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House crickets in circular food systems

From crop residue diets to frass-based farming

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Cover: Photo of the house cricket (*Acheta domesticus*). Image by Florian Denis, iStock. Licensed under standard agreement (2025).

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Abstract

Many elements in current food production are unsustainable, while population growth and increased meat consumption will further intensify food demands. Circular food systems offer a more sustainable model for food production by recycling organic residual streams from the food supply chain and promoting resource efficiency. Edible insect species can efficiently convert residual streams into protein and frass (a by-product made of faeces, shed exoskeletons, and leftover feed), making them ideal for circular food systems. This thesis examines how house crickets (*Acheta domesticus*) and their by-product, frass, can be integrated into circular food systems. In **Paper I**, the scientific literature on edible insects in circular food systems is reviewed, and key ecological knowledge gaps are identified. In **Paper II**, building on this conceptual overview, the performance of house crickets reared on crop residues from pea and tomato were assessed. Growth and final weights were reduced under both crop residue diets; however, a significant decline in survival was observed only in tomato residue. The quantity and mineral nutrient composition of frass also differed by diet type. In **Paper III**, the effects of house cricket frass on the vegetative growth and nutrient concentration of spring wheat (*Triticum aestivum*) were evaluated under different frass pre-treatments and application methods. The tallest plants were produced when non-heated frass was mixed into the substrate, the highest shoot biomass resulted from surface application, and the greatest leaf chlorophyll content was observed with delayed application. Nutrient uptake also varied by pre-treatment and application method. Finally, in **Paper IV**, the role of frass-associated microbial communities on spring wheat performance and aphid population growth was explored. While herbivory had the strongest impact on seedling growth, unsterile frass slightly improved root biomass and leaf chlorophyll content under aphid pressure. Aphid populations were generally lower on plants grown with sterile frass. Frass and aphid treatments also shaped the rhizosphere bacterial community, indicating that frass microbes can influence soil microbiota dynamics. Together, the findings highlight the potential of house crickets to transform crop residues into food and frass in circular food systems.

Keywords: *Acheta domesticus*, edible insects, insect frass, insect residual streams

Hussyrsor i cirkulära livsmedelssystem: Från dieter baserade på grödorester till frasbaserat jordbruk

Sammanfattning

Många inslag i dagens livsmedelsproduktion är ohållbara, och befolkningstillväxt samt ökad köttkonsumtion förväntas ytterligare öka efterfrågan på mat. Cirkulära livsmedelssystem erbjuder en mer hållbar modell för livsmedelsproduktion genom att återvinna organiska restströmmar och främja resurseffektivitet. Ätbara insektsarter, som hussyrsa (*Acheta domesticus*), omvandlar effektivt organiska restströmmar till protein och frass (en näringsrik biprodukt), vilket gör dem idealiska för cirkulära livsmedelssystem. Denna avhandling undersöker hur hussyrsor och deras frass kan bidra till cirkulära livsmedelssystems funktion och hållbarhet. I **Paper I** granskas den vetenskapliga litteraturen om ätbara insekter i cirkulära livsmedelssystem och viktiga kunskapsluckor i deras ekologiska integration identifieras. I **Paper II**, som bygger vidare på denna konceptuella översikt, utvärderas hussyrsors tillväxt och överlevnad vid uppfödning på ärt- och tomatrester. Tillväxten och slutvikterna var lägre på båda restdieterna, men en signifikant minskning av överlevnaden observerades endast vid tomatrester. Mängden och näringssammansättningen av frass varierade också mellan olika dieter. I **Paper III** utvärderades effekterna av hussyrsefrass på vegetativ tillväxt och näringsupptag hos vårvete (*Triticum aestivum*) under olika frassbehandlingar och appliceringsmetoder. De högsta plantorna erhölls när obehandlad frass blandades in i substratet, den största skottbiomassan vid ytapplicering, och det högsta klorofyllinnehållet i blad vid fördröjd applicering. Näringsupptaget varierade också med behandling och appliceringsmetod. Slutligen undersöktes i **Paper IV** frass-associerade mikrobiellas roll i vårvetets tillväxt och bladluspopulationers dynamik. Även om herbivori hade störst påverkan på planttillväxten, förbättrade osteriliserad frass något rotbiomassa och bladklorofyllinnehåll under bladlustryck. Bladluspopulationer var generellt lägre på plantor odlade med steril frass. Frass- och bladlusbehandlingarna påverkade också rhizosfärens bakteriesamhällen, vilket tyder på att frassmikrober kan påverka markens mikrobiotadynamik.

Nyckelord: *Acheta domesticus*, ätbara insekter, insektsfrass, insekters restströmmar

Grillos domésticos en sistemas alimentarios circulares: de dietas basadas en residuos de cultivo a la agricultura basada en frass

Resumen

Muchos aspectos de la producción alimentaria actual son insostenibles, y el crecimiento de la población y el consumo de carne aumentarán aún más la demanda de alimentos. Los sistemas alimentarios circulares, que reciclan residuos orgánicos y promueven la eficiencia en el uso de los recursos, ofrecen un modelo más sostenible. Los grillos (*Acheta domesticus*) convierten eficientemente los residuos orgánicos en proteína y frass rico en nutrientes, lo que los hace muy adecuados para estos sistemas. Esta tesis examina su contribución a los sistemas alimentarios circulares. El **Artículo I** revisa la literatura e identifica vacíos clave en la integración ecológica de los insectos comestibles. El **Artículo II** muestra que los grillos alimentados con residuos de cultivo de arveja y tomate presentaron menor crecimiento y peso final, con una supervivencia significativamente menor solo en residuos de tomate. La cantidad y composición nutricional del frass también varió según la dieta. El **Artículo III** demuestra que el pretratamiento y el método de aplicación del frass afectaron el crecimiento del trigo (*Triticum aestivum*): las plantas más altas crecieron con frass no tratado mezclado en el sustrato, la mayor biomasa aérea se logró con aplicación superficial y la mayor concentración de clorofila foliar se obtuvo con aplicación retardada. La absorción de nutrientes también varió según el tratamiento. En el **Artículo IV**, se encontró que los microbios asociados al frass influyeron en el crecimiento del trigo y la dinámica de los pulgones: el frass no estéril mejoró ligeramente la biomasa radicular y el contenido de clorofila bajo presión de pulgones, y las poblaciones de pulgones fueron menores en plantas con frass estéril. Los tratamientos con frass y pulgones también modificaron la microbiota de la rizosfera. En conjunto, estos estudios amplían nuestra comprensión sobre cómo los insectos comestibles y sus subproductos pueden contribuir a los sistemas alimentarios circulares.

Palabras clave: *Acheta domesticus*, insectos comestibles, frass de insectos, flujos residuales de insectos

Preface

Envisioning insect integration

Imagine this: You enter a grocery store. One entire aisle is now devoted to affordable and nutritious insect products—whole roasted insects, protein-rich powders, and insect oils. Even your favourite brand of snacks now features options with insect-based ingredients. In the produce aisle, you choose from vegetables and fruits grown with frass, a by-product of insect production. In the meat section, labels on chicken, pork, and fish proudly note: “insect-fed.”

Back home, you prepare dinner. You sauté potatoes—grown with frass—in insect oil with rosemary and salt. You sear an insect-fed chicken thigh with honey, lemon, and garlic. You toss a summer salad and sprinkle it with whole roasted crickets, which add a pleasant crunch and a nutty, almond-like flavour. For dessert: pound cake made with mealworm powder. After dinner, your food scraps go into an organic waste bin—waste that will be used as feed for insects, which in turn helps to produce more food, livestock feed, and agricultural inputs.

By consuming insect-based products, plants grown with frass, or animal products raised on insect feed, you are participating in a circular food system—one that reduces biological waste and supports sustainable crop and livestock production. This future is within reach—and through interdisciplinary research, advocacy, and openness to change, we can make it happen.

Dedication

For Lena.

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Berggren Å & **Capitán S**. Unlocking the potential for insects in circular food systems: paths for future research. (submitted)

II. **Capitán S**, Berggren, Å. Crop residues as feed for house crickets: Impacts on growth, survival, and frass quality. (submitted)

III. **Capitán S**, Berggren, Å. and Weih, M. (2025). Frass pre-treatment and application method impact spring wheat vegetative growth and nutrient concentration. *Journal of Insects as Food and Feed* (published online ahead of print 2025). https://doi.org/10.1163/23524588-bja10245

IV. **Capitán S**, Berggren Å, Weih M., Smith M. Microbial and nutrient contributions of *Acheta domesticus* frass to wheat performance and aphid population growth. (manuscript)

Paper III is published open access.

The contribution of Sara Capitán to the papers included in this thesis was as follows:

I. **Co-author**. Contributed to the review and editing of the final draft.

II. **Main author**. Conducted the experiment, collected data, contributed to analysis, and wrote the manuscript.

III. **Main author**. Contributed to experimental design, conducted the experiment, collected data, performed the analysis, and wrote the manuscript.

IV. **Main author**. Contributed to experimental design, conducted the main experiment (wheat growth, aphid counts, and harvest), participated in statistical analysis (half), and wrote the manuscript.

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Abbreviations

N	Total nitrogen
P	Phosphorus
K	Potassium
Mg	Magnesium
Ca	Calcium
Na	Sodium

1. Background

1.1 Challenges of current food systems

Many elements in current food production practices are unsustainable, with serious consequences for both environmental and human health. Much of these impacts stem from how we produce food, which largely depends on intensive, large-scale production of crops and vertebrate livestock. Intensive crop production practices—like monocropping and overuse of synthetic fertilisers, herbicides, and pesticides—accelerate land degradation by depleting soil organic matter, disturbing microbial communities, and increasing vulnerability to soil erosion (Bai et al. 2018; Ouyang & Norton 2020). These practices also contribute significantly to biodiversity loss by homogenizing landscapes, fragmenting habitats critical for wildlife, and harming beneficial organisms like pollinators and soil fauna (de Graaff et al. 2019; Raven & Wagner 2021). This makes crop production harder, as soil fertility and biodiversity support essential ecosystem services—such as pollination, nutrient cycling, and pest regulation—that directly affect crop productivity (Lanz et al. 2018).

Vertebrate livestock rearing (e.g., cattle, poultry, pigs) amplify these challenges. Livestock rearing contributes heavily to climate change through methane emissions from enteric fermentation by ruminants and nitrous oxide emissions from manure and slurry management (Herrero et al. 2016). Livestock rearing practices—characterised by high densities of genetically similar animals in confined spaces—also facilitates the spread and evolution of pathogens, while the widespread use of antibiotics, especially for non-therapeutic uses (e.g., as growth promoters), enables the development of antibiotic resistance (Mathew et al. 2007; Espinosa et al. 2020). Furthermore, feed production for livestock (e.g., soy and grain) competes for land, water, and nutrients that could otherwise support food production for humans while exacerbating ecosystem degradation through deforestation and land use change (Mottet et al. 2017; Grossi et al. 2019; Bidoglio et al. 2024).

