

The spatial dynamics of nutrient limitation in communities of generalist predators of crop pests

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Abstract

1. Generalist arthropod predators vitally control crop pests, but their ability to perform this role relies on them obtaining sufficient nutrients within simplified crop environments. Field margins are thought to provide habitat and resources for predators, such as ground beetles, but how far into fields this provision extends is poorly understood. Since arthropod nutrient contents can vary significantly over small spatial scales, resource scarcity within arable monoculture field interiors may drive nutrient limitation, impacting the fitness of natural enemies of crop pests.
2. Integrating field surveys, colorimetric assays and laboratory feeding trials, we investigated how distance into crop fields and crop stage affect nutrient limitation of ground beetles within arable crop fields. We specifically compared the community structure, nutrient contents and nutritional preferences of beetles at different distances into crops, and between crops before and after harvest to determine likely impacts to nutrient limitation.

3. Ground beetle communities and nutrient contents varied with distance into the crop and crop stage, but variation in nutritional preferences in relation to distance into the crop was species-specific and dependent on crop stage. Nutritional feeding trials indicated broad lipid limitation across all samples in the study.
4. These findings indicate taxon-specific variation in the nutritional dynamics of ground beetle communities at different distances into fields, with some species potentially being better adapted to crop interiors and post-harvest landscapes. Increasing in-field proximity to semi-natural habitat through intercropping and similar management strategies could support nutritionally healthier populations of natural enemies with likely benefits to pest suppression.

Keywords: arable, biocontrol, foraging ecology, macronutrients, optimal foraging theory, natural enemies

Introduction

Generalist arthropod predators play a vital role in controlling crop pests in agricultural systems (Michalko et al., 2019; Pekár et al., 2015; Symondson et al., 2002). The efficacy of generalist predators in providing this ecosystem service is, however, dependent on their persistence within crop environments and the capacity of those environments to sustain predator fitness (Harwood et al., 2009; Landis et al., 2000; Mansier & Van Rijn, 2024). For many years, field margins have been discussed as a means of enhancing communities of natural enemies of crop pests (Woodcock et al., 2005, 2007), particularly in relation to policies such as Europe's agri-environment schemes (Hasler et al., 2022), which demonstrably promote predators (Boetzi et al., 2019). Field margins provide suitable overwintering sites for natural enemies of crop

pests (Gallé et al., 2018), potentially buffering the ecologically disruptive impacts of harvest (Cuff, Gajski, et al., 2024; Opatovsky & Lubin, 2012). The efficacy of field margins in supporting the fitness and persistence of natural enemies of crop pests further into crop fields, and following perturbations like harvest, remains unclear.

According to optimal foraging theory, the exploitation time of consumers within a given patch or environment is predicated by the quality of that patch for foraging (MacArthur & Pianka, 1966; Pyke, 1984). Given the ubiquitous spatial variation in the types and quality of resources observed in natural and modified habitats, even within monocultural environments (Christopher et al., 2026; Landis et al., 2000), crops may present suboptimal foraging patches for generalist predators (MacArthur & Pianka, 1966). This spatial heterogeneity in patch quality can impact the persistence of generalist predators within crop fields and, therefore, their role in the biocontrol of pests. Among the key determinants of predator fitness is the nutritional content and quality of prey (Harrison et al., 2014; Wilder et al., 2025), which significantly drive foraging choices and trophic interactions (Cuff, Tercel, et al., 2024; Jensen et al., 2012; Mayntz et al., 2005). The nutritional quality of arthropod prey can vary significantly over very small spatial scales (e.g., < 5 m) based on crop management practices, likely due to nutritional differences in crops as basal resources cascading through herbivorous insects to their predators (Christopher et al., 2026). This is likely to alter the optimality of foraging patches across arable landscapes, potentially driving nutrient limitation and concomitant impacts to the fitness of natural enemies of crop pests.

Ground beetles (Coleoptera: Carabidae) are abundant generalist predators in arable landscapes and frequent natural enemies of crop pests (Cividanes, 2021; Lövei & Sunderland, 1996). The richness and functional diversity of ground beetles closely relates to landscape structure and habitat availability (Woodcock et al., 2010), with

many thought to enter crop fields from adjacent field margins (Varchola & Dunn, 2001). Grassy field margins are particularly effective for promoting ground beetle activity density and biocontrol (Mansion-Vaquié et al., 2017), but few studies have assessed the extent of their spillover into crop fields (but see, e.g., Neumann & Galpern, 2026; Varchola & Dunn, 2001) nor the nutritional implications of spillover. Despite their high activity density, ground beetles can exhibit a high degree of patch fidelity, sometimes travelling as little as 1 m per day (Schreiner & Irmeler, 2009). This likely restricts many ground beetles to specific locations within fields, potentially nutritionally isolating them in suboptimal patches, with potential concomitant impacts to their fitness and biocontrol activity.

Using a combination of field surveys, laboratory feeding trials and colorimetric assays, we investigated potential nutrient limitation in ground beetles at different distances into arable crop fields. We specifically investigated how beetle community structure, nutritional preferences and nutrient contents relate to distance into the crop and crop stage (i.e., desiccation, harvest). Using multivariate modelling, we tested the following hypotheses: (i) beetle community structure varies with distance into the crop and crop stage, with some species exclusively found in the margins and crop interior; (ii) beetles at different distances into the crop and from different crop stages seek specific nutrients in laboratory feeding trials, with crop interior and post-harvest beetles seeking more lipids due to resource scarcity interacting with broader lipid limitation in arthropod predators (Wilder et al., 2013); and (iii) beetles at different distances into the crop and from different crop stages will contain different nutrients, with crop interior and post-harvest beetle having lower lipid content, reflecting the aforementioned lipid limitation and resource scarcity. Elucidating the spatial dynamics of nutrition in natural enemies of crop pests is vital for understanding and potentially enhancing the fitness

and function of biocontrol agents, and for our wider comprehension of nutritional ecology in agroecosystems.

Methods

Field surveys

Field surveys were carried out at Cockle Park, Morpeth, UK (55.214° N, 1.685° W), a farm site operated by Newcastle University. Sampling took place across two rounds in July and August 2026 (14-15th July 2026 and 10-11th August 2026) in three fields. Two fields contained oats, which were desiccated during round one and harvested prior to round two, and one field contained peas, which were 'fresh' during round one and desiccated during round two. Pairs of dry 500 mL pitfall traps were set in the north margin at the approximate centre of each field, and then 5 m, 20 m, 50 m and 100 m into the crop (Figure 1). The selected margins were all relatively simple, short grass margins (~ 5 m wide) adjacent to either hedgerow or, in one case, a small patch of woodland. Pitfall traps contained clay balls to provide refuge to trapped invertebrates and prevent within-trap predation. Traps were collected after 24 h and the contents of each transferred to a 125 mL collection pot for transport to the lab. The beetles from one trap were frozen and stored at -20 °C for macronutrient analysis. The beetles from the other trap were taken forward for nutritional feeding assays.



Figure 1: Distribution of sampling locations within Cockle Park, Morpeth, UK. Three transects were established (pink dashed lines), each across a different field (yellow). Dark green indicates small patches of woodland or thicker hedgerow. Each transect comprised paired dry pitfall traps 0 m (i.e., margin), 5 m, 20 m, 50 m and 100 m into the crop field from the north crop margin. Each transect was sampled twice (July and August 2026).

Nutritional feeding assays

Nutritional feeding assays followed the 'double-test' procedure of pre-acclimation (i.e., following collection) and post-acclimation (i.e., following a week of acclimation under controlled conditions) feeding trials (e.g., see Christensen et al., 2020; Nielsen et al., 2022; Toft et al., 2019). The protocol used is broadly presented by Croft et al. (2026). Feeding arenas were prepared by pouring a ~5 mm thick plaster-charcoal base (5 g activated charcoal powder, 40 g plaster of Paris and 45 mL water per 90 mL) into 9 cm Petri dishes, which were allowed to set at room temperature for 24 h. Base

moisture was maintained throughout by applying ~2.5 mL of water to each arena when beginning to dry (determined by light grey colour of dried charcoal-plaster mix). Following field collection, beetles were separated into feeding arenas and left for 24 h before feeding assays were initiated. All beetles were kept in incubators at 25 °C with 12:12 light:dark cycles during initial incubation, feeding assays and satiation periods.

For the feeding trials, three artificial diets were prepared: high-carbohydrate, high-lipid and high-protein (Table S1). Each of these diets consisted of 50% dried, powdered mealworm, prepared by grinding commercially sold dried mealworms with a pestle and mortar, and sieving the fine powder. The remaining 50% consisted of an equal mixture of sucrose and dextrose powder, lard oil and casein for the high-carbohydrate, high-lipid and high-protein diets, respectively. These were stored at 4 °C for immediate use or -20 °C for longer-term storage. All artificial diets were precautionarily dried in an oven at 50 °C for 3 h prior to use, although none should have contained water.

Into each feeding trial arena, four inverted screw-cap 2 mL microcentrifuge cap lids were placed as feeding dishes. The inner recess of each lid was filled with one of the three foods, and the fourth was filled with water. Lids were labelled on their underside with the food mixture they contained, and each was weighed immediately before the assay. The lids were placed at cardinal points in the Petri dish, each ~10 mm from the Petri dish edge to allow beetles to freely follow the edge of the dish.

Beetles were weighed immediately before being placed in the centre of the arena. Beetles were allowed to feed for 24 h (pre-acclimation feeding trial), at which point the foods were collected, dried for 3 h in an oven at 50 °C (or up to 6 h if mass was still decreasing) and weighed. Beetles were allowed to feed ad libitum on dried mealworms and water for seven days (acclimation). The feeding trial was then repeated (post-acclimation feeding trial) as above. Following the conclusion of this second feeding

trial, beetles were weighed and killed by freezing. Beetles were identified to species level using a morphological key (Luff, 2007) and were digitally imaged on an Epson Perfection V850 Pro charged coupled device scanner using the settings described by Ong et al. (2025; Figures S1 and S2). The mass change of each artificial diet was calculated by subtracting the post-feeding trial mass from the pre-feeding trial mass for both pre- and post-acclimation feeding trials. In very few instances where artificial diet mass was apparently gained during a feeding trial, results were discounted unless the gain was less than 2 mg (to account for potential instrument error), at which point it was recorded as no mass change. Some data were lost due to beetles dying during one of the assays or between the two.

