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Arthropod predator nutrient content changes with wheat sowing period but is not driven by prey availability

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Research Paper

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Abstract

Conservation biocontrol is crucial for crop pest management, but the impact of agricultural management practices on natural enemies of crop pests is poorly characterised. The timing of crop sowing could impact arthropod communities by altering basal resource availability and quality, manifesting in altered nutrient availability for herbivorous arthropods and cascading impacts on natural enemy fitness and function. This study investigates how the timing of crop sowing impacts arthropod predator nutrition and whether associated differences relate to changes in prey availability. Arthropod predators and their prey were collected from adjacent plots of winter- and spring-sown wheat. The biochemical macronutrient (carbohydrate, lipid and protein) content of predators was determined by colourimetric assays and compared between winter- and spring-sown crops using multivariate models. Predator nutrient contents were compared to prey availability inferred using null network models based on both recent and current prey abundances. The nutrient contents of arthropod predators differed significantly between winter- and spring-sown wheat, driven by differences in carbohydrate content, and prey abundances similarly differed, but neither recent nor current prey availability explained differences in predator nutrition. These findings may indicate that prey quality, rather than identity, changes with the developmental stages of crops sown at different times. The different nutritional states of predators in crops sown at different times may have important implications for the spillover of natural enemies of crop pests between crops.

Introduction

Conservation biocontrol, the promotion of natural enemies of crop pests through land management, can contribute substantially to pest suppression (Symondson *et al.*, 2002; Tschumi *et al.*, 2018). Whilst it effectively suppresses disease vectors and crop herbivores (Moore *et al.*, 2010; Michalko *et al.*, 2019), inefficiencies in conservation biocontrol arise through the predation of fellow natural enemies of crop pests (Davey *et al.*, 2013; Cuff *et al.*, 2022) and other beneficial invertebrates, such as pollinators (Rosenheim *et al.*, 1995; Hodge, 1999; Tschumi *et al.*, 2018). These foraging decisions are usually motivated by complex interactions between biotic drivers, such as the need to redress nutritional deficits (Mayntz *et al.*, 2005), and abiotic drivers, such as the management and cycling of crops (Cuff *et al.*, 2021). To optimise the biocontrol activity of natural enemies of crop pests, we must understand how agricultural management decisions, including the myriad changes that arable land progresses through across the annual cycle, affect natural enemy populations and the drivers of their interactions with pests, including nutritional status (Cuff, Gajski *et al.*, 2024). From harvest practices (Opatovsky and Lubin, 2012; Cuff *et al.*, 2021), through tillage (Heimbach and Garbe, 1996; Jowett *et al.*, 2021), to the timing of sowing (Douglas *et al.*, 2010), management decisions can have profound, yet poorly characterised, implications for conservation biocontrol (Cuff, Gajski *et al.*, 2024).

The season within which crops are sown can greatly impact their management and productivity; for example, spring-sown crops can see improved disease delay relative to winter-sown crops (Landa *et al.*, 2004). As a result, land managers have developed a diverse range of crop management strategies and cycles. Such variations in crop management will also manifest in differences in invertebrate community structure and function due to cascading impacts arising from differences in crop developmental stages (Douglas *et al.*, 2010; Hsu *et al.*, 2021). Furthermore, it has the potential to impact the interactions between pests and their predators; for example, when crops sown at different times co-occur in an agricultural landscape, spillover of invertebrates and their interactions from one crop to another presents a significant opportunity for the spread of both pests and predators, especially when earlier-sown crops

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are harvested (Jaworski *et al.*, 2023; Cuff, Gajski *et al.*, 2024). By modifying invertebrate community structure (Douglas *et al.*, 2010), agricultural management decisions like crop sowing timing can also indirectly impact the nutrients available to and consumed by natural enemies of crop pests by altering crop development and senescence phenology. As crops senesce in their later developmental stages, nutrients are remobilised away from leaf tissues (Gregersen *et al.*, 2008), causing foliar herbivores and their predators to migrate or die (Watt, 1979). This is likely to have significant fitness consequences for natural enemies of crop pests, as nutritional deficits will alter their development, fecundity, survival, foraging choices and biocontrol potential (Bilde and Toft, 1997, 2001; Mayntz *et al.*, 2005).

Nutrients are the fundamental currency of trophic interactions, influencing population dynamics, physiology and species distributions, and driving biocontrol and other ecosystem services (Cuff, Evans *et al.*, 2024; Wilder *et al.*, 2025). Disruption to nutrient acquisition can cascade through consumers (Hedlund *et al.*, 2004), reducing energy transfer between trophic groups (Rosenblatt, 2018), ultimately disrupting ecosystem service provision. Generalist predators redress nutritional deficits that arise through such perturbations by engaging in nutrient-specific foraging, the selection of prey based on nutrient content, to optimise their nutrient intake, and therefore fitness (Mayntz *et al.*, 2005; Jensen *et al.*, 2012). Nutritional differences between prey are therefore important for the choices predators make, the trophic interactions they engage in, and the ecosystem services they provide, and are likely to be sensitive to agricultural land management practices. By understanding how nutritional dynamics drive ecological processes and are driven by human actions, agricultural land management can be optimised to promote the provision of ecosystem services, including conservation biocontrol, by ensuring sufficient nutrients are available to natural enemies (Cuff, Tercel, Vaughan *et al.*, 2024).

Here, we investigated how the timing of crop sowing affects the nutrient content of arthropod predators and whether this is driven by alterations to the prey community available to them. We collected arthropod predators and their prey from winter- and spring-sown wheat, and determined predator biochemical macronutrient (carbohydrate, lipid and protein) content. Using multivariate modelling and null network inference, we tested the following hypotheses: (i) invertebrate prey availability will differ between winter- and spring-sown crops; (ii) arthropod predator nutrient content will differ between winter- and spring-sown crops; (iii) differences in predator nutrient content will relate to recent, but not current, prey availability. By elucidating the nutritional consequences of management decisions such as sowing time for arthropod predators, further investigations can guide optimisation of management to safeguard the nutritional status of natural enemies of crop pests to sustain their beneficial action.