Compounding these environmental pressures, the food supply chain—a system encompassing agricultural production, storage, processing, distribution, consumption, and post-consumer disposal—generates vast amounts of organic waste[1], with 1.3 billion tonnes of food, or one-third of all food produced, lost annually (FAO 2011). This includes organic wastes such as unharvested produce, food processing leftovers like fruit peels and brewers' spent grain, spoiled food during transport, and household food scraps. Such waste represents lost resources and contributes to environmental degradation through carbon dioxide emissions from production and transport, air pollution from incineration, and methane release from anaerobic decomposition in landfills. It can also contaminate water sources through runoff and leaching, particularly when organic waste is mismanaged (Griffin et al. 2009; Thakali & MacRae 2021).

To make matters worse, the global population is projected to approach 10 billion by 2050, requiring substantial increases in food production to meet rising demand (FAO 2017). Additionally, urbanization and the increase of global incomes are shifting dietary preferences towards higher meat consumption, further intensifying pressure on agricultural and environmental resources (Thornton 2010; Tilman & Clark 2014). However, increasing food production through conventional methods would only worsen current problems with food production and waste generation. To meet the growing demand for food without further straining the environment, we must adopt more sustainable food production practices and explore alternative food sources. One promising solution is the use of insects as food.

1.2 Insects as food and feed

Insects have long played a vital role in food chains, serving as a primary food source for many insectivorous animals. Humans, too, have historically incorporated insects into their diets, and today, insects are still consumed in many parts of the world (Pal & Roy 2014). However, it is likely most humans have consumed insects at some point in their lives, as it is costly and nearly impossible to completely remove insects and their parts (eggs, fragments, etc.) from food. Furthermore, insects and their derivatives are routinely incorporated into various food products, medicines, and cosmetics without

[1] In this thesis, *waste* refers to discarded materials with no planned reuse. While this term reflects the typical fate of such materials, in later sections I refer to the same material as by-products and organic residual streams to emphasize differences in reuse potential. These distinctions are often context- and policy-dependent, highlighting the variability in how such materials are classified and managed.

much notice. For example, cochineal insects (*Dactylopius coccus*) produce carmine, a common red food colouring used in beverages and cosmetics, and shellac—derived from lac insects (*Kerria lacca*)—is commonly applied as a shiny coating on candies, pills, and even fruits (Yuan et al. 2021; Roque-Rodríguez 2022). But don't let this bother you, as eating insects can have a lot of great benefits.

Many insects are safe to eat. In fact, commercial insect production in the European Union is regulated under the same hygiene and safety standards that apply to other forms of animal farming, ensuring they are safe for human consumption. As of May 2025, the European Union has approved four insect species for human consumption: the house cricket (*Acheta domesticus*), migratory locust (*Locusta migratoria*), yellow mealworm (*Tenebrio molitor*), and buffalo mealworm (*Alphitobius diaperinus*) (Meijer et al. 2025). The feed given to insects reared for human consumption is generally restricted to plant-derived materials, with limited allowances for certain animal-derived ingredients (European Comission 2017). Insects are also a safe feed option for certain livestock species (i.e., poultry, pigs, and aquaculture) as they align with the animals' natural diets and help fulfil nutritional requirements. Approved insect species for livestock feed include: the black soldier fly (*Hermetia illucens*), common housefly (*Musca domestica*), yellow mealworm (*Tenebrio molitor*), buffalo mealworm (*Alphitobius diaperinus*), house cricket (*Acheta domesticus*), banded cricket (*Gryllodes sigillatus*), Jamaican field cricket (*Gryllus assimilis*), and the silkworm (*Bombyx mori*) (Meijer et al. 2025). Together, these approvals ensure insects are safe for human consumption—either directly as food or indirectly through the livestock we eat.

Insects are not only safe to eat, but also highly nutritious, offering a rich source of protein, fats, vitamins, and minerals (Oonincx & Finke 2021). The nutrients of edible insects are even comparable to meat products. For example, a 100 g portion of adult house crickets (*Acheta domesticus*) provides 20.5 g of protein, 5.06 g of fat, and 4.6 g of dietary fiber, while the same amount of beef sirloin contains slightly less protein (20.1 g) and fat (3.5 g) and lacks dietary fiber entirely (Orkusz 2021). Insects also offer unique flavour profiles that can vary across species, development stage, rearing methods (e.g., feed type), and preparation, with some insect flavours described as nutty, earthy, or umami-rich (Perez-Santaescolastica et al. 2022). Insects are an incredibly versatile food source: they can be eaten whole, roasted, or processed into powders[2] (Figure 1), oils, protein concentrates, or fermented products—which can further manipulate their flavour profile and makes them easy to integrate into a wide range of foods. For example, insect-fortified products like protein bars, chocolate, pasta, chips, beer, and sausage are already commercially available.

Figure 1: Cricket powder and whole crickets (*Gryllus bimaculatus*) as an edible protein product. Image sourced from iStock (Image ID: 1084970646) under a standard licensing agreement.

Emerging research also suggests that edible insects may offer additional health benefits. For example, chitin (a main component of insect exoskeletons) may serve as a source of dietary fiber with prebiotic potential, promoting beneficial bacteria in the human gut microbiome, such as *Bifidobacterium* and *Lactobacillus*, while also exhibiting antimicrobial activity against pathogens like *E. coli* and *Salmonella* (Aguilar-Toalá et al. 2022; Nowakowski et al. 2022; Alejandro Ruiz et al. 2025). So, if you've unknowingly eaten insects before, you might consider doing it again—this time on purpose.

[2] "Insect powder" is the more accurate term in scientific and regulatory contexts, while "insect flour" is often used in marketing to align with familiar food terms. Unlike cereal flours, insect powder lacks gluten and differs functionally, so regulators may avoid calling it "flour" to reduce confusion.

1.3 Insects as a sustainable resource

Another benefit of eating insects is that they can be produced more sustainably than vertebrate livestock. Insect rearing generally requires far fewer resources—such as land, feed, and water—and emits significantly lower levels of greenhouse gases and other pollutants (Alexander et al. 2017; van Huis & Oonincx 2017; Smetana et al. 2021). And some insects (e.g., mealworms) can even be farmed vertically, allowing for high yields in small spaces. Another advantage is that many insects act as waste bioconverters (Siddiqui et al. 2024), capable of transforming organic residual streams[3] that are inedible to humans and unsuitable for traditional livestock into edible biomass and other valuable by-products (Varelas 2019; Peer et al. 2021; Bruins et al. 2024). This not only reduces competition for arable land and feed resources but also offers a sustainable waste management solution by diverting organic residual streams from landfills and lowering associated environmental impacts. For example, insects can be reared on food processing leftovers (e.g., spent grains), slaughterhouse waste, or even livestock manure (Nyakeri et al. 2017; Bordiean et al. 2020; Cammack et al. 2021). However, the suitability of these materials as feed depends on the insect species, substrate composition, availability, and local regulations (Peer et al. 2021).

Insects also produce a valuable by-product, called frass. In a mass rearing context[4], frass is a mixture composed of faeces, shed exoskeletons, leftover feed, insect parts, dead insects, and eggs (Figure 2).

[3] Biological material that remains after agricultural production, food processing, or consumption, which is not intended as the primary product.

[4] In earlier ecological studies on the role of insects in nutrient cycling, frass was defined solely as faeces.

Figure 2: Unprocessed frass from the house cricket (*Acheta domesticus*), consisting of faeces, leftover feed, and visible insect parts. Photo by Sara Capitán.

This by-product holds substantial promise for use in agriculture, where it can function as a soil amendment for crop production (e.g., fertiliser, biostimulant, elicitor), feed for other animals, feedstock for biogas production, or a source of extractable compounds (e.g., chitin) (Yildirim-Aksoy et al. 2019; Chavez & Uchanski 2021; Wedwitschka et al. 2023; Mei et al. 2024). Among these, its role as a soil amendment is especially relevant to sustainable crop production. Frass is considered a nutrient-rich input, often containing significant levels of macronutrients (e.g., nitrogen, phosphorus, and potassium) and micronutrients (e.g., iron, manganese, zinc, boron) essential for plant growth (Beesigamukama et al. 2022). Moreover, due to the presence of chitin[5]—a structural biopolymer found in insect exoskeletons—frass may also influence the microbial communities in the rhizosphere. Chitin—and its derivative, chitosan—has been extensively researched for its agricultural benefits, which include enhancing plant growth and nutrient uptake, suppressing pests and pathogens, stimulating plant defence mechanisms, and promoting beneficial soil microbiota activity (Sharp 2013; Pichyangkura & Chadchawan 2015). However, most research

[5] Chitin is not unique to insect exoskeletons; it is also found in crustacean shells, the cell walls of fungi, and other organisms.

has focused on chitin derived from crustacean shells[6], while the properties and effects of insect-derived chitin remain comparatively understudied. These differences in chitin source may influence soil microbial communities and plant responses, as variations in physiochemical properties affect its solubility, reactivity, and biological activity (Arbia et al. 2013).

Other biological components may influence the efficacy of frass as a soil amendment. For example, microbes present in insect faeces could affect crop growth. Insects host a wide variety of microorganisms in their guts—including bacteria, fungi, archaea, and protists—which can influence plant growth and stress tolerance when passed into the environment via frass (Hongoh 2010; Porto de Souza Vandenberghe et al. 2017; Barcoto et al. 2020). The composition of these microbial communities is not fixed, and can vary depending on several factors, including the insect species, rearing conditions, development stage, and post-production handling (Yun et al. 2014). Pre-treatments such as heat sterilisation (currently required in the EU to control for pathogenic bacteria) may also potentially reduce beneficial microbial activity (European Comission 2011; European Commission 2021). Other processing methods, like grinding or chitin-enrichment (Wantulla et al. 2023; Kisaakye et al. 2024), may likewise affect the efficacy of frass as a soil amendment.

Taken together, all these qualities make insects valuable as a sustainable, alternative food source. Moreover, the ability of insects to transform organic residual streams into high-quality protein and nutrient-rich soil amendments makes them well suited to circular food systems—a concept explored further in the following section.

1.4 Circular food systems

A circular food system is not a new concept. It stems from the circular economy model—a term used to describe a regenerative system that minimizes "resource input and waste, emissions, and energy leakage by slowing, closing, and narrowing material and energy loops…through long-lasting design, maintenance, repair, reuse, remanufacturing, refurbishing, and recycling" (Geissdoerfer et al. 2017). The term itself has no clear origin

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[6] Currently, most industrial chitin is obtained as a by-product of marine food processing, particularly from the shells of crustaceans such as shrimp, crab, and krill

but was popularized in the 1990s and shaped by overlapping concepts from other fields (Winans et al. 2017) and earlier environmental discourses such as the long-standing "reduce, reuse, recycle" ethos. It has since evolved into many different definitions and iterations, often adapted to suit specific disciplines. A circular food system is one such iteration, applying the circular economy model to support resource reuse in agriculture.

Like its predecessor, a circular food system is not well defined and is frequently idealised as a "closed-loop". However, this concept should not be taken literally. In reality, agroecosystems face unavoidable thermodynamic constraints (entropy), leading to energy losses, while water, nutrients, and biomass dissipate through, for example, leaching, volatilization, and harvest removal. Even waste recycling—essential for "closing loops"—may require energy-intensive processing to mitigate contaminants, as organic waste is often biologically unstable, potentially pathogenic, and prone to rapid autoxidation (Oreopoulou & Russ 2007). A truly closed-looped circular food system does not exist; rather, it serves as a conceptual model for maximizing resource efficiency. Furthermore, circularity in agriculture generally depends on exchanges between different systems—such as repurposing organic residual streams from one agricultural sector as inputs for another. While intra-system recycling (i.e., reusing waste within the same sector) may technically be feasible, it remains controversial and is often prohibited in animal production due to disease risk[7]. Under EU legislation, feed for insects is mainly restricted to plant-based residual streams (European Comission 2017), as they pose lower risks compared to animal-derived materials.