Macronutrient analysis

Macronutrient analysis followed the Macronutrient Extraction and Determination from Invertebrates (MEDI) protocol (Cuff et al., 2021; Cuff & Wilder, 2023) which streamlines sulfo-phospho-vanillin, anthrone and bicinchoninic acid (BCA) colorimetric assays for lipid, carbohydrate and protein estimation, respectively. As per Christopher et al. (2026), assay volumes were adjusted for 384-well plates to increase throughput. Individual ground beetles were placed in 2 mL tubes of a 96-well rack and dried at 60 °C for 3 h. To each sample, 1 mL of 1:9 chloroform:methanol solution was added and incubated for 24 h at room temperature. After 24 h, 500 µL of the chloroform:methanol solution was removed and retained for lipid analysis. A further 500 µL of chloroform:methanol solution was added to the sample and incubated for 24 h at room temperature to reduce the prevalence of potential residual lipids. Following incubation, all chloroform:methanol solution was removed by pipetting, and any remaining solution evaporated by incubation at 60 °C for ~ 2 h.

To each sample, 1 mL 0.1 M NaOH was added and the samples incubated at 80 °C for 60 min, followed by room temperature incubation overnight (~ 16 h). From each sample, the supernatant was transferred directly into assay plates for protein and carbohydrate determination immediately following the overnight incubation. All assays were carried out in 384-well plate format, with all samples run in triplicate. 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 1:9 chloroform:methanol. Dilution series comprised 0-2 mg mL⁻¹ in eight increments (0, 25, 100, 300, 800, 1000, 1500, 2000 µg mL⁻¹). A quarter of each 384-well assay plate (96 wells) was reserved for repeats of these standards, except in one plate where 72 wells were used for standards to include eight additional samples in triplicate.

Lipid quantification

The sulfo-phospho-vanillin method was used to determine lipid content. The vanillin reagent was prepared by mixing 1.08 mg of vanillin with 180 µL of hot water and 720 µL 85 % phosphoric acid for every 1 mL of reagent. From each sample, three repeats of 20 µL were added to a 384-well plate alongside standards, as above, and heated to 90 °C for 10 min to evaporate the chloroform:methanol carrier. To each well, 10 µL of concentrated sulfuric acid was added, mixed briefly by vortexing and incubated at 90 °C for 10 min. Following this, 75 µL of vanillin reagent was added to each well and incubated at room temperature for 5 min. Absorbance at 490 nm was determined for each well in a spectrophotometer.

Carbohydrate quantification

The anthrone method was used to determine carbohydrate content. The anthrone reagent was prepared by mixing 1 mg of anthrone with 1 mL of concentrated sulfuric acid for every 1 mL of reagent. From each sample, three repeats of 20 μ L were added to a 384-well plate alongside standards, mixed with 80 μ L of the anthrone reagent and incubated at 90 °C for 6 min. The plate was incubated at room temperature for 5 min and absorbance at 620 nm was determined for each well in a spectrophotometer.

Protein quantification

The BCA method was used to determine protein content. From each sample, three repeats of 20 μ L were diluted with 180 μ L NaOH and 20 μ L of the diluted sample were added to a 384-well plate alongside standards. A BCA working reagent was prepared according to the manufacturer (Pierce™ BCA Protein Assay Kit, ThermoFisher). To each well, 80 μ L of BCA reagent was added and mixed briefly on a plate shaker. The plate was incubated at 37 °C for 10 min and absorbance at 562 nm was determined for each well in a spectrophotometer.

Nutrient content data processing

Absorbance values generated by the spectrophotometer were blank corrected by subtracting the mean absorbance for blank controls (i.e., controls with a concentration of 0 mg mL⁻¹) within each plate. A linear relationship between absorbance and concentration was assumed and a line of best fit generated for the standards included in each plate. If the R² for that line was below 0.95, outliers were identified and

removed (e.g., blank readings for a high concentration standard). Where most of the points for a given standard concentration were associated with a raw absorbance of 4.000 (the maximum reading), that standard concentration was discarded (which was only true for high concentrations of carbohydrate standards). The equation for the line of best fit was used to calculate concentration values for each sample based on their absorbance values. Negative concentration values were excluded, and mean concentrations calculated for each nutrient of each sample. Macronutrient data were generated for 389 beetles, of which data for five beetles were removed due to a lack of detections of at least one nutrient, and data for two beetles were removed due to detected nutrient contents exceeding 10 % above the highest standard concentration for at least one nutrient.

Data analysis

All data analyses were conducted in R version 4.5.2 (R Core Team, 2025). Data were processed and formatted using 'tidyverse' for reproducibility (Wickham et al., 2019). Beetle abundances and community structure were compared against distance into the field, crop stage, crop type and interactions between crop type and distance into the crop, and crop stage and distance into the crop. These relationships were tested in a multivariate generalised linear model (MGLM) using the 'manyglm' function in 'mvabund' with a Poisson distribution function (Wang et al., 2012). The model was analysed with Monte Carlo resampling and adjustment of p-values for univariate results to account for multiple testing using a step-down resampling procedure. Community differences were visualised using non-metric multidimensional scaling (NMDS) using the 'metaMDS' function in the 'vegan' package (Oksanen et al., 2022) with 999 'tries' and a Bray-Curtis dissimilarity matrix.

Nutrient intake data from the feeding trials were compared against distance into the field, crop stage, beetle species, crop type and interactions between beetle species and distance into the crop, beetle species and crop stage, crop type and distance into the crop, and crop stage and distance into the crop. Nutrient intake was represented as proportions of the total mass of feed consumed to account for differences in beetle size. These relationships were tested in two multivariate linear models using the 'manyglm' function in 'mvabund'. One model included data from the pre-acclimation feeding trials, whereas the other included data from the post-acclimation feeding trials. The models were analysed in 1000 iterations with p-values for univariate results adjusted for multiple testing using a step-down resampling procedure.

The difference in nutrient intake mass between pre-acclimation and post-acclimation (i.e., pre-acclimation intake subtracted from post-acclimation intake) for each of the three foods was compared against distance into the field, crop stage, beetle species, crop type and interactions between beetle species and distance into the crop, beetle species and crop stage, crop type and distance into the crop, and crop stage and distance into the crop. Intake mass differences were scaled using the 'scale' command and all values made positive by subtracting the minimum scaled value to adjust negative values. The relationships were tested in a multivariate linear model using the 'manyglm' function in 'mvabund', with models analysed as above.

The total food intake mass consumed during pre-acclimation and post-acclimation feeding trials were separately compared against distance into the field, crop stage, beetle species, crop type and interactions between beetle species and distance into the crop, beetle species and crop stage, crop type and distance into the crop, and crop stage and distance into the crop. These relationships were tested using generalised linear models, with total intake mass during each feeding trial as the dependent

variable. Model assumptions were checked using the 'testResiduals' function of the 'DHARMA' package (Hartig, 2022).

Beetle nutrient content data were compared against distance into the field, crop stage, beetle species, crop type and interactions between beetle species and distance into the crop, beetle species and crop stage, crop type and distance into the crop, and crop stage and distance into the crop. Beetle nutrient content data were represented as μg per beetle since proportional data violated the model assumptions, particularly normality. These relationships were tested in a multivariate linear model using the 'manyglm' function in 'mvabund', with models analysed as above. To meet the model assumptions, particularly normality, nutritional data were log-transformed. Nutritional data were visualised using ternary plots with the 'ggtern' package (Hamilton & Ferry, 2018) and scatterplots using 'ggplot2' (Wickham, 2016).

Results

Community composition

Ground beetle community composition significantly related to distance into the crop (MGLM: Dev = 87.48, d.f. = 1, $p = 0.001$; Figure 2), crop stage (MGLM: Dev = 279.81, d.f. = 2, $p = 0.001$; Figure 2), crop type (MGLM: Dev = 167.50, d.f. = 1, $p = 0.001$), and interactions between distance into the crop and crop type (MGLM: Dev = 17.96, d.f. = 1, $p = 0.010$), and distance into the crop and crop stage (MGLM: Dev = 44.21, d.f. = 2, $p = 0.001$).

Specifically, the abundances of *Pterostichus melanarius* (MGLM: Dev = 14.425, d.f. = 1, $p = 0.003$), *Bembidion* sp. (MGLM: Dev = 9.690, d.f. = 1, $p = 0.033$) and *Bembidion quadrimaculatum* (MGLM: Dev = 20.677, d.f. = 1, $p = 0.001$) increased with distance

into the crop (Figure S3). The abundances of *Pterostichus melanarius* (MGLM: Dev = 83.321, d.f. = 2, p = 0.001), *Pterostichus niger* (MGLM: Dev = 10.883, d.f. = 2, p = 0.010), *Bembidion* sp. (MGLM: Dev = 27.295, d.f. = 2, p = 0.001) and *Bembidion quadrimaculatum* (MGLM: Dev = 17.791, d.f. = 2, p = 0.002) were highest in desiccated crops, followed by fresh crops, and considerably lower in harvested crops (Figure S3). The abundance of *Harpalus rufipes* was highest in fresh crops, decreasing with desiccation and further again following harvest (MGLM: Dev = 43.178, d.f. = 2, p = 0.001; Figure S3). *Pterostichus vernalis* was exclusively found in fresh crops (MGLM: Dev = 14.138, d.f. = 2, p = 0.003; Figure S3). The abundance of *Trechus quadristriatus* was highest in harvested crops, followed by desiccated crops, and was absent in fresh crops (MGLM: Dev = 23.346, d.f. = 2, p = 0.001; Figure S3). The abundance of *Trechus quadristriatus* was higher in oats than peas (MGLM: Dev = 13.922, d.f. = 1, p = 0.001), and the abundances of *Harpalus rufipes* (MGLM: Dev = 43.704, d.f. = 1, p = 0.001), *Bembidion* sp. (MGLM: Dev = 63.962, d.f. = 1, p = 0.001), *Pterostichus madidus* (MGLM: Dev = 7.982, d.f. = 1, p = 0.019) and *Bembidion quadrimaculatum* (MGLM: Dev = 17.312, d.f. = 1, p = 0.001) were higher in peas than oats (Figure S3). The abundance of *Trechus quadristriatus* related to the interaction between distance into the crop and crop type (MGLM: Dev = 8.146, d.f. = 1, p = 0.021). The abundance of *Harpalus rufipes* related to the interaction between distance into the crop and crop stage (MGLM: Dev = 16.150, d.f. = 2, p = 0.002).