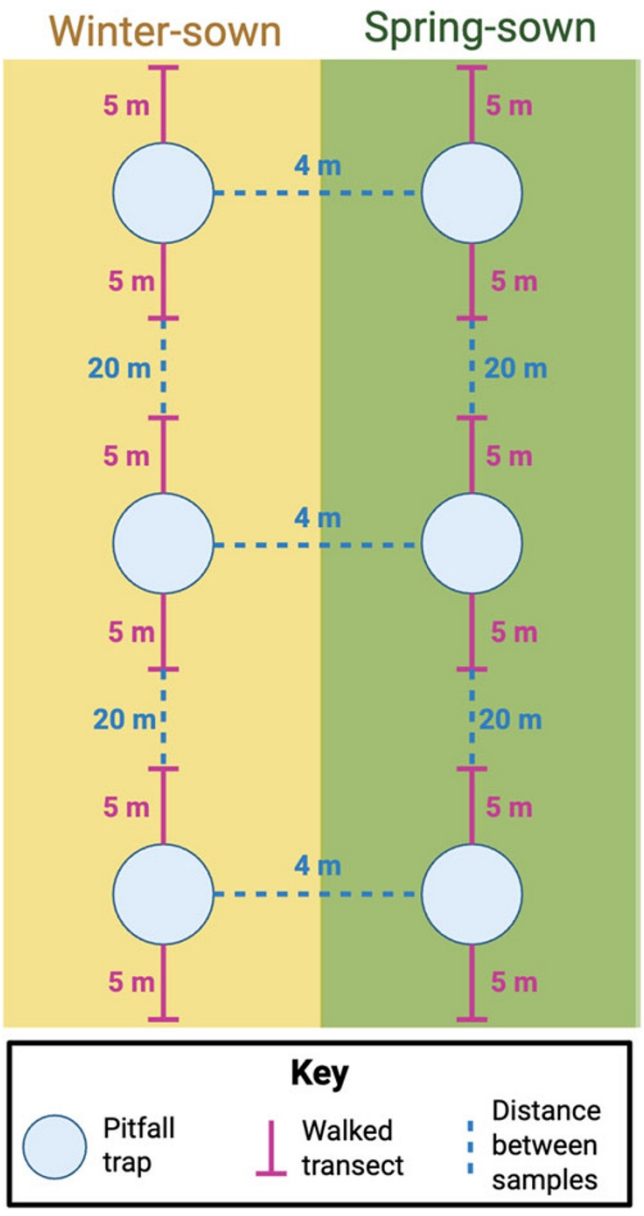


Figure 1. Experimental design for invertebrate sampling. Paired sampling locations were established 4 m apart in directly adjacent plots of winter- and spring-sown wheat. Created in BioRender. https://BioRender.com/6rd9udt.

Methods

Arthropod collection and identification

Arthropods were collected from Cockle Park (Morpeth, UK; 55°13′00.8″ N, 1°41′28.7″ W) in July 2024. Transects were established in a field containing adjacent plots of spring-sown and winter-sown wheat. Three pairs of belt transects were established 20 m apart within each crop, with 4 m between adjacent transects in the spring and winter-sown crops (fig.1). One pitfall trap was set at the centre of each transect (i.e. three per sowing period), filled with soapy water and deployed for 72 h. Pitfall trapping was conducted twice: once nine days prior to individual arthropod collection (to represent past prey availability) and once in parallel with individual arthropod collection (to represent current prey availability). Invertebrates within these traps were filtered in the field using an AeroPress® and stored in 80% ethanol for subsequent morphological identification. Within each transect, hand-searching was conducted for approximately 10 min, which was deemed sufficient to sample arthropods completely from both the ground and vegetation across the full length of the transect. Individual arthropods were collected directly from the ground or vegetation using a pooter. All arthropods found were collected, but, following morphological identification, only those from known natural enemy groups (i.e. Carabidae, Coccinellidae,

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Linyphiidae, Lithobiomorpha, Staphylinidae) were included in the analyses below, given the objectives of the study.

Following collection, the arthropods were frozen onsite at −20 °C to preserve their macronutrient contents for subsequent analysis. The samples were transported to the Molecular Diagnostics Facility at Newcastle University for morphological identification and nutritional analysis. Invertebrates were identified to family level or finer resolution using a stereomicroscope and morphological keys (Luff, 2007; Barber, 2008; Dallimore and Shaw, 2013; Tilling, 2014; Roberts, 2016). Some invertebrates from pitfall traps were, however, identified to order or suborder, where access to appropriate identification resources or damage to specimens limited identification. Individuals from each taxon were then counted to produce species-by-site abundance data.

Macronutrient quantification

Macronutrient analysis followed the Macronutrient Extraction and Determination from Invertebrates method (Cuff *et al.*, 2021; Cuff and Wilder, 2021), which streamlines sulfo-phospho-vanillin, anthrone and Lowry colourimetric assays for lipid, carbohydrate and protein estimation, respectively. This protocol was, however, adapted for compatibility with 384-well plates to facilitate a greater analysis throughput, with assay volumes adjusted accordingly. To extract macronutrients from whole arthropods, individuals were placed in 2 ml tubes of a 96-well rack and heated until dry (∼1 h) in an oven at 60 °C. To each sample, 500 µl of 1:12 chloroform:methanol solution was added and left at room temperature for 24 h. After 24 h, 400 µl of the chloroform:methanol solution was removed and retained separately for lipid analysis. A further 500 µl of chloroform:methanol solution was added to the sample and incubated at room temperature for 24 h to remove any residual lipids. All chloroform:methanol solution was removed by pipetting, and any residue was evaporated in an oven at 60 °C for ∼15 min.

To each dried sample, 500 µl 0.1 M NaOH was added, after which the samples were incubated at 80 °C for 30 min and at room temperature overnight (∼16 h). The samples were briefly centrifuged (∼2 min, 2,000× g) to avoid taking solid material through to the subsequent assays. From each sample, 400 µl of the supernatant was transferred into a separate tube for protein and carbohydrate determination. All assays were carried out in a 384-well plate format. For each assay, a stock standard dilution series of a known concentration was made with lard oil, glucose and bovine serum albumin (BSA) for lipid, carbohydrate and protein quantification, respectively. Stock solutions of 2 mg ml^{-1} glucose and BSA were made using distilled water and subsequently diluted in 0.1 M NaOH, whereas 2 mg ml^{-1} lard oil was made and diluted with 1:12 chloroform:methanol. Dilution series comprised 0–1 mg ml^{-1} in nine increments (0, 12.5, 62.5, 125, 250, 375, 500, 750, 1,000 µg ml^{-1}). A quarter of each 384-well assay plate (96 wells) was reserved for repeats of these standards.