The practice of circularity in agriculture long predates its modern conceptualisation. Traditional agroecosystems commonly recycled organic residual streams—for example, using crop residues as livestock feed and manure to fertilise crops (Oreopoulou & Russ 2007; Anal 2017). There are also many examples of circular practices adopted within the food industry, long before the concept of circularity was formalised—for instance, the marketing of pulp and molasses as by-products of sugar beet processing (Smetana et al. 2022). This is because the repurposing of organic residual streams in food production can be not only an ecologically sound option, but

[7] The outbreak of bovine spongiform encephalopathy, commonly known as mad cow disease, was linked to the practice of feeding cattle protein made from processed remains of other cattle. This enabled the spread of prions and led to widespread bans on feeding animals material from their own species.

an economically viable one (Andersen 2007). A circular food system is not a new innovative concept; however, today's technological, economic, and systemic innovations redefine its potential impact, and unlocking this potential requires targeted research to improve the effectiveness of recycling and reusing organic residual streams across diverse production systems. In this thesis, I explore the potential of edible insects and their by-product—frass—as integrated elements within a circular food system.

2. Objectives

This thesis aims to advance our understanding of how insects can be integrated into circular food systems. The focus is on two main products: house crickets (*Acheta domesticus*) and spring wheat (*Triticum aestivum*). House crickets were reared on crop residues—a by-product of crop production. Frass—a by-product of insect rearing—was then evaluated as a soil amendment for spring wheat cultivation. Together, the papers in this thesis link crop residues, cricket performance, and frass back to crop performance—offering concrete insights for integrating insects within circular food systems.

The research was guided by the following research questions:

- What is currently known about the ecological role of insects in circular food systems, and what are the most urgent research gaps for their integration into these systems? (**Paper I**)

- How does feeding house crickets with crop residues affect their growth, survival, and the quantity and nutrient composition of the resulting frass? (**Paper II**)

- How does frass pre-treatment and application method influence the vegetative growth and nutrient uptake of spring wheat? (**Paper III**)

- What role do frass-associated microbial communities play in shaping wheat performance and aphid population growth? (**Paper IV**)

To answer these questions, this thesis integrates insights from a literature review (**Paper I**) with findings from three controlled experiments (**Papers II–IV**) (Figure 3). The papers are sequentially linked: **Paper I** offers a structured review of the literature on edible insects in circular food systems, mapping existing studies and identifying key ecological knowledge gaps. This contextual overview informs the subsequent experimental studies. **Paper II** tests a research gap identified by evaluating the use of crop residues as feed for house crickets, assessing its effects on insect performance and frass quality. **Paper III** follows the repurposing of frass as a soil amendment and examines how different frass pre-treatments and application methods influence wheat growth and nutrient uptake. Finally, **Paper IV** builds on the previous findings by isolating whether plant responses to frass are driven by its nutrient content or microbial communities.

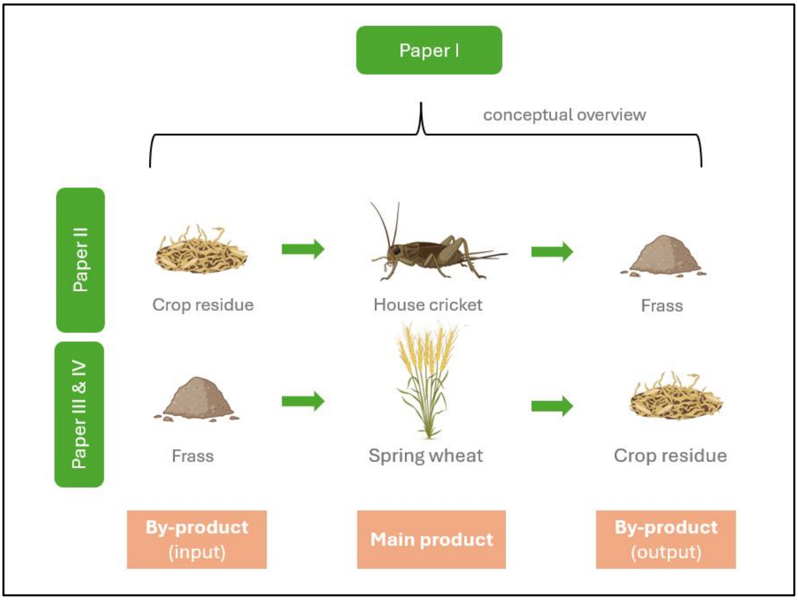

Figure 3: Conceptual linkages between the four papers in this thesis.

3. Methods

All experiments were conducted at the Swedish University of Agricultural Sciences (SLU; Uppsala, Sweden) between 2023 and 2024 to examine how house crickets (*Acheta domesticus*) and their frass contribute to circular food systems. The following section describes the main products and by-products used across experiments.

3.1 Main products, by-products, and source materials

House crickets (*Acheta domesticus*) and spring wheat (*Triticum aestivum*, var. 'Boett') are the main products within the circular food system evaluated in this thesis (Figure 4). House crickets, used in **Paper II**, are one of the most widely reared insect species globally due to their high protein content, broad natural distribution, and suitability for mass production (Gahukar 2016; Pilco-Romero et al. 2023). House crickets are hemimetabolous (i.e., no pupal stage) and, under rearing conditions, complete their life cycle in approximately 30–60 days, with some harvested at maturity (28–40 days) and others kept for egg-laying before being harvested (50–60 days) (Fernandez-Cassi et al. 2019; Kyllonen & Manzanares 2022). However, development time depends heavily on rearing conditions, especially diet.

Figure 4: The main study organisms used in this thesis: (right) House crickets (*Acheta domesticus*) and (left) spring wheat (*Triticum aestivum*). Photos sourced from iStock (purchased under a standard licencing agreement) and Pixabay.

The by-product used as feed input for crickets consisted of dried crop residues—stems and leaves remaining after harvest—from pea (*Pisum* *sativum*, var. 'Kelvedon Wonder') and tomato (*Solanum lycopersicum*, var. 'Ida Gold') (Figure 5 A, B). These plants were grown in a greenhouse at SLU under conditions recommended by the seed supplier (SW Horto, Hammenhög, Sweden), without the use of plant protection chemicals. Crop residues represent an abundant organic residual stream in the food supply chain (Peer et al. 2021), and as plant-derived material, comply with EU regulations for feed substrates in insect production intended for human consumption (Meijer et al. 2025). The selected crop species and varieties were chosen for their compatibility with greenhouse cultivation, which typically does not rely on pesticides—an important factor for insect rearing, as pesticide residues may harm insects.

Spring wheat (*Triticum aestivum*, var. 'Boett'), used in both **Papers III** and **IV**, served as the complementary main product in this circular system. 'Boett' is a modern spring wheat cultivar widely grown across northern Europe and suited to both organic and conventional systems (Liu 2021). Seeds were obtained from previous experiments conducted at the Department of Crop Production Ecology (SLU, Uppsala, Sweden) and had been stored under appropriate conditions to maintain viability. In **Paper IV**, half of the wheat plants were exposed to herbivory by the bird cherry-oat aphid (*Rhopalosiphum padi*), a major cereal pest that feeds on phloem sap and excretes honeydew, promoting fungal growth and reducing photosynthetic efficiency (Rabbinge et al. 1981). The bird cherry-oat aphid is also a vector of barley yellow dwarf virus, which can significantly reduce wheat yields under severe infestations (Smith 1963; Gaunce & Bockus 2015). Aphids used in the experiment were sourced from the company Biobasiq (Malmö, Sweden).

The by-product used as input for wheat production was frass—the residual stream of mass insect rearing (Figure 5C). Frass from house crickets was used as a soil amendment in **Papers III** and **IV** and sourced from a commercial food-grade cricket facility in the EU, where crickets were reared

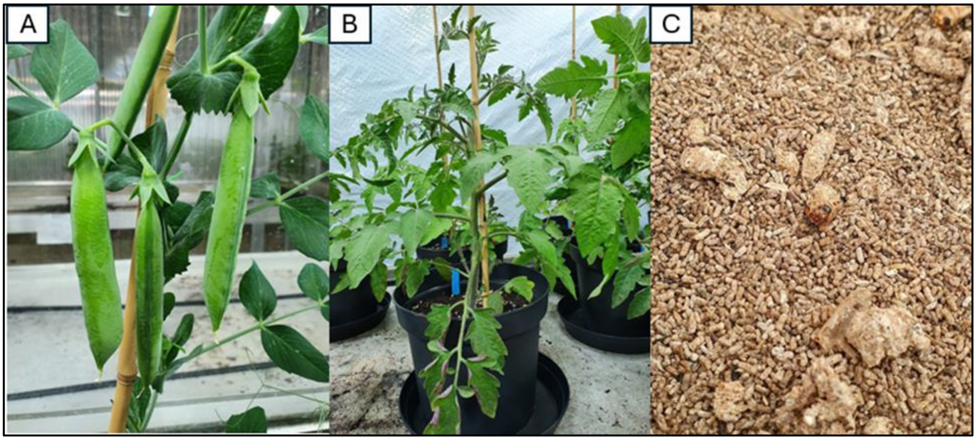

Figure 5: The by-products used for this thesis. (A) crop residue from greenhouse grown pea (*Pisum sativum*) (B) crop residue from greenhouse grown tomato (*Solanum lycopersicum*) (C) frass from house cricket (*Acheta domesticus*). Photos by Sara Capitán.

on a plant-based diet. Rearing practices at the facility adhered to current EU regulations on hygiene and feed standards for edible insect production.

3.2 Overview of methods by paper

3.2.1 Unlocking the potential for insects in circular food systems: paths for future research (**Paper I**)

This study synthesised current knowledge on the role of insects in circular food systems through a structured literature review. Peer-reviewed articles published through December 2024 were identified using targeted keyword searches in the Web of Science Core Collection (Figure 6). Inclusion criteria required that studies addressed both insects and circularity aspects—such as nutrient recycling, waste bioconversion, or system integration. Studies examining insects only as feed, without considering their integration at the system level, were excluded.

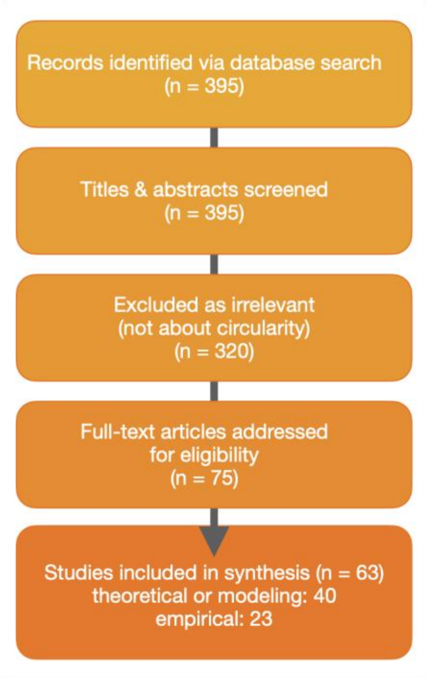

Figure 6: PRISMA flow diagram showing the process of identifying, screening, and selecting studies for this review on insects in circular food systems.

