip mean = 2·19 (+95% CI = 3·48, –95% CI = 1·20)]. The most abundant predator, *Pterostichus melanarius* (Illiger) ($n = 182$), similarly showed no effect of treatment ($F_{2,53} = 0 \cdot 356$, $P = 0 \cdot 678$). Over the season, quadrat data (total coverage = 36 m^{-2}) gave a similar picture to the pitfall traps, but the absolute density of invertebrates (total $n = 1304$) principally comprised three groups: carabid beetles, adult and immature linyphiid spiders and staphylinids (Fig. 2). Combining all invertebrate species, there were no effects of treatment [$F_{2,10} = 1 \cdot 99$, $P = 0 \cdot 188$; control mean = 4·62 (+95% CI = 5·56, –95% CI = 3·85); double strip mean = 6·01 (+95% CI = 7·25, –95% CI = 4·99); single strip mean = 5·48 (+95% CI = 6·33, –95% CI = 4·75)]. Nor was there an effect of distance ($F_{1,15} = 0 \cdot 71$, $P = 0 \cdot 411$) on field populations, not even when the untreated control was contrasted with the mean effect of the compost treatments ($F_{1,10} = 3 \cdot 49$, $P = 0 \cdot 091$). Although a strong effect of date was detected ($F_{3,90} = 14 \cdot 23$, $P \leq 0 \cdot 001$), this was a non-monotonic response over time, and the interaction between treatment and date was not significant. This analysis of all invertebrates species set the tone for all subsequent analyses of groups and species in that the effect of distance was relatively weak, with the exception of the numbers of staphylinids (all carabids $F_{1,15} = 0 \cdot 61$; $P = 0 \cdot 446$; all linyphiids $F_{1,15} = 0 \cdot 17$, $P = 0 \cdot 690$; all staphylinids $F_{1,15} = 5 \cdot 83$, $P = 0 \cdot 029$; *Trechus quadristriatus* (Schrank) $F_{1,15} = 1 \cdot 66$, $P = 0 \cdot 217$; *Notiophilus biguttatus* (F.) $F_{1,15} = 0 \cdot 24$, $P = 0 \cdot 630$). There was usually a strong effect of date although this was not always significant (all carabids $F_{3,90} = 52 \cdot 00$, $P \leq 0 \cdot 001$; all linyphiids $F_{3,90} = 9 \cdot 97$, $P \leq 0 \cdot 001$; all staphylinids $F_{3,90} = 7 \cdot 67$, $P \leq 0 \cdot 001$; *T. quadristriatus* $F_{2,60} = 52 \cdot 21$, $P \leq 0 \cdot 001$; *N. biguttatus* $F_{2,60} = 2 \cdot 75$, $P = 0 \cdot 072$). The two compost treatments and untreated control were not significantly different from each other (all carabids $F_{2,10} = 1 \cdot 04$, $P = 0 \cdot 388$; all linyphiids $F_{2,10} = 3 \cdot 41$, $P = 0 \cdot 074$; all staphylinids $F_{2,10} = 0 \cdot 28$, $P = 0 \cdot 762$; *T. quadristriatus* $F_{2,10} = 0 \cdot 48$, $P = 0 \cdot 634$; *N. biguttatus* $F_{2,10} = 1 \cdot 74$, $P = 0 \cdot 225$), not even when comparing the mean of the two compost
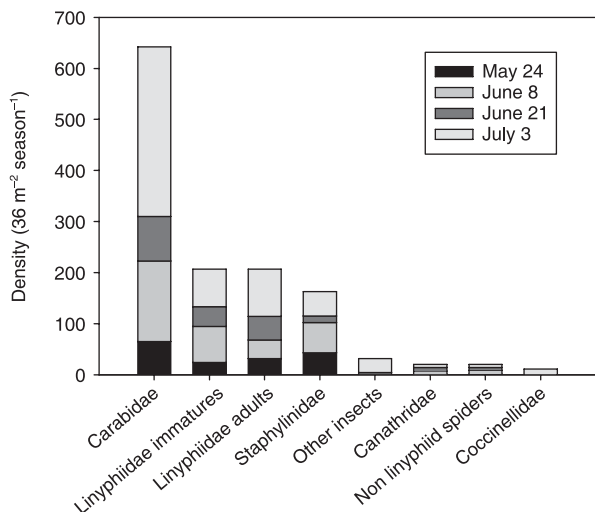
Fig. 2. Absolute densities of invertebrates taken from the quadrat samples over the whole season in 2005. In each month, 36 quadrats were taken (0·25 m^{-2}) representing an intensity of sampling of 9 m^{-2} per date, and thus 36 m^{-2} over the field season. Of the 17 species of carabids recorded, *Trechus quadristriatus* (n = 384; 10·66 m^{-2} season^{-1}) and *Notiophilus biguttatus* (n = 136; 3·77 m^{-2} season^{-1}) dominated the catch. Although adult spiders were much lower in total number, 14 species occurred which were dominated principally by three linyphiids; *Erigone atra* (n = 63; 1·75 m^{-2} season^{-1}), *Tenuiphantes tenuis* (n = 51; 1·41 m^{-2} season^{-1}) and *Bathyphantes gracilis* (n = 43; 1·19 m^{-2} season^{-1}). Excluding the Aleocharinae (n = 54; 1·50 m^{-2} season^{-1}), a diverse group of staphylind beetles which were not identified to below this sub-family level, the only other staphylinid species of a possible 15 which occurred at reasonable densities was *Tachyporus hypnorum* (n = 40; 1·11 m^{-2} season^{-1}).