Lipid quantification

The sulfo-phospho-vanillin method was used to determine lipid content. The vanillin reagent was prepared by mixing 0.108 mg of vanillin with 18 µl of hot water and 72 µl of 85% phosphoric acid for every 100 µl of reagent. From each sample, three repeats of 20 µl were added to a 384-well plate alongside standards and heated to 100 °C for 5 min to evaporate the chloroform:methanol carrier. To each well, 10 µl of concentrated sulfuric acid was added, mixed briefly on a plate shaker and incubated at room temperature for 15 min. Following this, 75 µl of vanillin reagent was added to each well, mixed briefly on a plate shaker and incubated at room temperature for 10 min. Absorbance at 490 nm for each was determined in a spectrophotometer.

Carbohydrate quantification

The anthrone method was used to determine carbohydrate content. The anthrone reagent was prepared by mixing 100 µg of anthrone with 100 µl of concentrated sulfuric acid for every 100 µl of reagent. From each sample, three repeats of 20 µl were added to a 384-well plate alongside standards, mixed with 80 µl of the anthrone reagent and incubated at 92 °C for 10 min. The plate was incubated at room temperature for 5 min, and absorbance at 620 nm for each well was determined in a spectrophotometer.

Protein quantification

The Lowry method was used to determine protein content. From each sample, three repeats of 20 µl were added to a 384-well plate alongside standards, and 60 µl of modified Lowry reagent was added to each well and mixed briefly on a plate shaker. The plate was incubated at room temperature for 10 min, and 6 µl of 1X Folin-Ciocalteu reagent was added and mixed briefly on a plate shaker. The plate was incubated at room temperature for 30 min, and absorbance at 750 nm for each well was determined in a spectrophotometer.

Statistical analysis

All analyses were conducted in R version 4.5.2 (R Core Team, 2025) and all data processing used the 'tidyverse' package for reproducibility (Wickham *et al.*, 2019). Data visualisations were generated using ggplot2 (Wickham, 2016).

The pitfall-trapped invertebrate communities (herein considered representative of prey available to the hand-collected arthropod predators) were compared between winter- and spring-sown crops, pitfall trapping rounds and an interaction between the two using multivariate generalised linear models (MGLMs) with a Poisson error family and Monte Carlo resampling in the 'mvabund' package via the 'manyglm' function (Wang *et al.*, 2012). These differences were visualised using non-metric multidimensional scaling with a Bray-Curtis dissimilarity matrix in the 'vegan' package (Oksanen *et al.*, 2022). Square-root-transformed macronutrient contents (i.e. percentage total macronutrient mass for each macronutrient) of arthropods were compared between taxa (based on the finest taxonomic resolution available for each predator taxon, mostly genus-level), winter- and spring-sown crops and the interaction between the two using multivariate linear models (MLMs) in the 'mvabund' package via the 'manylm' function (Wang *et al.*, 2012). Due to some taxa being present in only one of the two crops or fewer than three individuals being present overall, *Coccinella septempunctata, Loricera pilicornis, Patrobus atrorufus, Lamyctes emarginatus* and *Anchomenus dorsalis* were aggregated as 'other' for this comparison of nutrient content.

Null network models were run to infer density-dependent interactions for each of the individually collected arthropod predators based on prey availability and to determine if prey availability explains differences in predator nutrient content. Using pitfall trapping prey availability data, separately for the past and

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present prey availability based on the two rounds of pitfall trapping, null networks were generated for each of the individually collected predators included in the nutritional analyses above. These null network models assume that the trophic interactions of the predators were density-dependent (i.e. they interacted with the prey most available to them), providing a semi-realistic estimate of how prey availability would translate to trophic interactions.

To construct null networks, null diets were simulated using the 'generate_null_net' function in the 'econullnetr' package (Vaughan *et al.*, 2018) using the prey availability data from the pitfall traps with random placeholder interaction data. To generate null networks, we required dummy interaction data. We simulated these dummy interactions for each individual arthropod predator by randomly allocating interactions with three of the available prey taxa (approximately reflecting the interaction richness of arable arthropod predators from previous work; Cuff *et al.*, 2022). These dummy data were only required to run null network simulations and did not otherwise feature in any downstream analyses, with the exception of the fact that the node degree is invariable (i.e. a mean of three interactions per predator across all simulations). Using the 'generate_null_net_indiv' function (Cuff *et al.*, 2023), only the simulation data were extracted irrespective of the identities of the random interaction data input. Null networks were visually constructed using 'igraph' (Csardi and Nepusz, 2006) and plotted using 'ggnetwork' (Briatte, 2021). Null network-inferred predator-prey interactions based on both past and present prey availability were compared against predator nutrient content using redundancy analysis (RDA), and model outputs were analysed using analysis of variance (ANOVA) of the overall model, terms within the model and model axes.

Results

From the six transects, nutritional data were generated for 98 hand-collected predatory arthropods (Supplementary Table S1), 52 from the winter-sown wheat, and 46 from the spring-sown wheat. These belonged to five families: Carabidae ($n = 86$), Coccinellidae (2), Henicopidae (3), Linyphiidae (3) and Staphylinidae (4; Supplementary Table S1). The pitfall traps collected 668 individual invertebrates across 28 taxa resolved to family ($n = 22$), suborder ($n = 1$) or order level ($n = 5$; Supplementary Table S2), considered representative of prey available to the above predatory arthropods. These taxa included common wheat pests ($n = 4$), detritivores ($n = 7$) and natural enemies of crop pests ($n = 10$).