Relevant information was extracted and organised by insect species, waste or feed input, output products (e.g. frass, biomass), and the type of circular strategy involved. Thematic analysis was used to identify key patterns, research gaps, and potential leverage points for future study and application. The review aimed not only to describe the current evidence base but also to propose directions for integrating insects in circular food systems.

3.2.2 Crop residues as feed for house crickets: Impacts on growth, survival, and frass quality (**Paper II**)

A feeding trial was conducted to assess the performance of house crickets reared on dried crop residues from pea and tomato plants. Crickets were sourced from long-term laboratory colonies at SLU, originally collected from sites in mid- and southern Sweden and maintained as separate populations for over 20 generations. Crop residues were sourced from greenhouse-grown plants and dried (70°C for 48 h) before use. Three diets were tested: pea residue, tomato residue, and a standard grain-based control diet.

The experiment began with 200 cricket nymphs per diet, housed in 2L plastic cages (Figure 7) and reared for 56 days under controlled conditions. Weekly measurements included survival counts and mass of total surviving crickets (later presented as mass per cricket). Frass was collected weekly and weighed at the end of the trial.

All diets were analysed for dry matter, ash, crude protein, and amino acid content. Total frass output was measured for each diet, and frass was

Figure 7: Cage layout used in the experiment. Each 2 L plastic cage housed 10 cricket nymphs and included a water vial, a hiding structure, and one of three diet treatments: control, pea residue, or tomato residue. A total of 200 crickets were tested per diet type

analysed for mineral nutrient content (total N, P, K, Mg, S, Ca). Statistical analysis of average cricket mass per diet was conducted using a generalised linear model with a Gamma distribution, specifying day, diet, and their interaction as fixed effects. Survival across diet groups was analysed using a Cox proportional hazard model, with diet as the main covariate and the control diet set as the reference group. Cumulative mortality was illustrated using Kaplan–Meier survival curves.

3.2.3 Frass pre-treatment and application method impact spring wheat vegetative growth and nutrient concentration (**Paper III**)

A greenhouse experiment was conducted to assess how pre-treatment (heat-treated vs. non-heated) and application method (mixed into substrate, surface-applied, or delayed application) of house cricket frass influenced spring wheat growth and nutrient concentration. Frass was sourced from commercially reared house crickets. Heat treatment involved oven-drying at 70°C for 1 hour. Wheat was grown in pots filled with low-nutrient potting mix, and each frass treatment was applied at a rate of 7% (w/w) either by mixing frass into the soil before sowing (called "mix"), surface application after sowing (called "surface"), or delayed surface application 14 days after sowing (called "delay"). A control treatment with no frass added was included in the design.

Plant growth was evaluated after 56 days by measuring germination rate, final plant height, dry shoot biomass (dried at 70°C for 48 h), and leaf chlorophyll content (measured with a SPAD-502 meter). Shoot biomass was analysed for nutrient concentrations (N, P, K, Mg, S, Ca). Statistical analysis involved a one-way ANOVA, including the control treatment, to test for overall differences between frass-amended and control plants. In addition, a two-way ANOVA, excluding the control, was used to evaluate the main and interactive effects of frass pre-treatment (heat-treated vs. non-heated) and application method (surface, mixed, delayed). Where significant effects were detected ($p < 0.05$), Tukey's honest significant difference (HSD) test was applied for pairwise comparisons among treatment groups. For data that did not meet normality assumptions, the non-parametric Kruskal–Wallis test was applied instead, followed by Dunn's test for pairwise comparisons.

3.2.4 Microbial and nutrient contributions of *Acheta domesticus* frass to wheat performance and aphid population growth (**Paper IV**)

A controlled experiment tested how frass-associated microbes influence vegetative wheat performance, aphid population growth, and rhizosphere microbial communities. Treatments consisted of sterile frass (autoclaved twice at 121 °C for 90 min) or unsterile frass (no heat treatment), crossed with the presence or absence of aphids, yielding four treatment groups: sterile frass with aphids, sterile frass without aphids, unsterile frass with aphids, and unsterile frass without aphids.

Spring wheat was grown in sterilised low-nutrient potting mix amended with 7% (w/w) frass from commercially reared house crickets. Seeds were surface sterilised and pre-germinated prior to transplanting. Established seedlings were thinned to three plants per pot (n = 40 pots in total). Aphids (*Rhopalosiphum padi*) (Figure 8) were added to plants two weeks after transplanting. The experiment lasted 33 days and was conducted under controlled temperature, humidity, and light.

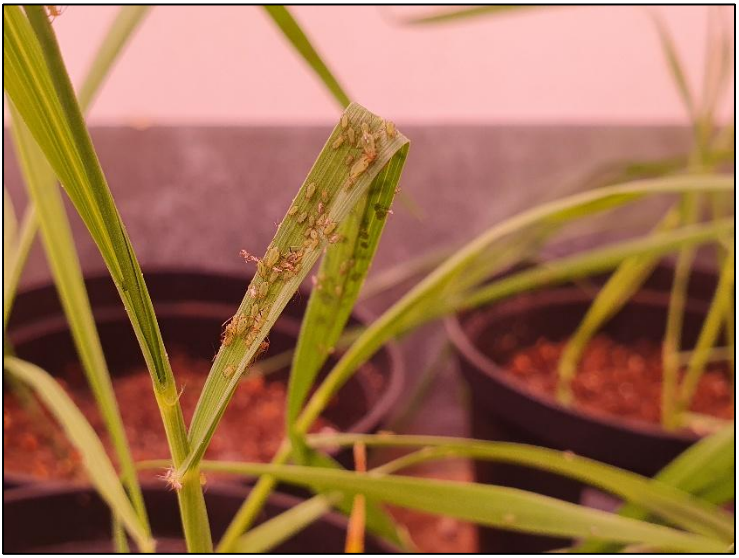

Figure 8: Cherry bird-oat aphids (*Rhopalosiphum padi*) on spring wheat (*Triticum aestivum*) seedlings. The image shows aphid populations on wheat leaves at 30 days post-transplant. Photo by Sara Capitán.

Aphid population growth was measured as a proxy for plant resistance, where higher aphid populations indicated a plant was less resistant to herbivory and vice versa. Aphids were counted every 3–4 days, for a total of 5 observations. Leaf chlorophyll content (SPAD) was measured before harvest. Shoot and root biomass were recorded after oven drying (70 °C, 48 h), and shoot nutrient concentrations (N, P, K, Mg, S, Ca) were subsequently measure. Rhizosphere soil was sampled for 16S rRNA amplicon sequencing to assess microbial richness and community composition.

Statistical analyses included a two-way ANOVA for plant traits, panel negative binomial regression for aphid counts, and PERMANOVA and homogeneity of multivariate dispersions tests for microbial community composition and dispersion, based on rarefied Bray-Curtis dissimilarities.

4. Results

4.1 Unlocking the potential for insects in circular food systems: paths for future research (**Paper I**)

This review analysed 63 peer-reviewed studies on insects in circular food systems, highlighting a large gap between theory and practice. Of these, 40 were theoretical or modelling contributions and only 23 empirical. Empirical research was limited: 10 studies measured insect growth or survival on residual streams, five tested frass as fertiliser and just one linked waste bioconversion with another trophic level. No study examined the full life-cycle performance in circular conditions or addressed multi-species interactions. Research has also concentrated on a few insect species: the black soldier fly (*Hermetia illucens*, 16 studies) and yellow mealworm (*Tenebrio molitor*, 5 studies) appeared most often, with others such as the house cricket (*Acheta domesticus*) appearing rarely. This narrow taxonomic scope limits system-level insights. Findings nevertheless confirm insects' potential to convert diverse residual streams into edible biomass and nutrient-rich frass. To advance insect integration into circular food systems, three research priorities were identified: (1) determining the suitability of different residual streams as feed, (2) understanding insect ecology, growth and reproduction in circular food systems and (3) examining ecological interactions among organisms in a circular food system.

4.2 Crop residues as feed for house crickets: Impacts on growth, survival, and frass quality (**Paper II**)

Diet significantly affected cricket mass (Figure 9). Crickets developed slower and had lower final mass on pea residues (27.6 mg) and tomato residues (25.7 mg) compared to the grain-based control feed (61.5 mg).

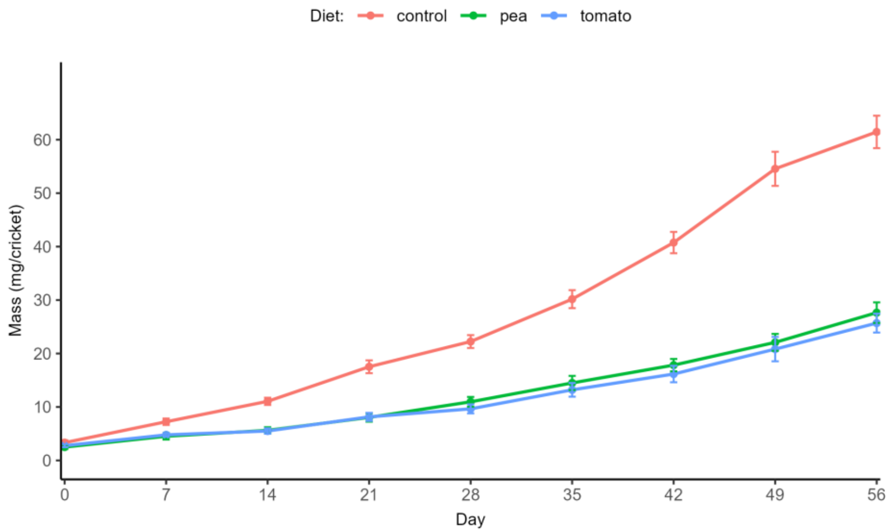

Figure 9: Mean individual mass (mg) ± SE of *Acheta domesticus* fed the grain-based control diet, pea residue diet (*Pisum sativum*), and tomato residue diet (*Solanum lycerpersicum*) over 56 days

Survival rate was also affected by diet. At day 56, crickets fed pea residue showed a survival rate (52.6%) similar to those on the control diet (58.2%), whereas tomato residue-fed crickets had markedly lower survival (38.6%). The Cox proportional hazards model indicated no significant difference in mortality risk between pea residue-fed and control crickets, whereas tomato residue-fed crickets had a significantly higher mortality risk compared to the control diet (Figure 10).