treatments and the untreated control, with the exception of the numbers of linyphiid spiders (all carabids $F_{1,10}$ = 0·09, P = 0·769; all linyphiids $F_{1,10}$ = 6·44, P = 0·030, all staphylinids $F_{1,10}$ = 0·18, P = 0·684, *T. quadristriatus* $F_{1,10}$ = 0·17, P = 0·690; *N. biguttatus* $F_{1,10}$ = 3·18, P = 0·105).

Discussion

These experiments support the hypothesis, conjectured by Settle *et al.* (1996), and later by Wise *et al.* (1999), that links exist between the detrital food web and the above-ground community. We found that up to a threefold difference in numbers of predators and potential prey is achievable in soils with enhanced levels of organic matter compared to those with unenriched soil. Such findings support previous studies (Idinger & Kromp 1997; Halaj & Wise 2002; Mathews, Bottrell & Brown 2004; Schmidt *et al.* 2004) suggesting that alternative prey subsidy transfers energy into the predator food web (Polis, Anderson & Holt 1997; Rypstra & Marshall 2005). In some years, we found that this subsidy was implicated in mediating a top–down reduction in aphid numbers: the 2000 experiment demonstrated a strong augmentative effect of compost on numbers of predators and non-aphid potential prey, and a concomitant significant decrease in numbers of aphids. This experiment was scaled up in 2001 and yielded

similar results to the previous year and other studies (Brown & Tworkoski 2004).

However, such top–down effects appear to be transient and determined strongly by between-year differences. In 2002, the potential prey decoupled themselves from predators; the latter were inconsistent between months and exerted no consistent pressure on the aphid populations in the compost treatment, which appeared to exceed the untreated control populations on a few occasions. Furthermore in 2005, when predators and aphids were sampled at a distance from the compost, all groups were unresponsive and showed no treatment effects. Collembola numbers were significantly greater in the compost strips than in unimproved soil in 2005, but predators did not percolate out from the compost strips. The 2005 experiment showed that compost increased wheat yields next to the compost strips. However, this also stimulated the weed population, particularly *Chenopodium album* L. (Family Chenopodiaceae), probably because of the slow release of nitrogen over time, and because an active seed bank was imported with the green waste compost.