A significant overall effect on prey community abundances related to sowing period and sampling round was identified (MGLM: Wald = 13.89, $p = 0.001$), specifically related to carabid beetles (MGLM: Wald = 6.276, $p = 0.001$), linyphiid spiders (MGLM: Wald = 6.709, $p = 0.001$) and platygastrid wasps (MGLM: Wald = 8.312, $p = 0.001$). Sequential multivariate ANOVA identified significant marginal effects of crop sowing period (MGLM: Dev = 213.55, df = 10, $p = 0.001$; fig. 2), sampling round (MGLM: Dev = 133.33, df = 9, $p = 0.001$) and the interaction between sowing period and sampling round (MGLM: Dev = 42.98, df = 8, $p = 0.001$). Specifically, the abundances of brachyceran flies (MGLM: Dev = 20.794, df = 10, $p = 0.001$), carabid beetles (MGLM: Dev = 28.456, df = 10, $p = 0.001$), ichneumonid wasps (MGLM: Dev = 8.662, df = 10, $p = 0.046$), linyphiid spiders (MGLM: Dev = 23.599, df = 10, $p = 0.001$), platygastrid wasps (MGLM: Dev = 83.939, df = 10, $p = 0.001$) and stratiomyid flies (MGLM: Dev = 9.704, df = 10, $p = 0.034$) differed between crops sown in winter and spring. Similarly, the abundances of brachyceran flies (MGLM: Dev = 20.794, df = 9, $p = 0.001$), carabid beetles (MGLM: Dev = 9.272, df = 9, $p = 0.044$), linyphiid spiders (MGLM: Dev = 31.662, df = 9, $p = 0.001$) and stratiomyid flies (MGLM: Dev = 9.704, df = 9, $p = 0.044$) differed between pitfall trapping rounds. No significant taxon-specific relationships were identified for the interaction between sowing period and pitfall trapping round. Coefficient-level tests also demonstrated that prey community abundances related to sowing period (MGLM: Wald = 6.948, $p = 0.001$; fig. 2), sampling round (MGLM: Wald = 6.062, $p = 0.001$) and the interaction between sowing period and sampling round (MGLM: Dev = 3.642, $p = 0.018$). Specifically, the abundances of linyphiid spiders (MGLM: Wald = 3.827, $p = 0.002$) and platygastrid wasps (MGLM: Wald = 4.079, $p = 0.001$) significantly differed

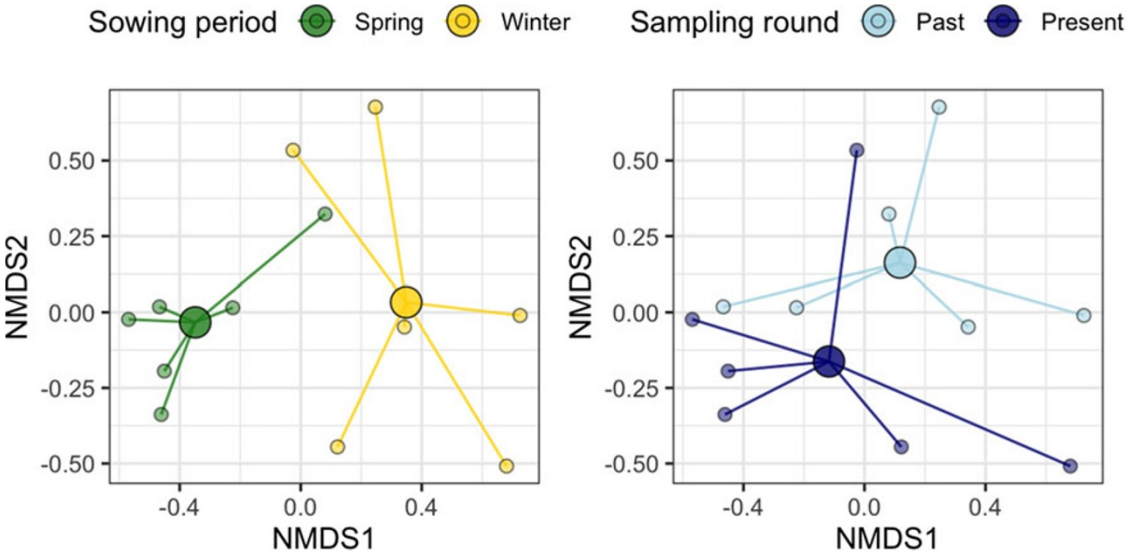


Figure 2. Non-metric multidimensional scaling of arthropod prey communities available in spring-sown ($n = 6$) and winter-sown ($n = 6$) wheat (left), and between pitfall trapping rounds (right; $n = 6$ per round). Stress = 0.103.

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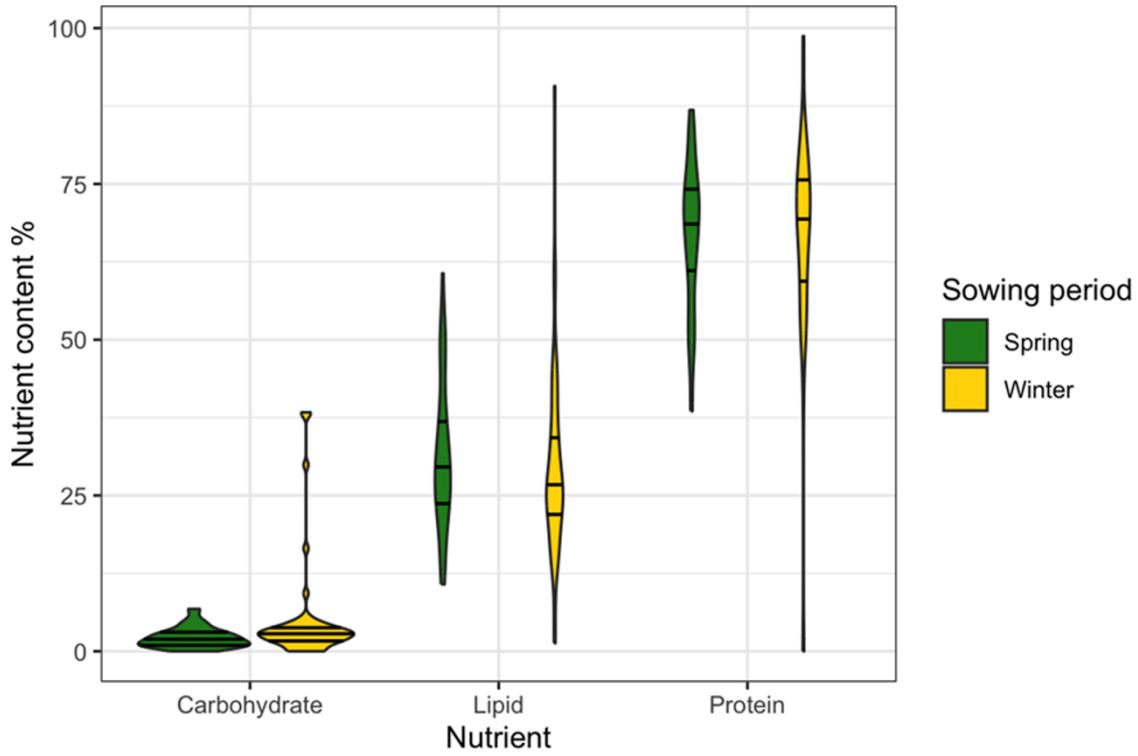


Figure 3. Violin plot of proportional macronutrient content (carbohydrate, lipid, protein) of predatory arthropods collected from winter-sown ($n = 52$) and spring-sown ($n = 46$) wheat. Horizontal lines within each violin represent the median and quartiles.

between sowing periods. Similarly, the abundances of carabid beetles (MGLM: Wald = 3.330, $p = 0.001$) differed between sampling rounds, and the abundances of platygastrid wasps related to an interaction between sowing period and sampling round (MGLM: Wald = 2.475, $p = 0.046$).