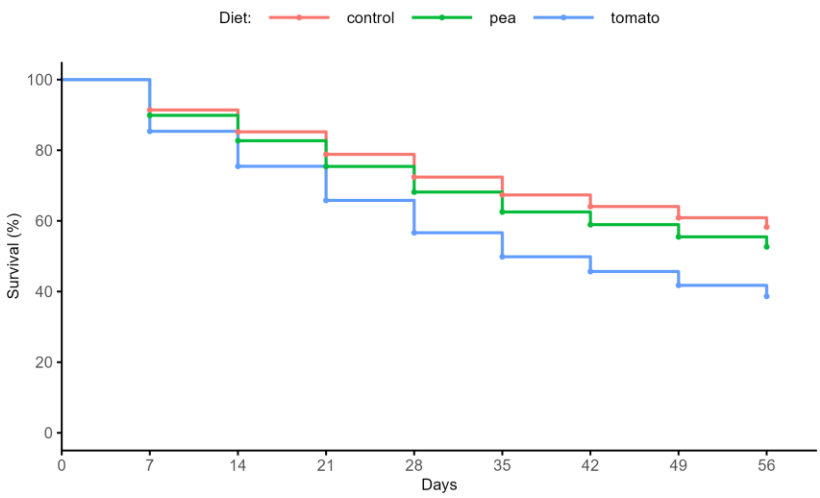

Figure 10: The Kaplan-Meier curve from the Cox proportional hazards mixed-effects model for *Acheta domesticus* fed the grain-based control, pea residue, and tomato residue diets. The experiment lasted 56 days, and each diet treatment began with 200 crickets.

Crop residue diets differed in nutrient composition compared to the control. Both diets had lower crude protein and essential amino acid levels; furthermore, the tomato residue diet had a lower protein content than both pea residue and control diets.

Frass production differed by diet, with the highest yield from tomato residue (7.03 g), followed by the control (6.45 g) and pea residue diets (3.68 g). Nutrient composition of the frass also varied across diets (Table 1).

Table 1: Nutrient composition (g/kg) of *Acheta domesticus* frass, collected cumulatively over 56 days, from crickets fed a standard grain-based diet, a pea residue diet, or a tomato residue diet.

Diet	N (g/kg)	P (g/kg)	K (g/kg)	S (g/kg)	Mg (g/kg)	Ca (g/kg)	Na (g/kg)
control	25.78	13.07	14.39	4.71	6.47	23.18	< 0.1
pea	24.28	6.77	38.45	4.96	5.18	41.94	0.62
tomato	10.19	5.58	19.54	13.30	5.18	44.20	1.09

4.3 Frass pre-treatment and application method impact spring wheat vegetative growth and nutrient concentration (**Paper III**)

Cricket frass influenced several aspects of wheat performance, with both heat pre-treatment and application method playing significant roles. Germination was highest when frass was mixed into the substrate (heat-treated) or applied two weeks after sowing (no-heat); however, germination decreased significantly with surface-applied, heat-treated frass (Figure 11A). The tallest plants grew with no-heat frass mixed into the soil (Figure 11B), while surface application—regardless of pre-treatment—produced the greatest shoot biomass (Figure 11C). Delayed application consistently resulted in the highest leaf chlorophyll content (SPAD) (Figure 11D). Frass also altered nutrient concentrations in wheat shoots (Figure 12), though results differed depending on the nutrient.

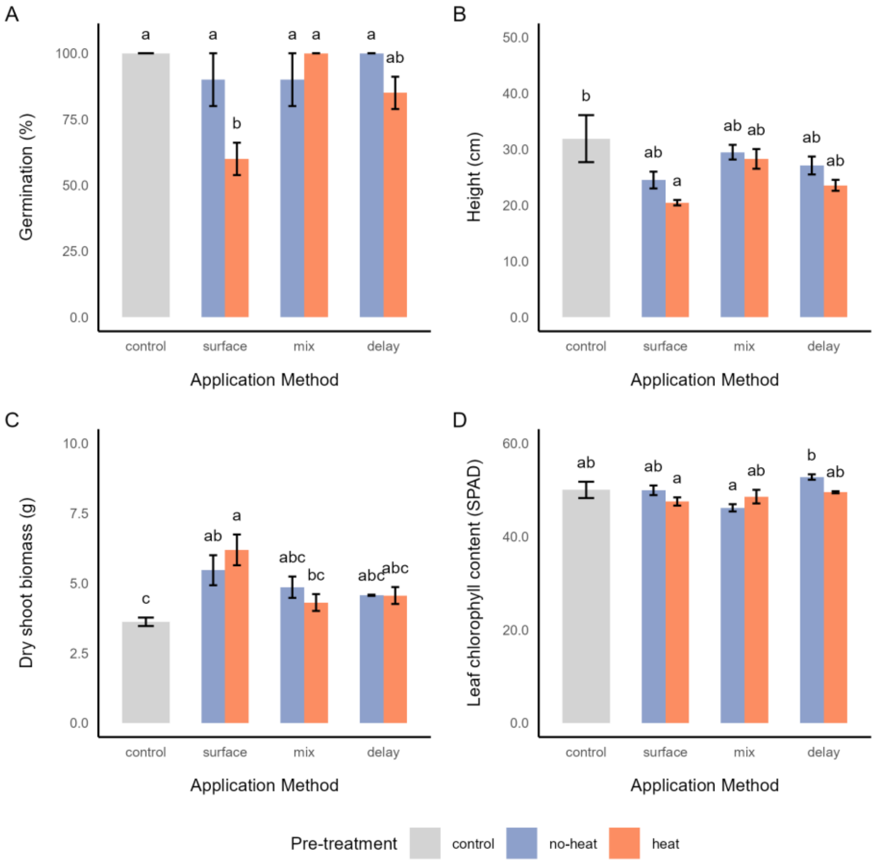

Figure 11: (A) germination (%), (B) plant height (cm), (C) dry shoot biomass (g), and (D) leaf chlorophyll content (SPAD units) of spring wheat grown in pots under greenhouse conditions for 8 weeks. Treatments included a control without frass, untreated frass (no-heat), and frass heat-treated at 70 °C for 1 h, applied either on the soil surface (surface), incorporated before sowing (mix), or placed on the soil surface two weeks after sowing (delay). Values are means of 5 pots per treatment ± SE. Different lowercase letters above bars denote significant differences among treatments (Tukey HSD, $p < 0.05$).

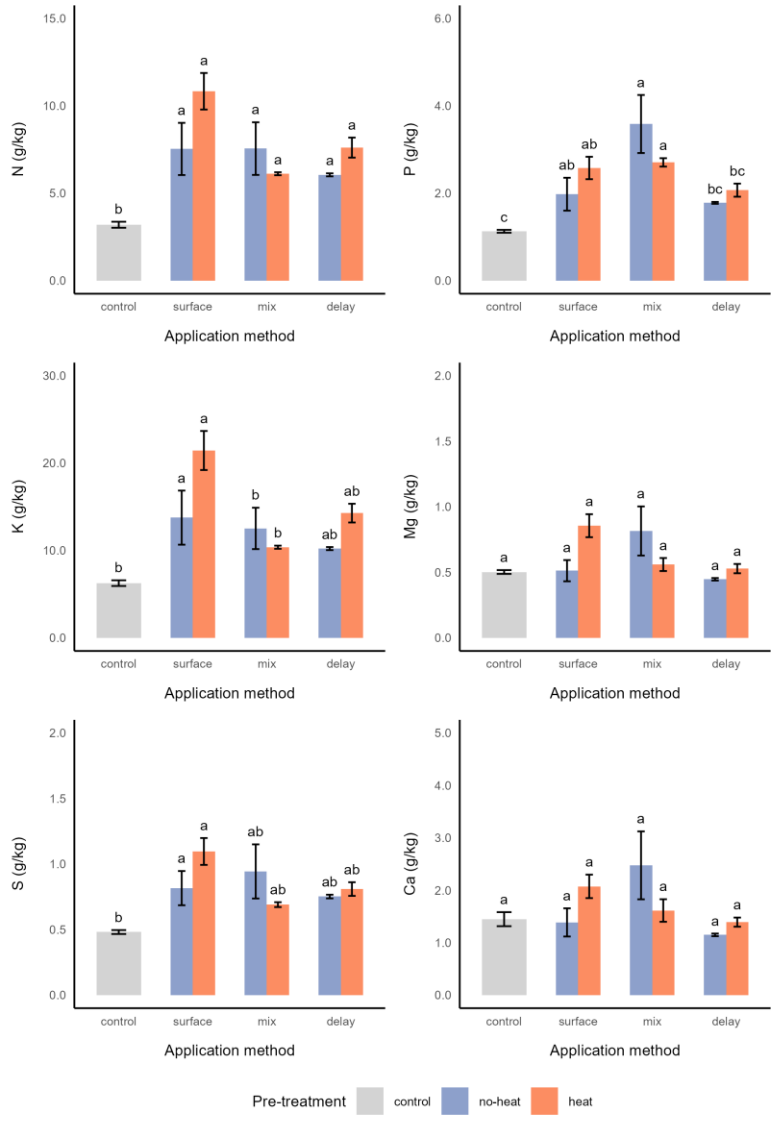

Figure 12: Concentrations of N, P, K, Mg, and S (g/kg) in shoots of spring wheat grown in pots under greenhouse conditions and harvested at 8 weeks. Treatments included a control without frass, untreated frass (no-heat), and frass heat-treated at 70 °C for 1 h, applied either to the soil surface (surface), incorporated before sowing (mix), or added to the soil surface two weeks after sowing (delay). Bars show means of 5 pots per treatment.

4.4 Microbial and nutrient contributions of *Acheta domesticus* frass to wheat performance and aphid population growth (**Paper IV**)

Herbivory had a strong negative effect on wheat growth: plants exposed to aphids had significantly lower shoot and root biomass compared to aphid-free plants. Frass sterilisation did not significantly affect biomass overall, but among aphid-infested plants, those grown with unsterile frass showed slightly higher shoot and root biomass than those with sterile frass (Figure 13A, B).

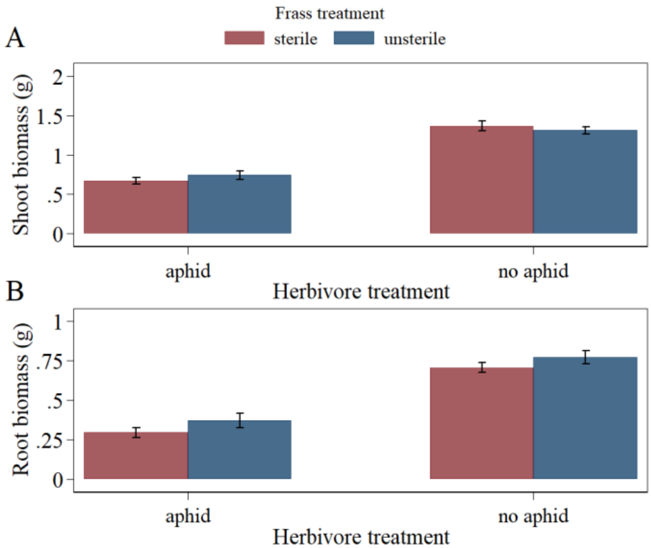

Figure 13: Dry shoot (A) and root (B) biomass of 33-day-old spring wheat (*Triticum aestivum*, var. 'Boett') harvested and dried at 70 °C for 48 hours. Plants were cultivated in pots within a controlled climate chamber at SLU (Uppsala, Sweden). Bars show mean values ± standard error for each combination of herbivore treatment (aphids or no aphids) and frass treatment (sterile or unsterile), with n = 10 pots per treatment.

Leaf chlorophyll content (SPAD) was also reduced by aphid infestation. While frass treatment had only a marginal effect on SPAD, unsterile frass tended to maintain slightly higher SPAD values, especially among aphid-infested plants (Figure 14).