In lieu of any further data on competitive interactions, it is difficult to suggest why such variation exists between years. Both spiders and beetles should benefit from a positive feedback on the size of the collembolan population (Toft & Bilde 2002; Agustí *et al.* 2003; Harwood *et al.* 2004), which remained significantly higher in the treated plots compared with the untreated controls in all years. The experimental rationale was different in 2005 compared to other years, but for 2000–2002 the mechanism could not have been caused by varying habitat quality between years as the source of the mushroom compost remained the same. A number of explanations as to why 2002 and 2005 deviated from the expected norm are possible.

First, aphid abundance in 2002 was less than in previous years and this correlated with an epizootic of entomopathogenic fungi (*Entomophthora* spp.) attacking the aphids. This did not occur in 2000 or 2001. Furthermore, the weather was warmer and drier in 2002 than in the previous 2 years, causing premature crop development in the face of the more slowly emerging predator community, giving rise to the possibility of higher levels of intraguild predation.

Secondly, in 2005 green waste was combined in equal proportions with mushroom compost which may have contributed to different predator–prey dynamics since green waste does not modify either bacterial or fungal densities (Pérez-Piqueres *et al.* 2006). This bottom–up resource and boost to the system may have been dampened as a result of diluting the mushroom compost with microbially different green waste. However, the 2002 experiment used pure spent mushroom compost, suggesting that on its own compost type does not have a strong enough effect to determine the variability observed between years.

Overall, these results may appear to be somewhat inconsistent, determined by strong temporal effects both within and between seasons. Whilst we cannot be certain why there was no consistent effect, these results strengthen the case for considering predators as top-down detrital-mediated biocontrol

agents because in years when predators were significantly boosted in number by the compost treatments, aphids were significantly suppressed (i.e. 2000 and 2001). Trophic cascades appeared to happen when predators achieved sufficiently high densities in compost-treated plots relative to the untreated control: when treatment differences were not expressed strongly in terms of increased predator numbers, aphids were not suppressed in the compost plots and, at times, numbers exceeded the populations in the untreated controls (i.e. 2002).

There may be mechanisms other than alternative prey subsidies, including the presence of a structurally more complex physical environment making conditions more conducive for predators (Riechert 1998), a reduction in intraguild predation pressure or the escalating effects of prey-switching (Finke & Denno 2003). There may also be complex indirect benefits such as the general improvement of the structure, water economy and fertility of the soil which have yet to be investigated explicitly and could contribute to survival of predatory beetle larvae (Traugott 1998).

Another potential cause for the variation between years is possible changes in the below-ground dynamics. However, we did not undertake observations on the below-ground community. As is usual for large experiments, new fields were commissioned each year to gain a representative sample of what a typical farm might do under a compost regime. These fields have their own particular soil management history and may have had unmeasured effects, especially in the view of Scheu (2001) and van der Putten *et al.* (2001) who both constructed strong arguments for multitrophic links that spanned the soil–plant network. Ultimately, an understanding as to why the 2002 and 2005 experiments gave an unexpected outcome compared to 2000–2001 will only be gained when the full multi-trophic links are revealed.

Conclusions

Our understanding of polyphagous predator food webs should not solely rest upon alternative prey subsidies as a means of supporting beneficial populations as it is clear that other factors, such as competition and microclimate, may also be capable of determining predator population size (Halaj & Wise 2002; van Veen *et al.* 2006). The mechanisms that caused differences in between-year patterns are not understood, making it difficult to provide specific pest management recommendations at this stage. Compost application may offer a useful technique for controlling aphids within an integrated pest management system, particularly for overwintering populations, but there is a need to understand the full trophic pathway. The latter could now be analysed effectively using molecular approaches based upon gut content analyses for predation on multiple prey species (Harper *et al.* 2005).

Acknowledgements

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Supplementary material

The following supplementary material is available for this article:

Fig. S1. Design of field experiments.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2664.2008.01479.x
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