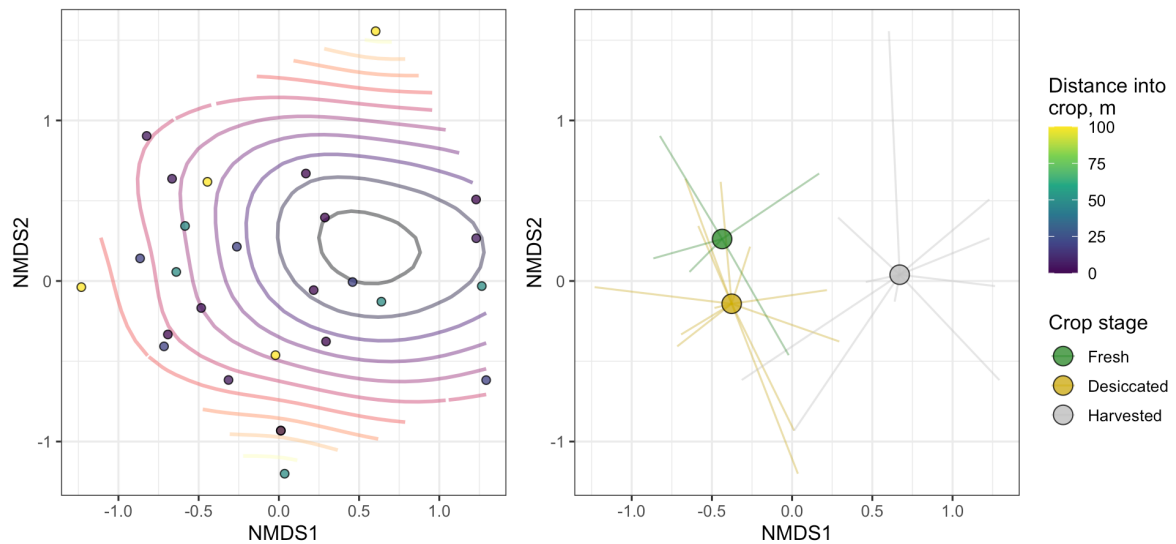


Figure 2: Non-metric multidimensional scaling of ground beetle communities in relation to distance into the crop (left) and crop stage (right). Axes represent two-dimensional variation in beetle communities. Each point represents the community composition of a single pitfall trap, with distance between them indicating their dissimilarity (i.e. proximate points are similar, distant points are dissimilar). Left: Contours represent an approximate relationship between distance into the crop and beetle community composition, with lighter colours relating to greater distances. Individual points are coloured according to the distance into the crop at which the beetle community was collected (blue through green to yellow denoting increasing distance) Right: Large bordered points represent mean coordinates for each group, and radial lines terminate at the coordinates of individual communities within each respective group. Green, yellow and grey denote fresh, desiccated and harvested crops, respectively. Stress = 0.157.

Nutritional feeding assays

In pre-acclimation feeding trials, most beetles exhibited a strong preference for the lipid-rich food, followed by the carbohydrate-rich and protein-rich foods, whereas post-acclimation, most beetles exhibited a strong preference for protein-rich food, followed by carbohydrate-rich and lipid-rich foods (Figures 3 and 4). There was, however, variation between groups, particularly during pre-acclimation feeding trials. Food intake during pre-acclimation feeding trials significantly related to beetle species

(MLM: $F_{6,76} = 12.670$, $p = 0.001$), crop type (MLM: $F_{1,66} = 4.132$, $p = 0.001$) and the interactions between beetle species and distance into the crop (MLM: $F_{6,60} = 1.191$, $p = 0.001$), and distance into the crop and crop stage (MLM: $F_{2,58} = 7.469$, $p = 0.027$), but not distance into the crop (MLM: $F_{1,75} = 0.137$, $p = 0.954$; Figure 3), crop stage (MLM: $F_{2,73} = 2.707$, $p = 0.489$; Figure 4), nor the interactions between beetle species and crop stage (MLM: $F_{12,48} = 0.388$, $p = 0.654$) nor crop type and distance into the crop (MLM: $F_{1,47} = 4.473$, $p = 0.156$). These results were driven by significant univariate relationships between independent variables and specific nutrients (Table 1).

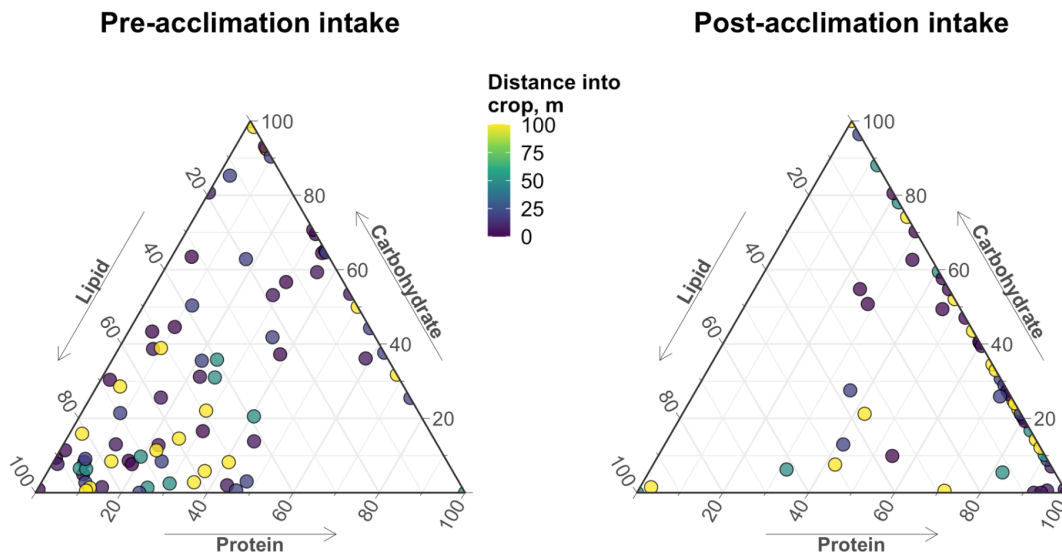


Figure 3: Proportional intake of food rich in carbohydrate, lipid or protein by ground beetles 24 h after collection (left; pre-acclimation) and following one week of ad libitum feeding (right; post-acclimation). Each point denotes the proportional intake of a single beetle. Points are coloured according to the distance into the crop at which the beetle was collected (blue through green to yellow denoting increasing distance).

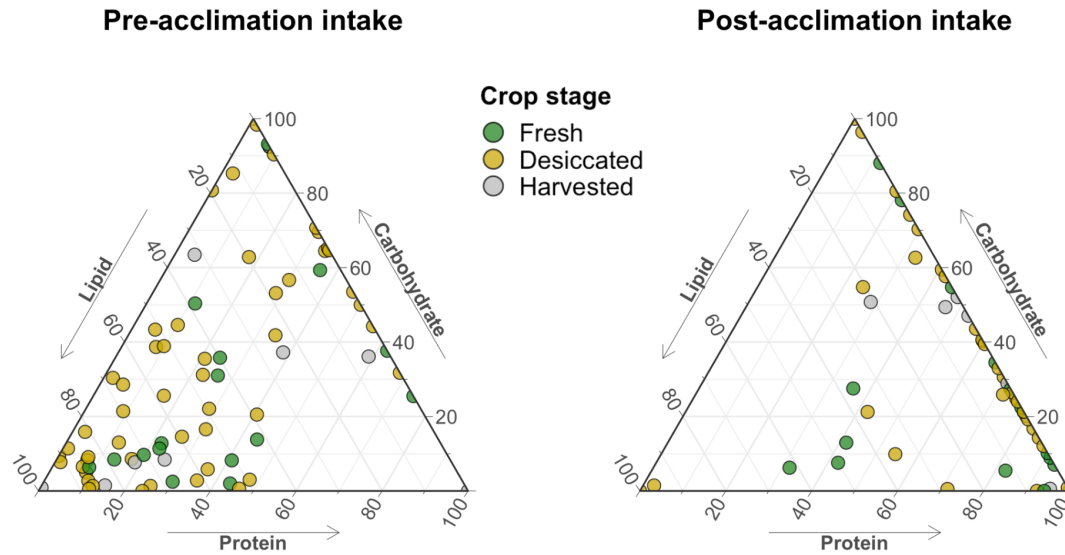


Figure 4: Proportional intake of food rich in carbohydrate, lipid or protein by ground beetles 24 h after collection (left; pre-acclimation) and following one week of ad libitum feeding (right; post-acclimation). Each point denotes the proportional intake of a single beetle. Points are coloured according to the stage of the crop at which the beetle was collected (purple, green and yellow denoting desiccated, fresh and harvested crops, respectively).

Table 1: Univariate results from the four nutritional multivariate linear models generated in this study. Insignificant relationships are given as 'ns'. Marginally insignificant results are given in italics. These results are written in full in Supplementary Information 1.

Model	Variable	Carbohydrate	Lipid	Protein
Pre-acclimation intake	Beetle species	$F_{6,76} = 7.112, p = 0.001$	$F_{6,76} = 3.451, p = 0.035$	$F_{6,76} = 2.108, p = 0.081$
	Crop type	$F_{1,66} = 2.347, p = 0.001$	$F_{1,66} = 1.753, p = 0.001$	$F_{1,66} = 0.032, p = 0.001$
	Beetle species and distance into the crop	$F_{6,60} = 0.637, p = 0.001$	$F_{6,60} = 0.043, p = 0.001$	$F_{6,60} = 0.511, p = 0.001$
	Crop stage and distance into the crop	$F_{2,58} = 2.772, p = 0.073$	$F_{2,58} = 3.190, p = 0.062$	ns
Post-acclimation intake	Crop type	$F_{1,46} = 0.049, p = 0.001$	$F_{1,46} = 2.044, p = 0.001$	$F_{1,46} = 1.697, p = 0.001$
	Beetle species and distance into the crop	$F_{5,41} = 0.017, p = 0.001$	$F_{5,41} = 0.043, p = 0.001$	$F_{5,41} = 0.001, p = 0.001$