A significant overall effect of sowing period and taxon on predatory arthropod nutrient contents was identified (MLM: Lawley–Hotelling trace = 5.614, $p = 0.014$), specifically on carbohydrates (MLM: $F = 1.629$, $p = 0.036$), lipids (MLM: $F = 2.888$, $p = 0.013$) and proteins (MLM: $F = 1.097$, $p = 0.046$). Sequential multivariate ANOVA identified no significant marginal effects of crop sowing period (MLM: $F_{1,96} = 5.265$, $p = 0.189$; fig. 3), taxon (MLM: $F_{5,91} = 6.141$, $p = 0.069$), or their interaction (MLM: $F_{5,86} = 4.788$, $p = 0.156$), with no significant underlying univariate relationships. Coefficient-level tests did, however, demonstrate that predator nutrient contents related to sowing period (MGLM: Wald = 9.847, $p = 0.006$; fig. 3), alongside specific taxon effects and the interaction between specific taxa and sowing periods. The proportional content of carbohydrate (MLM: $F = 9.119$, $p = 0.002$) significantly differed between crops sown in winter and spring, with carbohydrate being proportionally higher in winter-sown crops. Lipid (MLM: $F = 0.223$, $p = 0.104$) and protein (MLM: $F = 0.504$, $p = 0.098$) content did not significantly differ between sowing periods, although all three macronutrients were more variable in their content in winter-sown crops.

Null network predator–prey interactions did not significantly explain predator nutrient contents when considering past (RDA: $F = 0.851$, df = 19, $p = 0.673$; fig. 4) nor present (RDA: $F = 0.864$, df = 24, $p = 0.656$; fig. 4) prey availability, and most individual model terms (prey) did not significantly explain predator nutrient content, although there was a marginally insignificant relationship between past Keroplatidae abundance and predator nutrient contents (ANOVA: $F = 2.686$, df = 1, $p = 0.089$), and significant and marginally insignificant relationships involving present Collembola (ANOVA: $F = 6.361$, df = 1, $p = 0.013$) and Braconidae (ANOVA: $F = 2.662$, df = 1, $p = 0.096$) abundances, respectively.

Discussion

The nutrient content of arthropod predators was associated with the timing of crop sowing, even across the small spatial scales used in this study (i.e. parallel transects 4 m apart). Whilst the prey available to those predators also changed across those small spatial scales, neither current nor recent prey availability explained the nutritional differences. This could indicate density-independent foraging of the arthropod predators (i.e. foraging for prey disproportionate to their availability, observed in similar predatory assemblages; Cuff *et al.*, 2022), or a shift in prey quality, irrespective of taxonomic identity, associated with differences in the developmental stage of crops sown in winter and spring. The crops themselves will likely differ markedly in their nutrient content at different developmental stages given the remobilisation of nutrients away from leaf tissue over time (Gregersen *et al.*, 2008). This will possibly have concomitant impacts on the herbivorous insects feeding on them, which are then predated by the focal arthropod predators of this study. The greater variability in nutrient content in predators from the winter-sown wheat, for example, could relate to the scarcity of nutrients in the senescing wheat relative to the younger wheat in the spring-sown crop. Senescing crops can drive the death or dispersal of foliar herbivores and their predators (Watt, 1979), likely resulting in nutritional variation and decline in those that remain. Prey quality, rather than availability, may therefore be the primary driver of the observed nutritional differences

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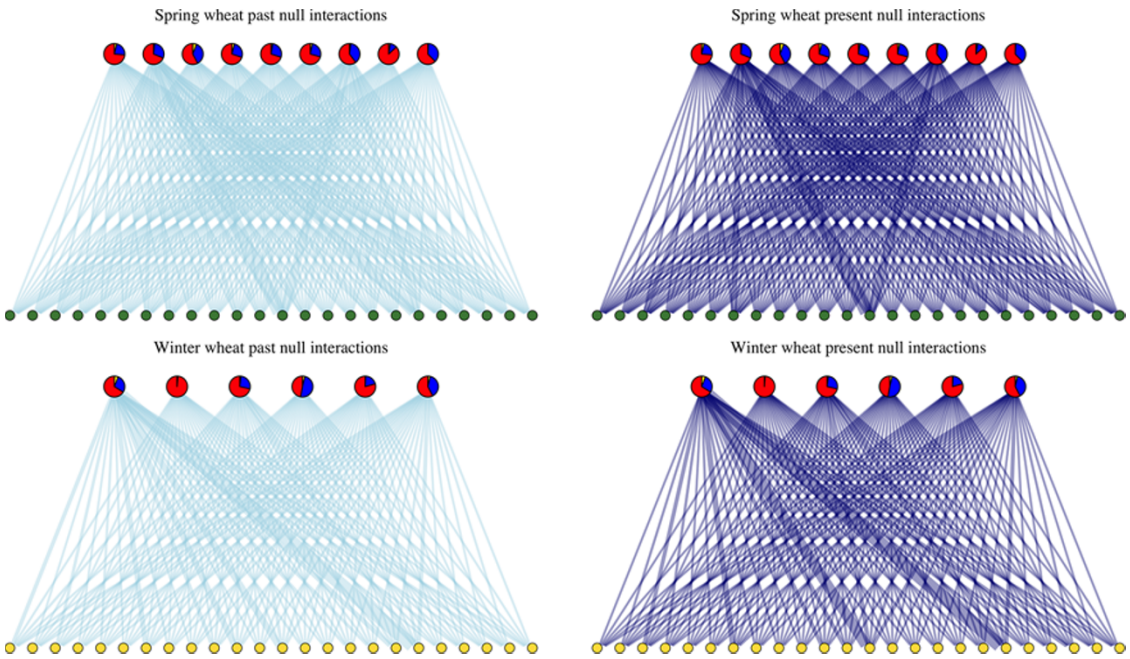


Figure 4. Inferred networks of predator-prey interactions based on prey availability for spring wheat (green prey nodes) and winter wheat (yellow prey nodes) based on data taken nine days before ('past'; light blue links) and in parallel with samples used for nutritional analysis ('present'; dark blue links). Upper nodes are predators when present nutrient data given with yellow, blue and red denoting carbohydrate, lipid, and protein proportional content, respectively.