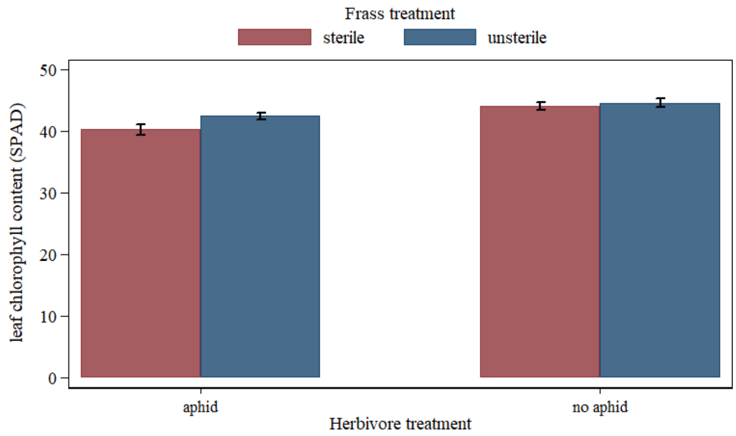

Figure 14: Leaf chlorophyll content (SPAD) in 33-day-old spring wheat plants (*Triticum aestivum*, var. 'Boett') grown in pots within a controlled climate chamber at SLU (Uppsala, Sweden). Results are shown for different herbivore (aphids vs. no aphids) and frass (sterile vs. unsterile) treatments. Bars display mean values ± standard error (n = 10 pots per treatment).

Nutrient concentrations in shoots varied by treatment (Figure 15). Phosphorus levels were influenced by both frass and herbivory, while potassium and magnesium were mainly affected by aphid feeding; potassium declined with aphids, whereas magnesium increased. Nitrogen, calcium, and sulphur were not significantly affected.

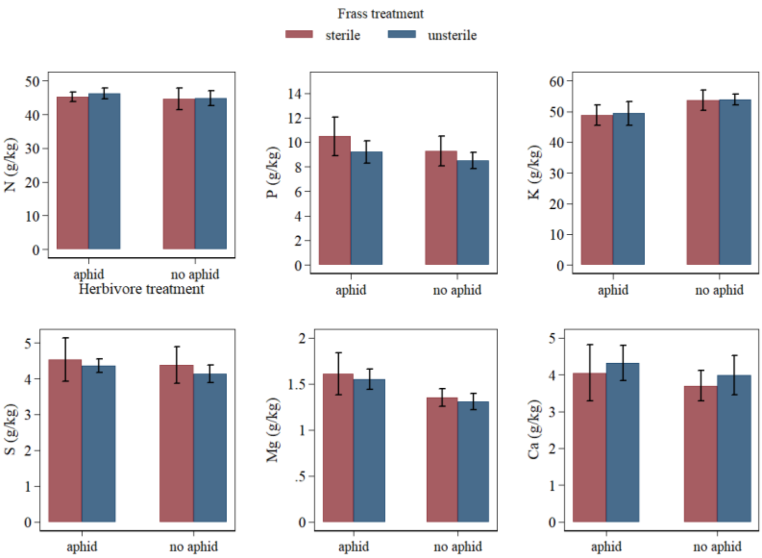

Figure 15: Shoot nutrient concentrations (g/kg) of N, P, K, Mg, and S of 33-day-old spring wheat (Triticum aestivum, var. 'Boett') grown a controlled climate chamber at SLU (Uppsala, Sweden). Data are presented for different herbivore (aphids vs. no aphids) and frass (sterile vs. unsterile) treatments. Bars indicate mean values ± standard error (n = 10 per group).

Aphid populations increased over time on all plants, but those grown with sterile frass generally supported fewer aphids, with a significant reduction observed on day 30 (Figure 16). Analysis of the rhizosphere bacterial communities revealed that both frass treatment and aphid presence shaped microbial diversity and composition. Notably, unsterile frass combined with aphid infestation led to higher bacterial richness (Figure 17).

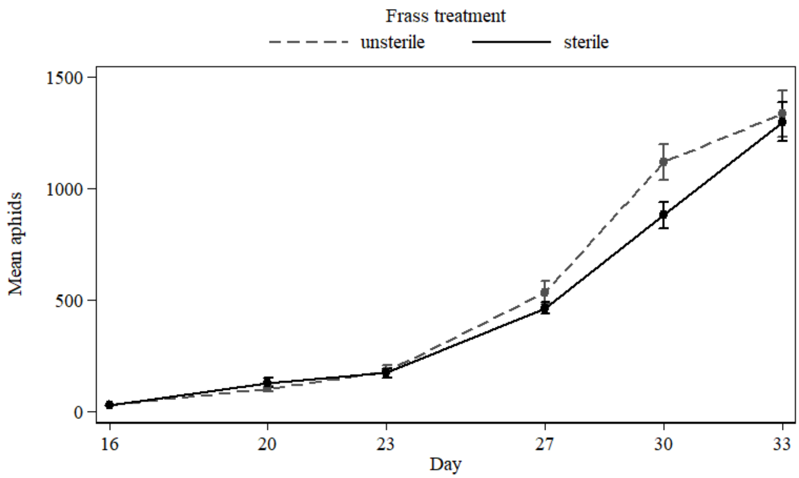

Figure 16: Mean aphid (*Rhopalosiphum padi*) counts ± SE per pot over time on spring wheat (*Triticum aestivum*, var. 'Boett') grown with either sterile or unsterile house cricket frass applied at a rate of 7% w/w. Aphids (30 per pot) were introduced on day 16 of growth, and aphid counts were taken until day 33 of wheat growth.

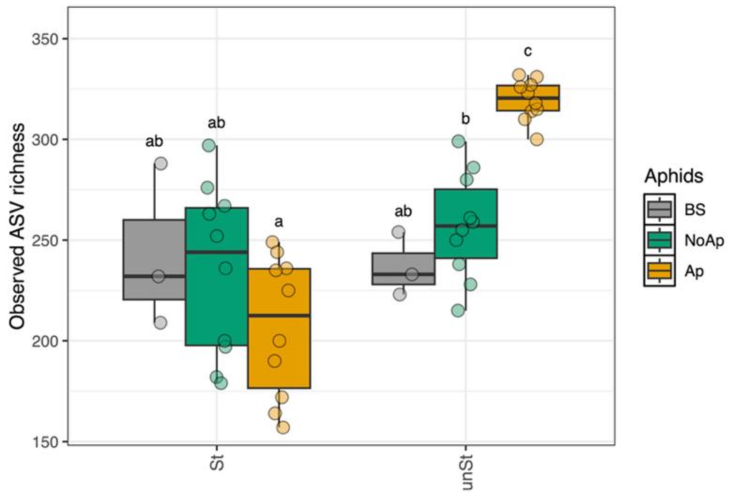

Figure 17: Observed bacterial richness in wheat rhizospheres and bulk soil (BS) controls under different frass treatments (sterile or unsterile) and herbivore treatments (aphids or no-aphids). Each point represents a sample, and boxplots display medians with interquartile ranges. Different letters mark significant pairwise differences according to Tukey's HSD post hoc test ($p < 0.05$).

5. Discussion

5.1 Insects as bioconverters of organic residual streams

Insects can be valuable components of circular food systems, capable of converting low-value organic residual streams into high-quality protein and nutrient-rich frass (Cadinu et al. 2020; Derler et al. 2021; Moruzzo et al. 2021). **Paper I** showed that while this concept has gained traction, empirical studies remain limited and often fail to assess ecological dynamics or production trade-offs. This gap motivated subsequent experiments evaluating both cricket performance on crop residues (**Paper II**) and the agronomic value of the resulting frass (**Papers III** & **IV**).

Paper II found that the type of crop residue fed to house crickets significantly influenced their growth and survival. Crickets fed tomato residue exhibited the lowest survival and weight gain, while pea residue-fed crickets performed moderately well (especially in terms of survival rate), though still underperforming compared to a standard grain-based diet. Notably, crickets did not reach maturity in any diet treatment, indicating potential nutritional limitations (e.g., lack of sodium in diets) or suboptimal rearing conditions. Furthermore, high mortality, combined with the absence of carcasses in frass, suggests that cannibalism may have occurred—a behaviour commonly observed in Orthoptera, often associated with dietary limitations and the density of the rearing environment (Simpson et al. 2006; Hansen et al. 2011; Gutiérrez et al. 2020).

These findings highlight a key limitation in using organic residual streams as feed: not all residues are suitable as sole feed inputs. Factors such as nutrient composition, physical properties of the feed, and behavioural responses to the feed can all affect insect performance. In commercial settings, many producers supplement insect diets with fresh feeds to help promote insect performance—an insight corroborated from informal communication with several insect producers. However, regulatory constraints play a pivotal role in diet selection. Under current EU regulations, insects intended for food and feed must primarily be reared on plant-based substrates, with limited exceptions for certain animal-derived materials;

additionally, strict feedstock sourcing rules apply (Elissen et al. 2023; Meijer et al. 2025).

Crop residues are a legally permitted feedstock for insect production in the EU that are widely available (Peer et al. 2021). When sourced from field grown crops, crop residues used as insect feed represent an alternative to conventional crop residue management methods (e.g., tilling, composting, burning, bioenergy production, use as livestock feed). However, using crop residues as insect feed presents multiple logistical challenges, including seasonal availability, the need for pre-processing (e.g., particle size reduction), competition with other residue uses, storage risks, and contamination (Meyer et al. 2021; El Deen et al. 2022; Ho et al. 2024)—all of which can impact insect yield, safety, and economic viability. Furthermore, crop residues sourced specifically from field crops may present additional challenges, since plant protection chemicals (in particular, pesticides) and secondary metabolites (defensive compounds produced by plants in response to stressors such as pests) in plants can compromise insect performance and pose risks for downstream use in circular food systems. Using crop residues from controlled growing environments (like greenhouses or hydroponic farms) may represent a safer feed option.

5.2 Frass as a soil amendment

Frass is widely promoted as a sustainable soil amendment (Poveda 2021), and may offer fertiliser, biostimulant, or elicitor effects (Ferruzca-Campos et al. 2023; Andrianorosoa Ony et al. 2024). In **Paper II**, frass quantity and composition varied by diet, demonstrating how upstream inputs (e.g., feed) shape frass properties. **Paper III** then tested the effects of frass pre-treatment and application method on wheat vegetative growth and nutrient concentration, while **Paper IV** isolated microbial and nutrient contributions of frass and tested effects under herbivore stress. Besides the presence of herbivory, a key distinction between the studies was the heat treatment: **Paper III** followed EU guidelines for processing of animal manures (70 °C for 1 h), while **Paper IV** used a more intensive heat treatment (twice autoclaved at 120 °C for 90 min) to suppress microbial activity. Recent studies highlight that while standard heat treatment is effective at reducing pathogenic bacteria (e.g., *Salmonella* and *E. coli*) its efficacy against other microorganisms varies, and frass properties—such as nutrient content and microbiota—are shaped by both insect species and production practices (Yun et al. 2014; Praeg & Klammsteiner 2024; Volder 2025).

In **Paper III**, frass improved various aspects of wheat performance, but effects depended strongly on application method and whether frass was heat-treated prior to use. For instance, surface application of heat-treated frass significantly decreased wheat seed germination. In **Paper IV**, microbial contributions of frass were more pronounced under herbivore pressure. While unsterile frass did not significantly improve plant growth overall, it slightly enhanced performance in aphid-infested plants, particularly in root biomass and SPAD values. Both studies raise important considerations for the use of frass as a soil amendment. Frass effects are not universal; they depend on several factors, including frass source, pre-processing, application rate, application method, crop species, and external stressors.