Intake difference between pre- and post-acclimation	Beetle species	$F_{5,45} = 9.047, p = 0.001$	$F_{5,45} = 5.525, p = 0.003$	$F_{5,45} = 4.159, p = 0.003$
	Crop type	$F_{1,44} = 0.480, p = 0.001$	$F_{1,44} = 0.876, p = 0.001$	$F_{1,44} = 2.922, p = 0.001$
	Beetle species and distance into the crop	$F_{5,39} = 0.152, p = 0.001$	$F_{5,39} = 0.065, p = 0.001$	$F_{5,39} = 0.005, p = 0.001$
	Beetle species and crop stage	$F_{10,29} = 0.301, p = 0.001$	$F_{10,29} = 0.422, p = 0.001$	$F_{10,29} = 0.188, p = 0.001$
	Crop type and distance into the crop	$F_{1,28} = 0.193, p = 0.001$	$F_{1,28} = 0.117, p = 0.001$	$F_{1,28} = 0.000, p = 0.001$
Beetle nutrient content	Distance into the crop	$F_{1,381} = 18.406, p = 0.001$	$F_{1,381} = 7.225, p = 0.013$	$F_{1,381} = 7.355, p = 0.013$
	Crop stage	$F_{2,379} = 15.286, p = 0.001$	$F_{2,379} = 4.116, p = 0.024$	$F_{2,379} = 4.372, p = 0.024$
	Beetle species	$F_{22,357} = 105.740, p = 0.001$	$F_{22,357} = 29.694, p = 0.001$	$F_{22,357} = 61.528, p = 0.001$
	Crop type	$F_{1,356} = 5.172, p = 0.001$	$F_{1,356} = 8.138, p = 0.001$	$F_{1,356} = 81.125, p = 0.001$
	Beetle species and distance into the crop	$F_{22,334} = 0.689, p = 0.001$	$F_{22,334} = 0.374, p = 0.001$	$F_{22,334} = 0.225, p = 0.001$
	Beetle species and crop stage	ns	$F_{44,290} = 0.828, p = 0.002$	ns
	Crop type and distance into the crop	$F_{1,289} = 4.277, p = 0.001$	$F_{1,289} = 1.665, p = 0.001$	$F_{1,289} = 1.326, p = 0.001$

Nutrient intake during post-acclimation feeding trials significantly related to beetle species (MLM: $F_{5,47} = 7.265, p = 0.046$), crop type (MLM: $F_{1,46} = 3.790, p = 0.001$) and the interaction between beetle species and distance into the crop (MLM: $F_{5,41} = 0.061, p = 0.001$), but not distance into the crop (MLM: $F_{1,54} = 3.007, p = 0.402$; Figure 3), crop stage (MLM: $F_{2,52} = 1.099, p = 0.843$; Figure 4), nor the interactions between beetle species and crop stage (MLM: $F_{10,31} = 0.458, p = 0.623$), crop type and distance into the crop (MLM: $F_{1,30} = 0.004, p = 0.998$), nor and distance into the crop and crop

stage (MLM: $F_{2,39} = 0.175$, $p = 0.979$). These results were driven by significant univariate relationships between independent variables and specific nutrients (Table 1).

The difference in nutrient intake mass between pre-acclimation and post-acclimation feeding trials (Figure 5) significantly related to beetle species (MLM: $F_{5,45} = 18.731$, $p = 0.001$), crop type (MLM: $F_{1,44} = 4.277$, $p = 0.001$; Figure S6), and the interactions between beetle species and distance into the crop (MLM: $F_{5,39} = 0.222$, $p = 0.001$), beetle species and crop stage (MLM: $F_{10,29} = 0.911$, $p = 0.001$) and crop type and distance into the crop (MLM: $F_{1,28} = 0.310$, $p = 0.001$), but not distance into the crop (MLM: $F_{1,52} = 1.212$, $p = 0.676$; Figure S4), crop stage (MLM: $F_{2,50} = 0.671$, $p = 0.921$; Figure S5), nor the interaction between distance into the crop and crop stage (MLM: $F_{2,37} = 0.683$, $p = 0.850$). These results were driven by significant univariate relationships between independent variables and specific nutrients (Table 1).

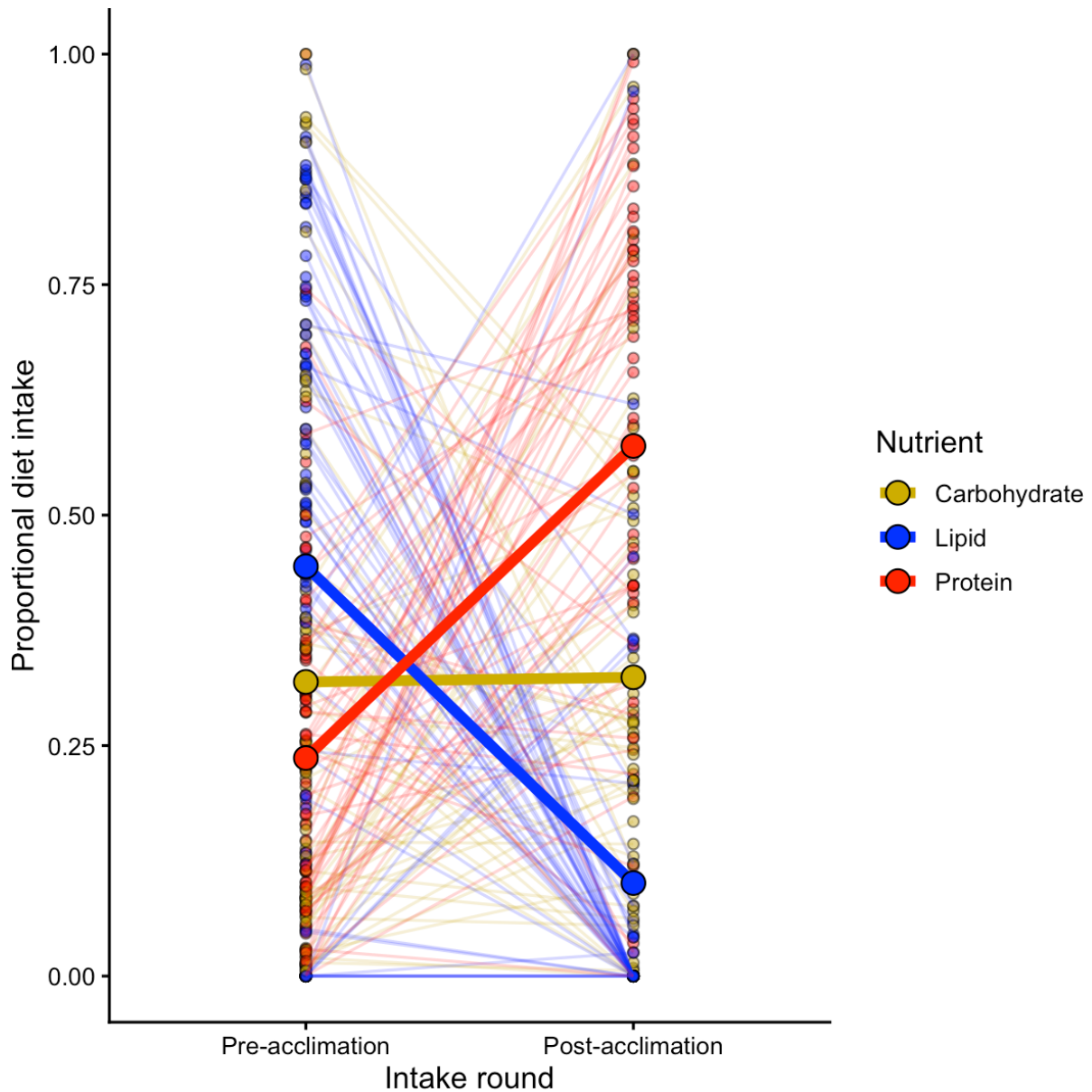


Figure 5: Differences in pre-acclimation and post-acclimation proportional intake of foods rich in carbohydrate (yellow), lipid (blue) and protein (red). Lines join points associated with the same beetle across both feeding trials. Thicker lines and larger points represent mean intake across all beetles. Figures S4, S5 and Figure S6 show the same data separated by distance into the crop, crop stage and crop type, respectively.

Total food intake mass during pre-acclimation feeding assays significantly related to beetle species (GLM: $F_{5,46} = 4.790$, $p = 0.002$), crop type (GLM: $F_{1,45} = 11.454$, $p = 0.002$) and the interaction between beetle species and distance into the crop (GLM: $F_{1,44} = 4.546$, $p = 0.040$), but not the interactions between crop type and distance into the crop (GLM: $F_{1,40} = 0.309$, $p = 0.581$), nor crop stage and distance into the crop

(GLM: $F_{2,38} = 0.706$, $p = 0.500$). Pre-acclimation total food intake did marginally insignificantly relate to distance into the crop (GLM: $F_{1,53} = 4.007$, $p = 0.052$; Figure 6), crop stage (GLM: $F_{2,51} = 2.631$, $p = 0.085$; Figure 6) and the interaction between beetle species and crop stage (GLM: $F_{3,41} = 2.547$, $p = 0.070$). Total food intake mass during post-acclimation feeding assays marginally insignificantly related to crop type (GLM: $F_{1,45} = 3.634$, $p = 0.064$) but not distance into the crop (GLM: $F_{1,53} = 1.908$, $p = 0.175$; Figure 6), crop stage (GLM: $F_{2,51} = 0.229$, $p = 0.796$; Figure 6), beetle species (GLM: $F_{5,46} = 0.926$, $p = 0.475$), nor the interactions between beetle species and distance into the crop (GLM: $F_{1,44} = 0.846$, $p = 0.364$), beetle species and crop stage (GLM: $F_{3,41} = 1.187$, $p = 0.328$), crop type and distance into the crop (GLM: $F_{1,40} = 2.427$, $p = 0.128$), nor crop stage and distance into the crop (GLM: $F_{2,38} = 0.394$, $p = 0.677$).