(Wilder *et al.*, 2010; Schmidt *et al.*, 2012; Rendon *et al.*, 2019). Since prey nutrient content influences the nutrition and trophic interactions of predators (Wilder *et al.*, 2019; Cuff, Tercel, Vaughan *et al.*, 2024), this could indicate a nutritional cascade from the crop as a basal resource to the arthropod predators, although this requires further investigation in a larger-scale study.

This hypothetical nutritional cascade could have important implications for subsequent biocontrol and the spillover of arthropods and interactions from winter- to spring-sown crops continuously and particularly following harvest. The greater nutritional variation in predators in the winter-sown wheat could indicate increased rates of nutritional imbalance, which would then be likely redressed through nutrient-specific foraging as they migrate to other crops (Mayntz *et al.*, 2005). Given the larger variation in nutrient contents of winter-sown wheat predators, it may be harder to predict the interactions and nutritional dynamics of these predators as they migrate to other locations, such as spring-sown crops. Harvest of winter-sown crops, which will increase community turnover through physical disturbance (Opatovsky and Lubin, 2012; Cuff *et al.*, 2021), is likely to propagate this migration through spillover, especially between adjacent plots (Cuff, Gajski *et al.*, 2024).

This work was intentionally carried out at a small spatial scale, with only 4 m separating the transects in winter- and spring-sown crops. The intention was to determine either that differences could be resolved at such small spatial scales, or that arthropods were spilling over between the two adjacent crops. Whilst a significant difference in nutrient content was detected at this resolution, this was not consistent across analyses, and spillover is likely nonetheless, especially given that many of the arthropod predators studied are mobile. Most of the predators collected were small ground beetles such as *Bembidion* spp., the foraging range of which is poorly characterised; however, other larger ground beetles are known to travel less than 1 m per day (Schreiner and Irmler, 2009). This could imply that the 'present' prey availability data were representative of their recent prey availability, even if the 'past' prey availability data were less likely to be representative. That some significant difference in nutrient content was observed could support the notion that the difference between the two crop stages resulted in the divergent nutritional states of predators. Alternatively, the nutritional state of the predators could have driven them to forage in a specific crop stage, seeking nutrients that were deficient in the other crop stage. The latter would be consistent with optimal foraging theory if each 'patch' presented different nutritional opportunities (Pyke *et al.*, 1977). Both eventualities do, however, indicate a nutritional effect of crop developmental stage with implications for wider foraging, predator fitness and biocontrol, which requires further investigation.

This study was a brief snapshot of a potentially complex and continuously evolving dynamic between crop development and predator nutrition. Given the indirect link between predators and crops, other nutrients, including elemental macronutrients and micronutrients, may be important drivers of interactions (Kaspari, 2021; Wilder *et al.*, 2025). This study provides the foundations from which to investigate this dynamic deeper, ideally by linking nutrient flow through each trophic level to determine how nutrients structure the wider ecological system (Cuff, Evans *et al.*, 2024). Whilst the interactions inferred based on prey availability data are likely to reflect the pool of prey accessible to the predators studied and null models can generate semi-accurate interaction data (Cuff, Tercel, Windsor *et al.*, 2024), trophic interactions are often density-independent (Vaughan *et al.*, 2018; Cuff *et al.*, 2022; Gajski *et al.*, 2024), the deviations of which from our models are unknown. The interactions inferred should therefore be interpreted with caution, and future investigations should identify trophic interactions empirically.

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Conclusions

We have demonstrated that, at least in this small-scale snapshot study, the nutrient contents of arthropod predators can change with the sowing period of crops on even very small spatial scales. Whilst prey availability concomitantly changes, it does not explain this nutritional variation, possibly indicating a more complex set of mechanisms, potentially relating to cascading impacts to the nutritional quality of prey as a result of different stages of crop development and senescence. That basal resource quality could underpin predator nutritional fitness through trophic cascades has important implications for the management of crops to sustain healthy natural enemy populations. This is likely to be particularly relevant in monocultural arable systems where alternative basal resources are scarce if available at all. The potential spillover of nutritionally distinct predator and pest populations from winter- to spring-sown crops, either continuously or following harvest, has the potential to rewire nutritional networks in adjacent spring-sown crops. This study provides the foundations for further investigation of this crucial nutritional dynamic, ideally with greater replication across a broader range of contexts to enable greater generalisability of the results. Expansion of the spatiotemporal scope of this study could identify novel management strategies to optimise natural enemy population health and conservation biocontrol.

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References

Barber AD (2008) *Key to the Identification of British Centipedes*, 1st Edn. Preston Montford, UK: Field Studies Council.

Bilde T and Toft S (1997) Limited prédation capacity by generalist arthropod predators on the cereal aphid, *Rhopalosiphum padi*. *Biological Agriculture & Horticulture* **15**(1–4), 142–150. https://doi.org/10.1080/01448765.1997.9755188.

Bilde T and Toft S (2001) The value of three cereal aphid species as food for a generalist predator. *Physiological Entomology* **26**(1), 58–68. https://doi.org/10.1111/j.1365-3032.2001.00218.x.

Briatte F (2021) *Ggnetwork: Geometries to plot networks with 'ggplot2'*. [Computer software].

Csardi G and Nepusz T (2006) The igraph software package for complex network research. *InterJournal Complex Systems* **1695**, 1–9.

Cuff JP, Drake LE, Tercel MPTG, Stockdale JE, Orozco-terWengel P, Bell JR, Vaughan IP, Müller CT and Symondson WOC (2021) Money spider dietary choice in pre- and post-harvest cereal crops using metabarcoding. *Ecological Entomology* **46**(2), 249–261. https://doi.org/10.1111/een.12957.