5.3 Design implications for circular food systems

Together, the papers in this thesis link crop residues, cricket performance, and frass back to plant performance—offering concrete insights for integrating insects within circular food systems (see Figure 3). First, not all organic residues are suitable as sole feed—the nutrient composition of the feed can limit insect performance and impact the quality of frass. Second, the properties of frass are not fixed but shaped by upstream inputs (e.g., diet) and downstream decisions (e.g., heat-treatment, application method). Third, microbes in frass may emerge as important drivers of plant response, particularly under herbivore stress. These results highlight the importance of deliberate system design: choices made at one stage (e.g., crop selection, residue handling, insect diet) cascade through the system, influencing outcomes downstream (e.g., frass quality, plant performance). For insects and frass to meaningfully contribute to circularity at scale, production must expand—supported not only by technical innovation, but also by supply, market demand, regulatory support, and social acceptance (Wade Hoelle, J. 2020; Veldkamp et al. 2022). In parallel, more empirical work is needed to guide decisions on feed selection, pre-processing, and frass application strategies across systems. Insects thus represent a powerful biological tool for transforming organic residual streams into resources, advancing the development of resilient and circular food systems.

5.4 Afterthoughts on circularity and circular food systems

Starting this PhD was my first encounter of the term "circular economy" and "circular food system", though it was not my first encounter of the concept. As I explored the terminology and theoretical framing of circularity, I became aware of the many different definitions, as well as the vague and overly idealistic wording that obscured the concept's practical limitations. For instance, phrases such as "closed-loop" and "zero waste" are often used in tandem with circularity, promoting a vision of infinite recycling where no resource is lost. The term "circular economy"—the predecessor to the concept of circular food systems—has been in circulation for decades (Geissdoerfer et al. 2017), and critical perspectives have emerged alongside its popularity. For instance, Kirchher (2023) argues that much of the research invoking circular economy exemplifies an archetype of "scholarly bullshit": work built on recycled research and academic buzzwords, unclear or missing theoretical framework, analyses lacking replicability, and conclusions that are wide-sweeping. Others argue that the concept is not grounded in economic reasoning and that, without assessing environmental costs of implementation, many reuse and recycling options will not be viable (Andersen 2007).

Circularity is a simplified framework intended to encourage the reuse of organic residual streams in agriculture. In practice, however, circularity can be difficult to apply. For example, resource constraints were a major barrier in my experiments, even in the small scale I worked at (frass is extremely difficult to source and not all companies who rear insects sell it). This highlights a central challenge of using edible insects and frass in circular food systems: developing a reliable, cost-effective supply chain is difficult because the insect industry (particularly insects reared as food and feed for humans and livestock) remains niche, with both limited supply and demand. This is not to say circular practices are unachievable, but applying these practices with insects poses substantial logistical and economic challenges.

Another challenge I struggled with was how to apply circularity to my experiments. Vague and varied interpretations of circularity make implementation inconsistent and difficult to evaluate. The circular food system framework offered no practical toolset nor measurable metrics, and at times I felt that it hindered rather than supported the biological questions I sought to answer. In striving to be "circular", I made design choices that, in retrospect, were missteps—prioritising perceived alignment with the circular food system framework over experimental feasibility. Furthermore, in reviewing studies within the circular food system paradigm, I found that it often does not fully capture empirical studies that indirectly support its functioning; valuable contributions can be overlooked if they fall outside formal definitions or do not explicitly label their approach as "circular". These reflections are not a rejection of my work; valuable insights emerged from the experiments. However, they have left me with a more grounded perspective of circularity. I support the ethos of circularity—waste less, use resources more efficiently—while remaining acutely aware of the gap between concept and execution.

6. Conclusion

This thesis examined how edible insects—specifically the house cricket (*Acheta domesticus*)—can be integrated into circular food systems by converting crop residues into insect biomass and frass, and by assessing the efficacy of frass as a soil amendment for spring wheat (*Triticum aestivum*).

Paper I reviewed the existing scientific knowledge on insects in circular food systems, highlighting strong theoretical support but limited empirical studies. It identified key research gaps, including the evaluation of residual streams as insect feed, the study of insect performance within circular food systems, and the examination of ecological interactions among organisms in these systems.

Paper II tested whether crop residues from pea and tomato plants could serve as sole feed for house crickets. Crickets could survive on these diets—particularly pea residues—but grew more slowly than on a standard grain-based diet. Furthermore, the frass produced had varied nutrient profiles.

Paper III evaluated the use of cricket frass as a soil amendment for spring wheat. Results showed that both frass pre-processing (heat treatment) and application method (surface applied, mixed into the substrate, or a 2-week delayed surface application) influenced plant performance. Mixing untreated frass into the soil promoted greater plant height, while surface application increased biomass. Different treatments also affected nutrient concentration in shoots.

Paper IV explored the role of frass-associated microbial communities in wheat performance and aphid population dynamics. Herbivory was the dominant factor reducing wheat performance, but unsterile frass showed subtle benefits under aphid pressure, maintaining slightly higher root biomass and leaf chlorophyll content. Contrary to expectations, plants with sterile frass tended to host fewer aphids. Herbivory and frass treatments also shaped rhizosphere bacterial communities, with unsterile frass and aphids driving greater microbial richness and distinct community composition. These results indicate that, under the tested conditions, microbial inputs had little direct effect on early wheat growth or aphid population growth, but they demonstrate that frass-associated microbes can influence rhizosphere community structure, particularly when plants face herbivory.

Together, these studies demonstrate that insects and their frass can contribute meaningfully to circular food systems, but their effective integration depends on careful design choices—from feed selection to frass pre-processing and application.

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Popular science summary

Our current way of producing food is putting serious pressure on the environment—causing pollution, loss of biodiversity, and inefficient use of resources. At the same time, the world's population is growing, and so is the demand for food, especially meat. To meet these challenges, we need to rethink how food is produced and what new food sources can be used. One promising solution is the use of insects as food.

This thesis explores how insects, specifically house crickets (*Acheta domesticus*), can play a key role in circular food systems—a type of food system where waste is recycled into resources to help produce more food. House crickets can eat waste and turn it into two valuable products: high-protein food and a nutrient-rich by-product called frass (a mix of insect poop, shed exoskeletons, and leftover feed). Frass can then be added to soil to help grow new crops and make crops more resilient to stress. In a series of studies, I looked at how this system works in practice:

Paper I reviewed what has been studied about insects in circular food systems. While there's a lot of excitement about the idea, very few real-world studies exist. **Paper II** tested whether crop harvest leftovers—specifically stems and leaves from pea and tomato plants—could be used to feed house crickets. The results showed that crickets can survive on these materials, especially pea residues, but they grow more slowly than when fed a standard grain-based feed. However, the frass they did produce had different nutrient profiles. **Paper III** focused on what happens when frass is used as a fertilizer for spring wheat. The way frass was processed before use and how it was applied to crops had a big impact. Heating frass and applying it to the surface after planting reduced the number of plants that germinated. However, mixing untreated frass into the soil helped plants grow taller, while surface application increased above-ground biomass growth. Different treatments also affected the amount of nutrients in the aboveground biomass. **Paper IV** examined how the microbes in frass influence wheat growth, nutrients in the aboveground biomass, and resistance to aphids. By comparing sterilised and unsterilised frass, we found that frass microbes had limited effects on early wheat growth overall, but there were subtle benefits under aphid attack—plants with unsterile frass tended to maintain slightly more root biomass and leaf chlorophyll content when infested. We also saw clear changes in the soil microbial community depending on both frass treatment and aphid presence, suggesting that frass microbes can shape the rhizosphere in ways that may matter over time.

Together, these studies show that edible insects and frass can make food production more sustainable—but only if we carefully design how these systems work. Everything is connected: the type of crop waste used to feed insects affects cricket growth and frass quality; the frass then affects plant performance depending on how it’s processed and applied; finally, the microbes present in frass can influence plant growth and resilience against pests. By better understanding these interactions, we can move one step closer to creating circular food systems that reduce waste and help feed the world more sustainably.

Populärvetenskaplig sammanfattning

Vårt nuvarande sätt att producera mat sätter stor press på miljön—det orsakar föroreningar, förlust av biologisk mångfald och ett ineffektivt resursutnyttjande. Samtidigt växer världens befolkning, liksom efterfrågan på mat, särskilt kött. För att möta dessa utmaningar behöver vi tänka om kring hur mat produceras. Ett lovande alternativ är konceptet cirkulära livsmedelssystem, där organiska reströmmar inte kasseras utan återanvänds som en resurs.

Denna avhandling undersöker hur ätliga insekter, i synnerhet hussyrsan (Acheta domesticus), kan spela en central roll i cirkulära livsmedelssystem. Hussyrsor kan äta organiska reströmmar och omvandla dem till två värdefulla produkter: proteinrik mat och en näringsrik biprodukt som kallas frass (en blandning av insektsavföring, ömsade exoskelett och foderrester). Frass kan sedan tillföras jorden för att hjälpa nya grödor att växa och göra dem mer motståndskraftiga mot stress. I en serie studier undersökte jag hur detta system fungerar i praktiken:

Artikel I granskade vad som hittills har studerats om insekter i cirkulära livsmedelssystem. Trots det stora intresset finns det få verkliga fallstudier. Mer forskning behövs, särskilt kring hur insekter samspelar med andra delar av systemet, såsom växter och markmikrober. **Artikel II** testade om restprodukter från skörd—specifikt stjälkar och blad från ärt- och tomatplantor—kunde användas som föda för hussyrsor. Resultaten visade att syrsor kan överleva på dessa material, särskilt ärtrester, men de växte långsammare än när de fick ett standardfoder baserat på spannmål. Däremot hade den frass som producerades olika näringsprofiler. **Artikel III** fokuserade på vad som händer när frass används som gödsel till vårvete. Hur frassen behandlades innan användning och hur den applicerades på grödan hade stor betydelse. Upphettad frass som lades på ytan efter sådd minskade antalet plantor som grodde. Däremot gynnade obehandlad frass som blandades in i jorden plantans höjd, medan ytlig applicering ökade tillväxten av ovanjordisk biomassa. Olika behandlingar påverkade också näringsinnehållet i den ovanjordiska biomassan. **Artikel IV** undersökte hur mikroberna i frass påverkar vetets tillväxt, näringsinnehåll i ovanjordisk biomassa och resistens mot bladlöss. Genom att jämföra steriliserad och osteriliserad frass fann vi att mikroberna hade begränsade effekter på tidig vetetillväxt i stort, men det fanns vissa fördelar under bladlusangrepp—plantor med osteril frass behöll något mer rotbiomassa och klorofyll vid angrepp. Vi såg också tydliga förändringar i markens mikrobiella sammansättning beroende på både frassbehandling och bladlusnärvaro, vilket tyder på att frassmikrober kan forma rhizosfären på sätt som kan få betydelse över tid.

Tillsammans visar dessa studier att ätliga insekter och frass kan bidra till ett mer hållbart livsmedelssystem—men bara om vi noggrant utformar hur systemen ska fungera. Allt hänger ihop: vilken typ av växtrester som används som foder påverkar syrsornas tillväxt och frassens kvalitet; frassen påverkar i sin tur grödornas utveckling beroende på hur den behandlas och appliceras; slutligen kan mikroberna i frass påverka både tillväxt och växternas motståndskraft mot skadegörare.