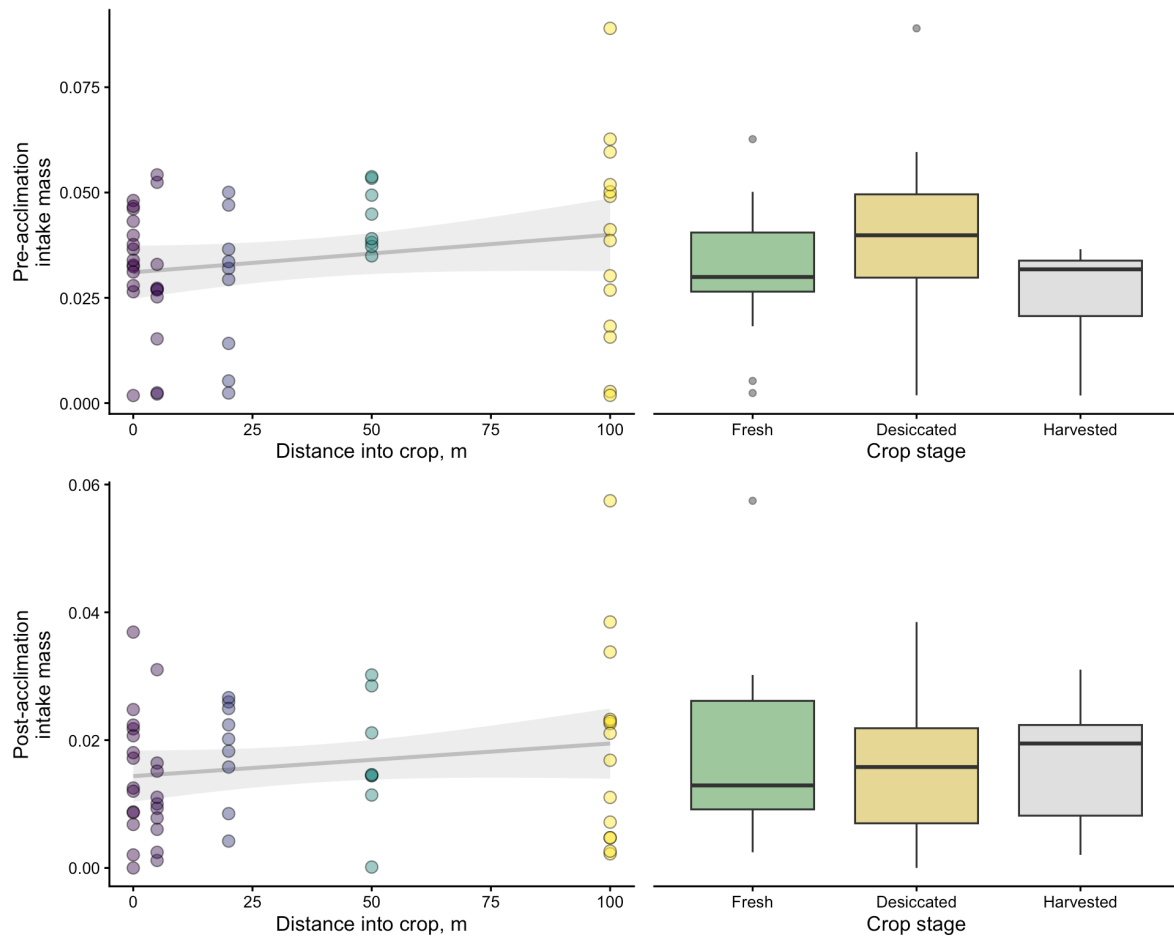


Figure 6: Differences in the total food intake of ground beetles during pre- and post-acclimation feeding trials between beetles taken from different distances into the crop and from different crop stages.

Macronutrient content

Beetle nutrient contents significantly related to distance into the crop (MLM: $F_{1,381} = 32.99$, $p = 0.001$; Figure 7; Figure 8), crop stage (MLM: $F_{2,379} = 23.77$, $p = 0.001$; Figure 7; Figure 8), beetle species (MLM: $F_{22,357} = 196.96$, $p = 0.001$; Figure S7), crop type (MLM: $F_{1,356} = 94.43$, $p = 0.001$) and interactions between distance into the crop and beetle species (MLM: $F_{22,334} = 1.29$, $p = 0.001$), crop stage and beetle species (MLM: $F_{44,290} = 1.35$, $p = 0.003$), and distance into the crop and the crop type (MLM: $F_{1,289} = 7.27$, $p = 0.001$), but not distance into the crop and crop stage (MLM: $F_{2,333} =$

4.55, $p = 0.112$). These results were driven by significant univariate relationships between independent variables and specific nutrients (Table 1).

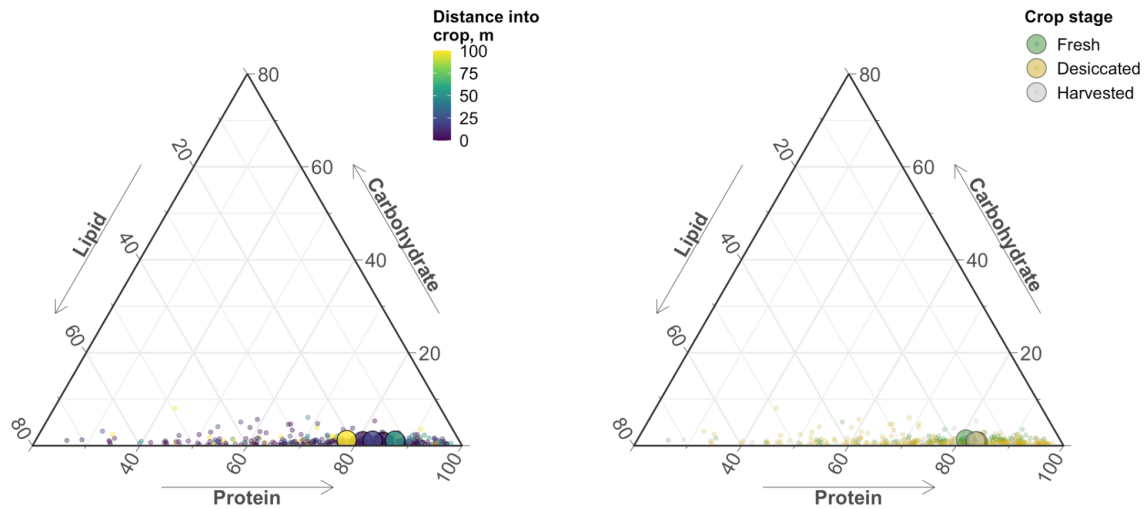


Figure 7: Proportional carbohydrate, lipid and protein content of ground beetles collected at different distances into the crop (left) and at different crop stages (right). Each small point denotes the proportional nutrient content of a single beetle. Each larger, bordered point denotes the mean proportional nutrient content of beetles from a given group. Points are coloured according to the distance into the crop at which the beetle was collected (left; blue through green to yellow denoting increasing distance) or the stage of the crop at which the beetle was collected (right; purple, green and yellow denoting desiccated, fresh and harvested crops, respectively).

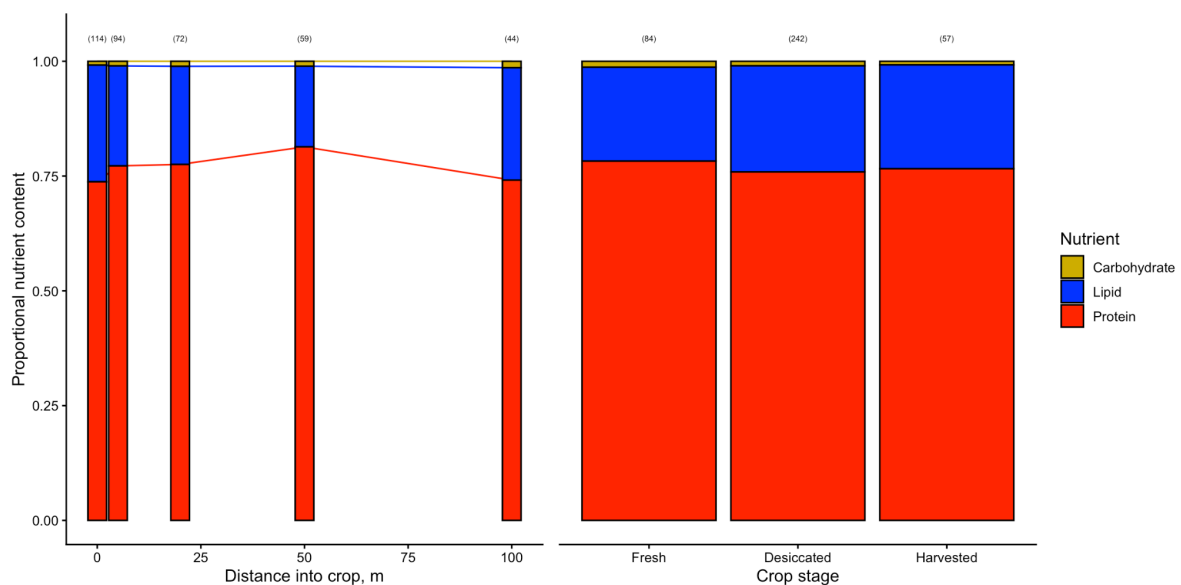


Figure 8: Proportional carbohydrate, lipid and protein content of ground beetles collected at different distances into the crop (left) and at different crop stages (right). Plot elements are coloured according to the nutrient they pertain to (i.e., yellow, blue and red denote carbohydrate, lipid and protein, respectively). Small bracketed numbers above bars display the number of individual beetles represented by that bar. Species are represented in Figure S7.

Discussion

We demonstrate that ground beetle body nutrient contents vary with distance into crop fields and with different stages of crop cycling, notably following harvest. Whilst we provide evidence supporting lipid limitation in ground beetle population feeding across the study, this was not broadly related to distance into the crop alone, other than some species-specific effects, and similarly did not relate to crop stage. Together, these results indicate that the nutritional dynamics of ground beetle communities at different distances into fields may be predominantly driven by differences in community structure, with some species perhaps being better adapted to crop interiors, where resources may be scarcer, lower quality or at least more homogeneous as crops senesce and are harvested.

Nutrient content varies with distance into the crop and crop stage

The difference in ground beetle nutrient content with increasing distance into the crop, and across crop stages, aligns with previous research evidencing nutritional differences across small spatial scales and between crop developmental stages (Christopher et al., 2026). In this case, the variation in nutrient content with distance into the crop appears to be driven primarily by the protein:lipid ratio, with lower lipid content further into the crop, except for the furthest distance included (100 m), where the protein:lipid ratio broadly reflects that of the margin. This trend does, however,

appear to vary between beetle species. The difference in ground beetle communities with distance into the crop may reflect previous results that demonstrate changes in ground beetle diversity with distance into the crop (Neumann & Galpern, 2026). Given the significant interaction between distance into the crop and beetle species, this community turnover may drive the non-linear pattern of nutrient content with distance into the crop. Beetles further into the field may be represented more frequently by species better adapted to seeking specific nutrients in the field interior, or species that are metabolically adapted to resource scarcity.

Importantly, ground beetles are not exclusively predatory, with many being seed predators and otherwise being omnivorous (Charalabidis et al., 2019; Kulkarni et al., 2015; Petit et al., 2014), although most of the species collected are known predators. Even primarily predatory beetles are known to exploit plant resources to obtain specific nutrients, such as sterols, to enhance their fitness and redress deficiencies (Pilorget et al., 2010; Ugine et al., 2020). This opportunistic herbivory can be motivated by poor prey quality (Ugine et al., 2019), which could lead to consumption of crop seeds and tissues (Boetzi & Knapp, 2024; Brygadyrenko & Reshetniak, 2014), but only when crops are available, accessible and digestible. Desiccation and harvest of crops may therefore remove a potential resource from some granivorous or opportunistically herbivorous ground beetles, potentially driving the species-specific effects of crop stage on nutrient content. Equally, some species naturally peak during typical harvest periods, perhaps indicating some adaptation to such conditions, and these species can see enhanced nutritional states and abundances in the presence of field margins (Labruiere et al., 2016).