Cuff JP, Evans D, Vaughan I, Wilder S, Tercel M and Windsor F (2024) Networking nutrients: How nutrition determines the structure of ecological networks. *Journal of Animal Ecology* **93**(8), 974–988. https://doi.org/10.1111/1365-2656.14124.

Cuff JP, Gajski D, Michalko R, Košulič O and Pekár S (2024) Biomonitoring of biocontrol across the full annual cycle in temperate climates: Post-harvest, winter and early-season interaction data and methodological considerations for its collection. *Agricultural and Forest Entomology*, afe.12635. https://doi.org/10.1111/afe.12635.

Cuff JP, Tercel MPTG, Drake LE, Vaughan IP, Bell JR, Orozco-terWengel P, Müller CT and Symondson WOC (2022) Density-independent prey choice, taxonomy, life history, and web characteristics determine the diet and biocontrol potential of spiders (Linyphiidae and Lycosidae) in cereal crops. *Environmental DNA* **4**(3), 549–564. https://doi.org/10.1002/edn3.272.

Cuff JP, Tercel MPTG, Vaughan IP, Drake LE, Wilder SM, Bell JR, Müller CT, Orozco-terWengel P and Symondson WOC (2024) Prey nutrient content is associated with the trophic interactions of spiders and their prey selection under field conditions. *Oikos*, e10712. https://doi.org/10.1111/oik.10712.

Cuff JP, Tercel MPTG, Windsor FM, Hawthorne BSJ, Hambäck PA, Bell JR, Symondson WOC and Vaughan IP (2024d) Sources of prey availability data alter interpretation of outputs from prey choice null networks. *Ecological Entomology* **49**(3), 418–432. https://doi.org/10.1111/een.13315.

Cuff JP, Windsor FM, Tercel MPTG, Bell JR, Symondson WOC and Vaughan IP (2023) Temporal variation in spider trophic interactions is explained by the influence of weather on prey communities, web building and prey choice. *Ecography* **2023**(7), e06737. https://doi.org/10.1111/ecog.06737.

Dallimore T and Shaw PJA with Field Studies Council (Great Britain) (2013) *Illustrated Key to the Families of British Springtails (Collembola)*. Preston Montford, UK: FSC Publications.

Davey JS, Vaughan IP, Andrew King R, Bell JR, Bohan DA, Bruford MW, Holland JM and Symondson WOC (2013) Intraguild predation in winter wheat: Prey choice by a common epigeal carabid consuming spiders. *Journal of Applied Ecology* **50**(1), 271–279. https://doi.org/10.1111/1365-2664.12008.

Douglas DJT, Vickery JA and Benton TG (2010) Variation in arthropod abundance in barley under varying sowing regimes. *Agriculture, Ecosystems & Environment* **135**(1–2), 127–131. https://doi.org/10.1016/j.agee.2009.09.002.

Gajski D, Mifková T, Košulič O, Michálek O, Serbina LŠ, Michalko R and Pekár S (2024) Brace yourselves, winter is coming: The winter activity, natural diet, and prey preference of winter-active spiders on pear trees. *Journal of Pest Science* **97**(1), 113–126. https://doi.org/10.1007/s10340-023-01609-5.

Gregersen PL, Holm PB and Krupinska K (2008) Leaf senescence and nutrient remobilisation in barley and wheat. *Plant Biology* **10**(s1), 37–49. https://doi.org/10.1111/j.1438-8677.2008.00114.x.

Hedlund K, Griffiths B, Christensen S, Scheu S, Setälä H, Tscharntke T and Verhoef H (2004) Trophic interactions in changing landscapes: Responses of soil food webs. *Basic and Applied Ecology* **5**(6), 495–503. https://doi.org/10.1016/j.baae.2004.09.002.

Heimbach U and Garbe V (1996) Effects of reduced tillage systems in sugar beet on predatory and pest arthropods. *Acta Jutlandica, Arthropod Natural Enemies in Arable Land II: Survival, Reproduction and Enhancement* **71**(2), 195–208.

Hodge MA (1999) The implications of intraguild predation for the role of spiders in biological control. *The Journal of Arachnology, Proceedings of the XIV International Congress of Arachnology and a Symposium on Spiders in Agroecosystems* **27**(1), 351–362.

Hsu G, Ou J and Ho C (2021) Pest consumption by generalist arthropod predators increases with crop stage in both organic and conventional farms. *Ecosphere* **12**(7), e03625. https://doi.org/10.1002/ecs2.3625.

Jaworski CC, Thomine E, Rusch A, Lavoir A-V, Wang S and Desneux N (2023) Crop diversification to promote arthropod pest management: A review. *Agriculture Communications* **1**(1), 100004. https://doi.org/10.1016/j.agrcom.2023.100004.

Jensen K, Mayntz D, Toft S, Clissold FJ, Hunt J, Raubenheimer D and Simpson SJ (2012) Optimal foraging for specific nutrients in predatory beetles. *Proceedings of the Royal Society B: Biological Sciences* **279**(1736), 2212–2218. https://doi.org/10.1098/rspb.2011.2410.

Jowett K, Milne AE, Garrett D, Potts SG, Senapathi D and Storkey J (2021) Above- and below-ground assessment of carabid community responses to crop type and tillage. *Agricultural and Forest Entomology* **23**(1), 1–12. https://doi.org/10.1111/afe.12397.

Cuff JP and Wilder SM (2021) MEDI: Macronutrient Extraction and Determination from Invertebrates. protocols.io. https://dx.doi.org/10.17504/protocols.io.buj9nur6

Kaspari M (2021) The invisible hand of the periodic table: How micronutrients shape ecology. *Annual Review of Ecology, Evolution, and Systematics* **52**(1), 199–219. https://doi.org/10.1146/annurev-ecolsys-012021-090118.

Landa BB, Navas-cortés JA and Jiménez-díaz RM (2004) Integrated management of Fusarium wilt of chickpea with sowing date, host resistance, and biological control. *Phytopathology®* **94**(9), 946–960. https://doi.org/10.1094/PHYTO.2004.94.9.946.

Luff ML (2007) *Handbooks for the Identification of British Insects. Vol. 4, Pt. 2: The Carabidae (Ground Beetles) of Britain and Ireland*, 2nd Edn. Hertfordshire, UK: Royal Entomological Society.