It is important to note that nutrient contents do not directly relate to nutritional requirements, which can be driven by metabolism, energetic demands and other

variables (Raubenheimer et al., 2007; Wilder et al., 2025; Wilder & Eubanks, 2010). Instead, nutrient contents may mirror nutritional requirements, with lipid-limited individuals likely having low lipid content and a preference for lipid-rich resources. Consequently, whilst these results can indicate a potential paucity of one or more nutrients in a given location, the feeding trials discussed below are a more direct indicator of nutrient limitation. That said, the variation in nutrient contents of ground beetles at different distances into the crop and different crop stages indicates the variable availability of some nutrients to predators of ground beetles, including confamilials through intraguild predation (Davey et al., 2013).

Nutritional niche differences

Our data, demonstrating strong evidence of widespread lipid limitation in ground beetle populations, aligns closely with the findings of Wilder et al. (2013) that arthropod food webs become lipid-limited at higher trophic levels. Predatory arthropods can sometimes extract lipids selectively from their resources, with lipid-rich diets leading to enhanced growth and reproduction (Mayntz & Toft, 2001; Raubenheimer et al., 2007), so this limitation may reflect a paucity of lipids in the prey and wider resources available to these ground beetles. The greater total food intake mass of beetles pre-acclimation similarly supports the notion that beetles were food-limited in the field. The particularly high total food intake mass of beetles from desiccated crops could indicate that crops were particularly resource-poor at this stage. As above, this could relate to the availability of plant resources for opportunistic herbivores or granivores.

Total food intake was higher for beetles taken at intermediate distances into the crop (i.e., 20 m, 50 m), perhaps similarly driven by resource scarcity or, as above, the

presence of poorly adapted generalist species. Importantly, whilst overall food limitation influences specific nutrient limitation, a paucity of high quality prey may have a much stronger effect on nutritional imbalance (Toft et al., 2021). Variation in the nutritional niches of different beetle species (Toft et al., 2019) will also have a profound impact on the ability of different predators to persist in habitat patches with different assemblages of available resources. When considering nutrient limitation, it is important to note that generalisations about predator nutrition are often inaccurate (Wilder & Eubanks, 2010). Importantly, life history traits, such as sex, can have important implications for nutritional requirements and preferences (Cuff, Tercel, et al., 2024), but were not considered here and could explain some variation to the results.

The difference in results between pre-acclimation and post-acclimation feeding trials, other than demonstrating a consistent inversion from lipid-seeking to protein-seeking across groups, nicely demonstrated the aforementioned lipid limitation. The nutrient intake during the post-acclimation feeding trials did, however, still significantly relate to specific beetle groups. This could indicate longer term nutritional imbalances in some groups, potentially driven by the transcriptome or epigenome of those individuals (Costa et al., 2020; Jones et al., 2023). Equally, this could indicate that the acclimation was ineffective in some individuals. Acclimation was carried out with *ad libitum* dried mealworms, may have equilibrated diets between beetles to some degree, but might not have redressed nutritional deficiencies fully. Most of the data do, however, indicate that this experimental approach was successful in identifying nutrient limitation.

Management implications

Our findings, particularly those related to beetle nutrient content, indicate that the spillover of nutrients and nutritionally supplemented ground beetles from field margins may be relatively modest, and may be restricted to the crop immediately adjacent to field margins. These margins may, however, allow otherwise poorly adapted species to persist further into crops than might otherwise be the case, even if they do so in a suboptimal state of nutrition. Indeed, generalist predators are thought to exist mostly in a suboptimal state of nutrition (Symondson et al., 2002), which may motivate predation of crop pests through nutrient-specific foraging (Cuff, Tercel, et al., 2024).

The structural complexity of field margins can be an important determinant of beetle diversity and spillover into crops (Neumann & Galpern, 2026), although some studies report little difference between margin types on ground beetle communities (Jowett et al., 2024). While the focal margins of this study were relatively simple grass strips, future studies could compare results across a gradient of margin complexity, especially given the emergence of increasingly accessible methods for vegetation complexity measurement (Erland et al., 2026). Although in-field semi-natural habitat strips, such as ‘beetle banks’ do not always provide a comparable diversity of natural enemies (Thomas et al., 2002), they could provide sufficient habitat continuity to support a greater provision of nutrients to in-field populations of natural enemies (MacLeod et al., 2004). This could similarly be true of intercropping or strip cropping, which similarly maintain natural enemy populations within crop fields (Cuperus et al., 2024). Some studies, however, report a negative impact of margins on in-field abundances of some ground beetles (e.g., larvae; Jowett et al., 2024), so careful consideration and validation of any wider impacts may be beneficial.

Conclusions

We show that broadly lipid-limited ground beetle populations have nutrient contents that vary with distance into crop fields and crop stage. The nutritional dynamics of ground beetle communities appear to be driven, at least in part, by community turnover over spatial gradients, with nutritional requirements and the ability of beetles to meet them in sometimes suboptimal habitat patches varying between species. Nutrient intake substantially impacts overwintering success (Knapp & Uhnová, 2014), reproduction (Macartney et al., 2019) and competition (Lenski, 1984), rendering the nutrition of natural enemies of crop pests vital for the provision of biocontrol. By expanding our understanding of arthropod predator nutrition to the flow of nutrients through ecosystems and across spatial gradients, we could enhance our understanding of the resilience of arable arthropod communities (Cuff, Evans, et al., 2024) and the services they provide.

Author contributions

Annabel Smyth: conceptualisation; funding acquisition; data curation; formal analysis; investigation; methodology; visualisation; writing - original draft; writing - review and editing. Raul Costa-Pereira: investigation; writing - review and editing. Mia Croft: investigation; methodology; writing - review and editing. Jordan P. Cuff: conceptualisation; supervision; funding acquisition; data curation; formal analysis; investigation; methodology; visualisation; writing - original draft; writing - review and editing.

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Data availability

All data are openly available via Zenodo: <https://doi.org/10.5281/zenodo.23242041>

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Supplementary Information 1: Univariate test results

Nutritional feeding assays: pre-acclimation intake

The intake of carbohydrate-rich food in the pre-acclimation feeding trials specifically significantly related to beetle species (MLM: $F_{6,76} = 7.112$, $p = 0.001$), crop type (MLM: $F_{1,66} = 2.347$, $p = 0.001$) and the interaction between beetle species and distance into the crop (MLM: $F_{6,60} = 0.637$, $p = 0.001$), and marginally insignificantly related to the interaction between distance into the crop and crop stage (MLM: $F_{2,58} = 2.772$, $p = 0.073$). The intake of lipid-rich food in the pre-acclimation feeding trials specifically significantly related to beetle species (MLM: $F_{6,76} = 3.451$, $p = 0.035$), crop type (MLM: $F_{1,66} = 1.753$, $p = 0.001$) and the interaction between beetle species and distance into the crop (MLM: $F_{6,60} = 0.043$, $p = 0.001$), and marginally insignificantly related to the interaction between distance into the crop and crop stage (MLM: $F_{2,58} = 3.190$, $p = 0.062$). The intake of protein-rich food in the pre-acclimation feeding trials specifically significantly related to crop type (MLM: $F_{1,66} = 0.032$, $p = 0.001$) and the interaction between beetle species and distance into the crop (MLM: $F_{6,60} = 0.511$, $p = 0.001$), and marginally insignificantly related to beetle species (MLM: $F_{6,76} = 2.108$, $p = 0.081$).

Nutritional feeding assays: post-acclimation intake

The intake of carbohydrate-rich food in the post-acclimation feeding trials specifically significantly related to crop type (MLM: $F_{1,46} = 0.049$, $p = 0.001$) and the interaction between beetle species and distance into the crop (MLM: $F_{5,41} = 0.017$, $p = 0.001$). The intake of lipid-rich food in the post-acclimation feeding trials specifically significantly related to crop type (MLM: $F_{1,46} = 2.044$, $p = 0.001$) and the interaction between beetle species and distance into the crop (MLM: $F_{5,41} = 0.043$, $p = 0.001$). The intake of protein-rich food in the post-acclimation feeding trials specifically significantly related to crop type (MLM: $F_{1,46} = 1.697$, $p = 0.001$) and the interaction between beetle species and distance into the crop (MLM: $F_{5,41} = 0.001$, $p = 0.001$).

Nutritional feeding assays: intake difference between pre- and post-acclimation

The difference in carbohydrate intake specifically significantly related to beetle species (MLM: $F_{5,45} = 9.047$, $p = 0.001$), crop type (MLM: $F_{1,44} = 0.480$, $p = 0.001$), and the interactions between beetle species and distance into the crop (MLM: $F_{5,39} = 0.152$, $p = 0.001$), beetle species and crop stage (MLM: $F_{10,29} = 0.301$, $p = 0.001$) and crop type and distance into the crop (MLM: $F_{1,28} = 0.193$, $p = 0.001$). The difference in lipid intake specifically significantly related to beetle species (MLM: $F_{5,45} = 5.525$, $p = 0.003$), crop type (MLM: $F_{1,44} = 0.876$, $p = 0.001$), and the interactions between beetle species and distance into the crop (MLM: $F_{5,39} = 0.065$, $p = 0.001$), beetle species and crop stage (MLM: $F_{10,29} = 0.422$, $p = 0.001$) and crop type and distance into the crop (MLM: $F_{1,28} = 0.117$, $p = 0.001$). The difference in protein intake specifically significantly related to beetle species (MLM: $F_{5,45} = 4.159$, $p = 0.003$), crop type (MLM: $F_{1,44} = 2.922$, $p = 0.001$), and the interactions between beetle species and distance into the crop (MLM: $F_{5,39} = 0.005$, $p = 0.001$), beetle species and crop stage (MLM: $F_{10,29} = 0.188$, $p = 0.001$) and crop type and distance into the crop (MLM: $F_{1,28} = 0.000$, $p = 0.001$).

Beetle nutrient content

Carbohydrate content specifically significantly related to distance into the crop (MLM: $F_{1,381} = 18.406$, $p = 0.001$; Figure 7; Figure 8), crop stage (MLM: $F_{2,379} = 15.286$, $p =$

0.001; Figure 7; Figure 8), beetle species (MLM: $F_{22,357} = 105.740$, $p = 0.001$; Figure S7), crop type (MLM: $F_{1,356} = 5.172$, $p = 0.001$), and interactions between distance into the crop and beetle species (MLM: $F_{22,334} = 0.689$, $p = 0.001$), and distance into the crop and the crop type (MLM: $F_{1,289} = 4.277$, $p = 0.001$).