Mayntz D, Raubenheimer D, Salomon M, Toft S and Simpson SJ (2005) Nutrient-specific foraging in invertebrate predators. *Science* **307**(5706), 111–113. https://doi.org/10.1126/science.1105493.

Michalko R, Pekár S, Dul'a M and Entling MH (2019) Global patterns in the biocontrol efficacy of spiders: A meta-analysis. *Global Ecology and Biogeography* **28**(9), 1366–1378. https://doi.org/10.1111/geb.12927.

Moore SM, Borer ET and Hosseini PR (2010) Predators indirectly control vector-borne disease: Linking predator-prey and host-pathogen models. *Journal of the Royal Society, Interface* **7**(42), 161–176. https://doi.org/10.1098/rsif.2009.0131.

Oksanen J, Simpson GL, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'hara RB, Solymos P, Stevens MHH, Szoecs E, Wagner H, Barbour M, Bedward M, Bengtsson H, Bolker B, Borcard D, Borman T, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista HBA, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Heida I, Hill MO, Lahti L, Martino C, McGlinn D, Ouellette M-H, Cunha ER, Smith T, Stier A, Ter Braak CJF and Weedon J (2022) *Vegan: Community Ecology Package* (Version 2.6-2). [Computer software]. Available at https://CRAN.R-project.org/package=vegan.

Opatovsky I and Lubin Y (2012) Coping with abrupt decline in habitat quality: Effects of harvest on spider abundance and movement. *Acta Oecologica* **41**, 14–19. https://doi.org/10.1016/j.actao.2012.03.001.

Pyke GH, Pulliam HR and Charnov EL (1977) Optimal foraging: A selective review of theory and tests. *The Quarterly Review of Biology* **52**(2), 137–154.

R Core Team. (2025) *R: A Language and Environment for Statistical Computing* (Version 4.5.2). [Computer software]. R Foundation for Statistical Computing. Available at https://www.R-project.org/.

Rendon D, Taylor PW, Wilder SM and Whitehouse MEA (2019) Does prey encounter and nutrient content affect prey selection in wolf spiders inhabiting Bt cotton fields? *PLOS ONE* **14**(1), e0210296. https://doi.org/10.1371/journal.pone.0210296.

Roberts MJ (2016) *Spiders of Britain and Northern Europe*. (Reprint).

Rosenblatt AE (2018) Shifts in plant nutrient content in combined warming and drought scenarios may alter reproductive fitness across trophic levels. *Oikos* **127**(12), 1853–1862. https://doi.org/10.1111/oik.05272.

Rosenheim JA, Kaya HK, Ehler LE, Marois JJ and Jaffee BA (1995) Intraguild predation among biological-control agents: Theory and evidence. *Biological Control* **5**(3), 303–335. https://doi.org/10.1006/bcon.1995.1038.

Schmidt JM, Sebastian P, Wilder SM and Rypstra AL (2012) The nutritional content of prey affects the foraging of a generalist arthropod predator. *PLoS ONE* **7**(11), e49223. https://doi.org/10.1371/journal.pone.0049223.

Schreiner R and Irmler U (2009) Mobility and Spatial use of the Ground Beetle species Elaphrus cupreus and Elaphrus uliginosus (Coleoptera: Carabidae). *Entomologia Generalis* **32**(3), 165–179.

Symondson WOC, Sunderland KD and Greenstone MH (2002) Can generalist predators be effective biocontrol agents? *Annual Review of Entomology* **47**(1), 561–594. https://doi.org/10.1146/annurev.ento.47.091201.145240.

Tilling S (2014) *A Key to the Major Groups of British Terrestrial Invertebrates*, 2nd Edn. Preston Montford, UK: FSC.

Tschumi M, Ekroos J, Hjort C, Smith HG and Birkhofer K (2018) Predation-mediated ecosystem services and disservices in agricultural landscapes. *Ecological Applications* **28**(8), 2109–2118. https://doi.org/10.1002/eap.1799.

Vaughan IP, Gotelli NJ, Memmott J, Pearson CE, Woodward G and Symondson WOC (2018) econullnetr: An R package using null models to analyse the structure of ecological networks and identify resource selection. *Methods in Ecology and Evolution* **9**(3), 728–733. https://doi.org/10.1111/2041-210X.12907.

Wang Y, Naumann U, Wright ST and Warton DI (2012) Mvabund– an R package for model-based analysis of multivariate abundance data. *Methods in Ecology and Evolution* **3**(3), 471–474. https://doi.org/10.1111/j.2041-210X.2012.00190.x.

Watt AD (1979) The effect of cereal growth stages on the reproductive activity of Sitobion avenue and Metopolophium dirhodum. *Annals of Applied Biology* **91**(2), 147–157. https://doi.org/10.1111/j.1744-7348.1979.tb06485.x.

Wickham H (2016) *Ggplot2: Elegant Graphics for Data Analysis*, 2nd Edn. Cham, Switzerland: Springer International Publishing : Imprint: Springer. https://doi.org/10.1007/978-3-319-24277-4.

Wickham H, Averick M, Bryan J, Chang W, D'Agostino McGowan L, François R, Grolemund G, Hayes A, Henry L, Hester J, Kuhn M, Lin Pedersen T, Miller E, Milton Bache S, Müller K, Ooms J, Robinson D, Seidel DP, Spinu V, Takahashi K, Vaughan D, Wilke C, Woo K and Yutani H (2019) Welcome to the Tidyverse. *Journal of Open Source Software* **4**(43), 1686. https://doi.org/10.21105/joss.01686.

Wilder SM, Barnes CL and Hawlena D (2019) Predicting predator nutrient intake from prey body contents. *Frontiers in Ecology and Evolution* **7**, 42. https://doi.org/10.3389/fevo.2019.00042.

Wilder SM, Herzog C, Reeves J, Knowles O and Cuff JP (2025) Bridging digestive physiology and ecology for a more integrative understanding of invertebrate predators. *Journal of Experimental Biology* **228**(14), jeb249697. https://doi.org/10.1242/jeb.249697.

Wilder SM, Mayntz D, Toft S, Rypstra AL, Pilati A and Vanni MJ (2010) Intraspecific variation in prey quality: A comparison of nutrient presence in prey and nutrient extraction by predators. *Oikos* **119**(2), 350–358. https://doi.org/10.1111/j.1600-0706.2009.17819.x.

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