Lipid content specifically significantly related to distance into the crop (MLM: $F_{1,381} = 7.225$, $p = 0.013$; Figure 7; Figure 8), crop stage (MLM: $F_{2,379} = 4.116$, $p = 0.024$; Figure 7; Figure 8), beetle species (MLM: $F_{22,357} = 29.694$, $p = 0.001$; Figure S7), crop type (MLM: $F_{1,356} = 8.138$, $p = 0.001$), and interactions between distance into the crop and beetle species (MLM: $F_{22,334} = 0.374$, $p = 0.001$), crop stage and beetle species (MLM: $F_{44,290} = 0.828$, $p = 0.002$), and distance into the crop and the crop type (MLM: $F_{1,289} = 1.665$, $p = 0.001$).

Protein content specifically significantly related to distance into the crop (MLM: $F_{1,381} = 7.355$, $p = 0.013$; Figure 7; Figure 8), crop stage (MLM: $F_{2,379} = 4.372$, $p = 0.024$; Figure 7; Figure 8), beetle species (MLM: $F_{22,357} = 61.528$, $p = 0.001$; Figure S7), crop type (MLM: $F_{1,356} = 81.125$, $p = 0.001$), and interactions between distance into the crop and beetle species (MLM: $F_{22,334} = 0.225$, $p = 0.001$), and distance into the crop and the crop type (MLM: $F_{1,289} = 1.326$, $p = 0.001$).

Table S1: Artificial diet mixture and ingredient compositions. Nutrient compositions for specific ingredients were derived from product information for these or directly comparable products.

Component	Carbohydrate (%)	Lipid (%)	Protein (%)	Source
Dried mealworms	1.8	28.0	53.0	Chubby Mealworms
Casein	0.1	1.0	89.4	Sigma-Aldrich
Lard oil	0.0	99.7	0.0	Sigma-Aldrich
Dextrin from potato starch	95.5	0.0	0.0	Sigma-Aldrich
Caster sugar	100.0	0.0	0.0	Marks & Spencer
High carbohydrate diet	49.8	14.0	26.5	50% dried mealworms, 25% caster sugar, 25% dextrin
High lipid diet	0.9	63.9	26.5	50% dried mealworms, 50% lard oil
High protein diet	1.0	14.5	71.2	50% dried mealworms, 50% casein



Figure S1: High resolution charged coupled device scan of beetles included in the feeding trials, collected during the first round of surveys.



Figure S2: High resolution charged coupled device scan of beetles included in the feeding trials, collected during the second round of surveys.

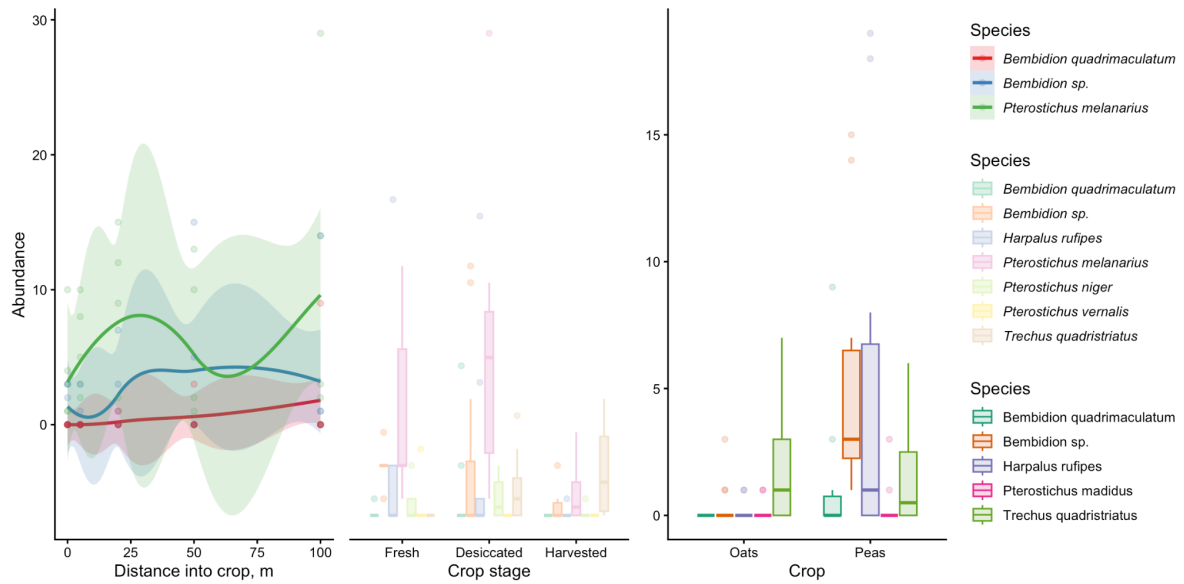


Figure S3: The abundance of ground beetles in relation to distance into the crop (left), crop stage (centre) and crop (right). Only species for which abundance had a significant relationship to each variable in the multivariate generalised linear model reported in the main text are shown.

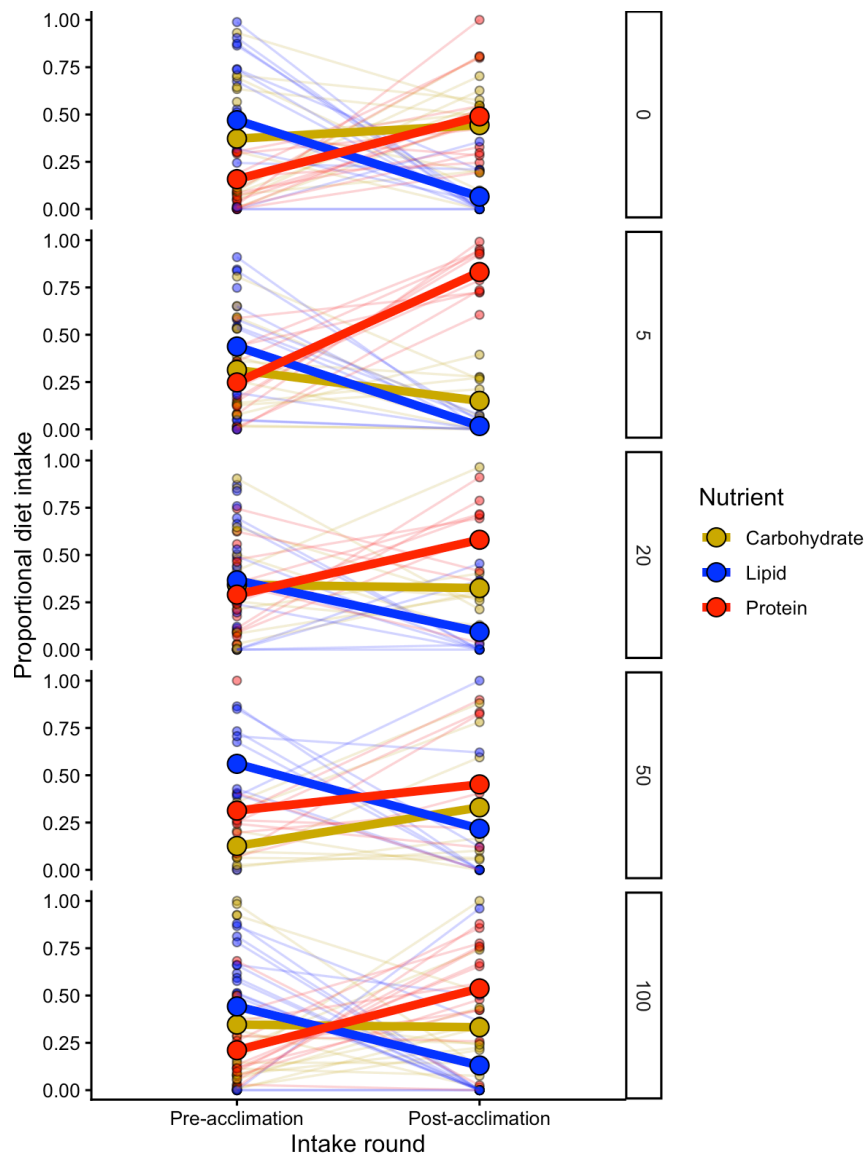


Figure S4: Differences in pre-acclimation and post-acclimation proportional intake of foods rich in carbohydrate (yellow), lipid (blue) and protein (red) for beetles collected at different distances into the crop. Distances are given on the right of the plot in metres. Lines join points associated with the same beetle across both feeding trials. Thicker lines and larger points represent mean intake across beetles at each distance. Figure 5 shows the same data together for all distances and Figures S5 and S6 show the same data separated by crop stage and crop type, respectively.

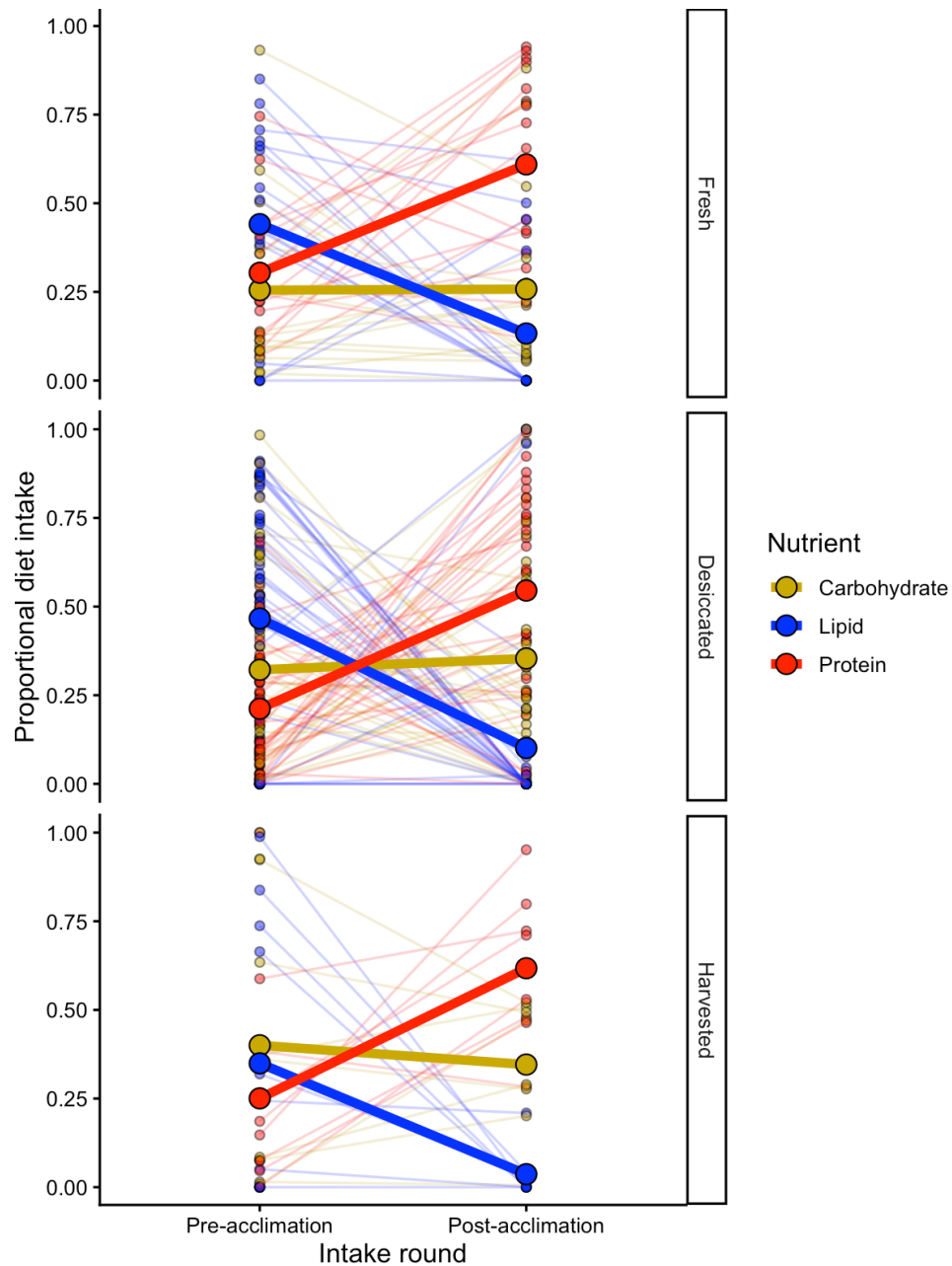


Figure S5: Differences in pre-acclimation and post-acclimation proportional intake of foods rich in carbohydrate (yellow), lipid (blue) and protein (red) for beetles collected from crops at different stages. Crop stages are given on the right of the plot. Lines join points associated with the same beetle across both feeding trials. Thicker lines and larger points represent mean intake across beetles at each crop stage. Figure 5 shows the same data together for all distances and Figures S4 and S6 show the same data separated by distance into the crop and crop type, respectively.

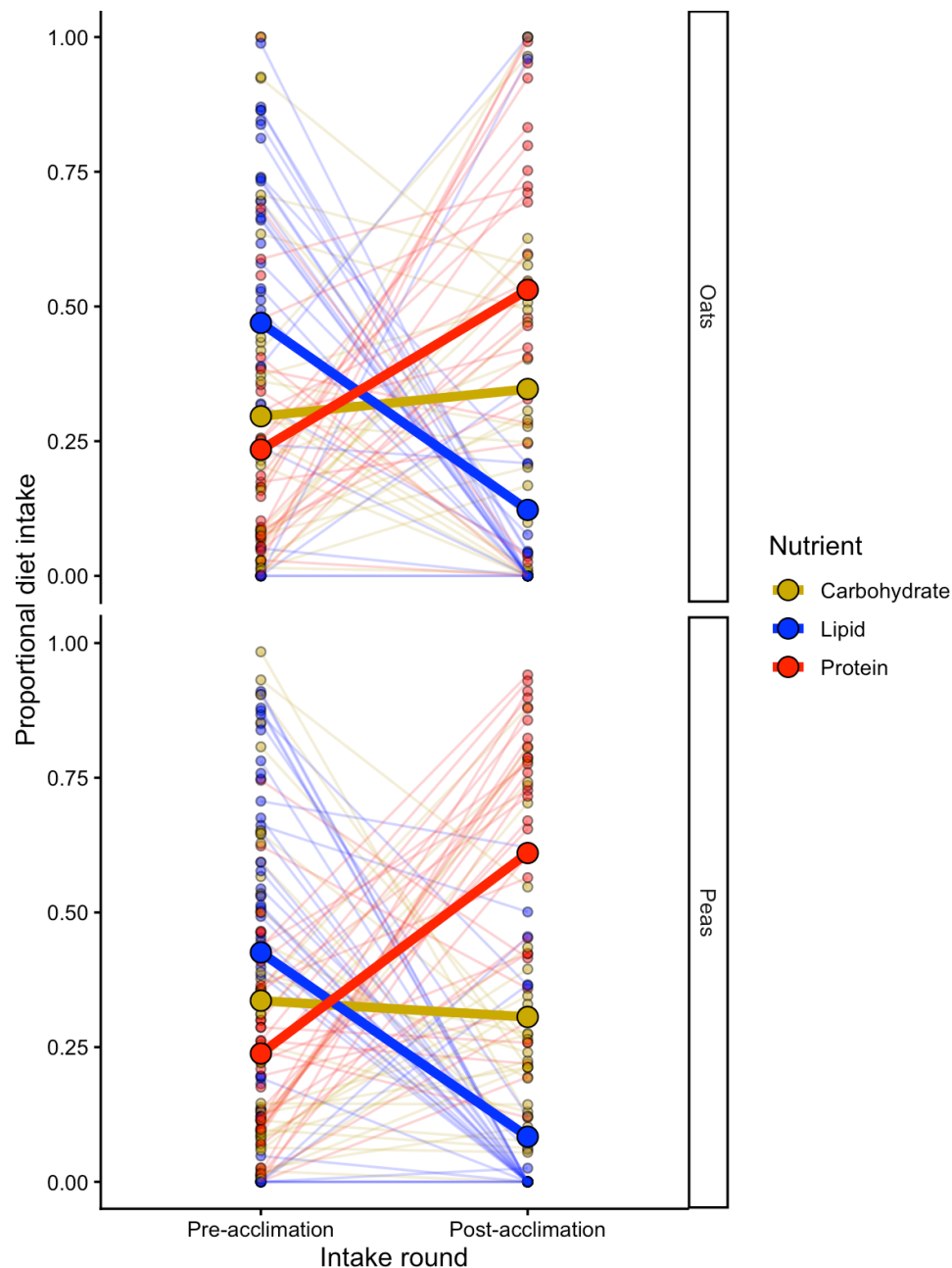


Figure S6: Differences in pre-acclimation and post-acclimation proportional intake of foods rich in carbohydrate (yellow), lipid (blue) and protein (red) for beetles collected from different crops. Crops are given on the right of the plot. Lines join points associated with the same beetle across both feeding trials. Thicker lines and larger points represent mean intake across beetles at each crop stage. Figure 5 shows the same data together for all distances and Figures S4 and S5 show the same data separated by distance into the crop and crop stage, respectively.

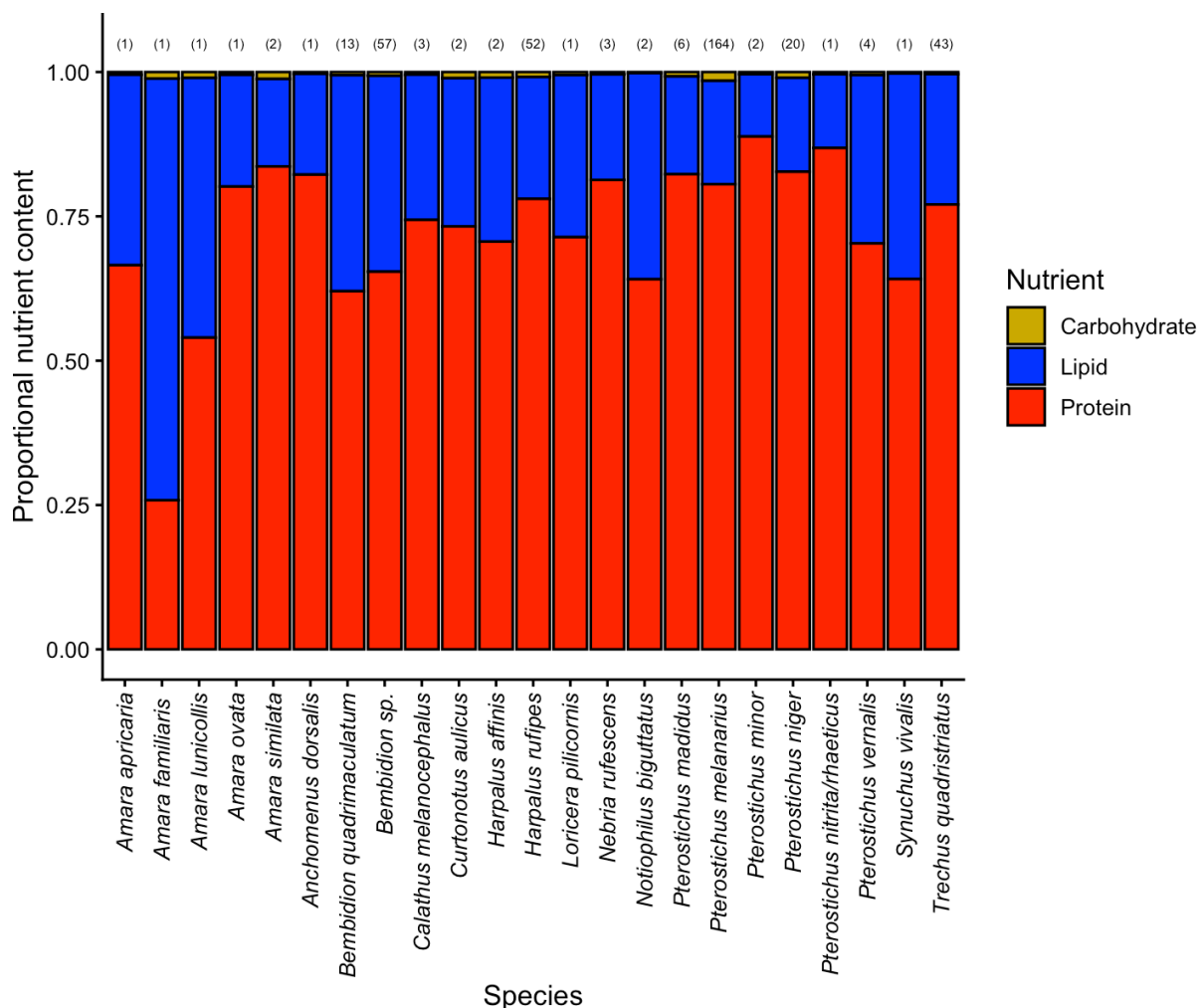


Figure S7: Proportional carbohydrate, lipid and protein content of different ground beetle species collected in the study. Bars are coloured according to the nutrient they pertain to (i.e., yellow, blue and red denote carbohydrate, lipid and protein, respectively). Small bracketed numbers above bars display the number of individual beetles represented by that bar. Figure 8 shows the same data separated by distance into the crop and crop stage.