Genom att bättre förstå dessa samband kan vi ta ett steg närmare att skapa cirkulära livsmedelssystem som minskar svinn och bidrar till att mätta världens befolkning på ett mer hållbart sätt.

III

BRILL
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RESEARCH ARTICLE

Frass pre-treatment and application method impact spring wheat vegetative growth and nutrient concentration

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Abstract

The house cricket (*Acheta domesticus*) is a widely farmed edible insect species, and its by-product – frass – has potential as a sustainable soil amendment. However, the efficacy of frass may depend on how it is pre-treated and applied. This study evaluated the effects of cricket frass on the vegetative growth and nutrient concentration of spring wheat (*Triticum aestivum*) under different frass pre-treatments and application methods. Wheat was pot-grown in a greenhouse for eight weeks — from seed germination to flowering — with one control (no frass) and six experimental treatments, combining two pre-treatments (non-heated and heat-treated frass) and three frass application methods (surface application, mixed into the substrate, and 2-week delayed application). Germination, plant height, shoot biomass, leaf chlorophyll content, and shoot nutrient concentration were measured. Frass pre-treatment and application method significantly influenced wheat growth and nutrient concentration. Germination reached 100% with heat-treated frass mixed into the substrate and delayed application of no-heat frass but dropped to 60% with surface-applied heat-treated frass. The tallest plants grew with no-heat frass mixed into the substrate, while surface application, regardless of heat treatment, produced the greatest shoot biomass. Delayed application, regardless of pre-treatment, resulted in the highest leaf chlorophyll content. Surface-applied heat-treated frass increased plant nitrogen and potassium concentrations, whereas no-heat mixed frass enhanced phosphorus levels. These findings demonstrate that cricket frass can improve wheat growth and nutrient concentration, but its effects vary by pre-treatment and application method. Optimising these factors could maximise its potential as a sustainable soil amendment in crop production.

Keywords

Acheta domesticus – biostimulant – edible insects – insect faeces – organic fertiliser

1 Introduction

The edible insect sector is expected to expand significantly within the coming years, offering an alternative solution to global food security challenges (Siddiqui *et al.*, 2023). However, alongside supplying food, the growth of the edible insect sector will result in an increased production of waste, such as frass. In the context of mass insect rearing, frass is a mixture of insect faeces, shed exoskeletons, dead insects, insect parts, and leftover feed. This mixture frequently contains an array of essential nutrients for plant growth

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that can be valuable as an organic fertiliser (Beesigamukama *et al.*, 2022). Frass can also be used as a biostimulant – a substance that enhances plant growth, nutrient acquisition, stress tolerance, and/or crop quality – due to the presence of chitin (a main component of the insect exoskeleton) and potentially beneficial microbes (Poveda *et al.*, 2019; Barragán-Fonseca *et al.*, 2022; Ferruzca-Campos *et al.*, 2023). The use of frass as a soil amendment, whether as a fertiliser or biostimulant, has therefore the potential to increase the sustainability of edible insect production by reducing the reliance on synthetic inputs in crop production and supporting the development of food system circularity (Smetana *et al.*, 2022).

Cereal crops, such as wheat (*Triticum aestivum*), are among the most widely cultivated staple crops globally, making them an important target for evaluating the agronomic potential of frass as a soil amendment. Several recent studies have investigated the potential of frass as a soil amendment, primarily testing frass sourced from black soldier fly larvae (*Hermetia illucens*) or mealworms (*Tenebrio molitor*). For example, black soldier fly frass applied at a rate of 7.5 t/ha increased maize grain yield by 27% compared with mineral fertilisers at equivalent nitrogen rates, highlighting the potential of frass to replace synthetic fertilisers (Beesigamukama *et al.*, 2020), and the same type of frass also increased vegetative shoot biomass and foliar nutrient content of barley, oats, spelt and triticale (Carroll *et al.*, 2023). Mealworm frass was also found to significantly improve barley vegetative biomass and nutrient uptake (Houben *et al.*, 2020). These findings suggest that frass may hold significant promise for improving plant growth and nutrient concentration in cereal crops.

However, while frass has shown benefits in certain growing conditions, the effectiveness of frass as a soil amendment can vary depending on several factors. For example, the type of insect that produced the frass and the composition of the frass (i.e. faeces or shed exoskeletons) can influence plant growth and rhizosphere communities (van de Zande *et al.*, 2024). Furthermore, the way frass is applied can affect the accessibility of nutrients to plants. While no studies have specifically compared frass application methods, a review and meta-analysis on fertiliser placement suggests that subsoil application of nutrients can enhance yield and nutrient uptake compared to surface broadcasting (Mehdi *et al.*, 2016). Additionally, heat pre-treatment of frass – commonly required for its use as fertiliser – may influence microbial composition, activity, and biomass (Praeg and Klammsteiner 2024).

As the edible insect sector grows, evaluating the effectiveness of frass as a soil amendment is crucial for understanding its agronomic potential. In this study, we investigated the use of frass from the house cricket (*Acheta domesticus*) as a soil amendment in spring wheat (*Triticum aestivum*) cultivation. *Acheta domesticus* is one of the most widely farmed insect species for food and feed due to the species' high protein content, efficient feed conversion, and rapid reproduction (Gahukar 2016; Pilco-Romero *et al.*, 2023). Despite its commercial significance, research on *Acheta domesticus* frass remains limited. The aim of this study was to evaluate the effects of *Acheta domesticus* frass on the vegetative growth and nutrient concentration of spring wheat, focusing on how these outcomes are influenced by different heat pre-treatments applied to the frass and by different frass application methods. We hypothesised that (H1) *Acheta domesticus* frass applied as fertiliser will enhance shoot biomass growth and nutrient concentration of young spring wheat plants; (H2) heat pre-treatment of the frass will impact the plant responses; and (H3) different frass application methods (surface application, mixed into the substrate, and 2-week delayed application) will influence the plant responses.

2 Materials and methods

Spring wheat (*Triticum aestivum*, var. 'Boett') was grown in a greenhouse for 8 weeks – from seed germination to flowering – at the Swedish University of Agricultural Sciences (Uppsala, Sweden) from September 10th to November 5th, 2023. During the growing period, the temperature in the greenhouse ranged between 22 and 25 °C and relative humidity between 28 and 61%. The greenhouse environment included artificial light conditions with a 16-hour light period and watering three times a week.

Four wheat seeds were planted directly into a 7.5-litre pot (d = 26 cm, h = 21 cm) at a depth of 2.5 cm, spaced 7.6 cm apart. Each pot had its own tray underneath to prevent nutrient leaching and cross contamination between frass treatments. For the growing medium, a low-nutrient potting mix (Supplementary Table S1) was used. The potting mix was composed of light and dark peat, perlite, sand/rock milk, lime, mineral fertiliser, and root powder, with a pH of 5.5–6.5.

TABLE 1 Nutrient content of the *Acheta domesticus* frass applied in the experiment, expressed in grams per kilogram of frass sample

Nutrients	Amount
Total nitrogen (N)	38.40
Phosphorous (P)	8.07
Potassium (K)	9.49
Calcium (Ca)	10.84
Magnesium (Mg)	4.71
Sodium (Na)	2.01
Sulphur (S)	4.58

Frass treatment and composition

Raw (untreated) frass was sourced from *Acheta domesticus* reared commercially as food for humans by an EU-based company, where the crickets were fed a grain-based diet, primarily consisting of barley, oats, and other plant-derived ingredients. The frass provided nitrogen, phosphorous, and potassium (NPK) in the proportions 4.7:1:1.2 (Table 1), which is similar to the corresponding proportions of 5.8:1:1.9 in many commercial NPK fertilisers. Before the experiment, all frass was stored at −10 °C for 2 days to kill viable eggs, cricket nymphs, and other insect pests that may be present. Frass was subsequently sieved (3 mm) to separate carcasses, large pieces of leftover feed, shed exoskeletons, and inorganic rearing material.

Experimental design

To evaluate the impact of application method, three common fertiliser application techniques – surface application, subsoil application, and side-dressing – were simulated to replicate standard agricultural practices (Jones, 2002). In the first method (henceforth *surface*), frass was applied to the surface of the pot after sowing, simulating surface broadcast fertilisation. In the second method (henceforth mix), frass was mixed into the substrate before sowing, simulating subsoil application, where fertiliser is incorporated below the surface using techniques such as ploughing, harrowing, or rotary tillage. In the third method (henceforth delay), frass was surface-applied two weeks after sowing, simulating side-dressing, where fertiliser is applied alongside crops after emergence.

To assess the effect of heat pre-treatment, each application method included two experimental groups. In the first group, non-heated frass (henceforth no-heat frass) was used, and in the second group heat-treated frass was used. The heat-treated frass was exposed to 70 °C for 1 h, following EU regulations on minimum processing requirements for animal by-products used as fertiliser (European Commission, 2021). The three application methods, each with frass either heat-treated or not, resulted in six experimental groups. In addition, a control group to which no frass was applied was included in the set-up.

For all seven treatment groups there were five replicates (i.e. pots). In each pot, four wheat seeds were planted in 2 kg of substrate (potting mix with or without frass). The potting mix provided 0.94 g of available nitrogen. To all groups except the control, 150 g of frass was added, corresponding to 7% (w/w) of the total substrate. This addition increased the total nitrogen availability by 5.76 g to a total of 6.70 g per pot (calculated as N concentration of frass (%) × frass amount (g)/100). A randomised design was implemented, with pot positions in the greenhouse rotated weekly to minimise potential side effects from light and temperature variations.

Measured outcomes

To assess how *Acheta domesticus* frass affects wheat growth – and how heat pre-treatment and application method influence vegetative growth and nutrient concentration – we measured germination, shoot height, and dry shoot biomass. Germination was measured as the percentage of wheat seeds that germinated out of the total number of seeds sown (i.e. the number of seeds germinated out of 20 seeds planted per treatment). Plant height was measured from the base of the stem to the highest node (the point on the stem where leaves emerge) using a hand-held ruler for each wheat seedling at week 8. To measure dry shoot biomass, wheat shoots from all plants were harvested at week 8, dried in an oven at 70 °C for 48 h, and weighed using a precision balance (ML1602T/00, Mettler-Toledo, Greifensee, Switzerland). Week 8 was selected as the endpoint for vegetative measurements because it coincided with the initial signs of reproductive development in the control group (i.e. seed head development), while all frass-treated plants remained in the vegetative stage, ensuring consistency in developmental phase across treatments.

To assess differences in plant nutrient concentration, leaf chlorophyll content and shoot nutrient concentration were measured. Leaf chlorophyll content, as assessed by SPAD, is commonly closely correlated with leaf nitrogen content (Uddling *et al.*, 2007). Therefore, leaf chlorophyll content was measured non-destructively using a SPAD chlorophyll meter (SPAD-502, Konica Minolta Sensing Inc., Japan), averaging three readings taken from the middle of the uppermost leaf of each seedling before harvest (week 8). The total nitrogen (N) concentration of shoot biomass was determined using the Kjeldahl method with a 2520 Digestor, Kjeltec 8400 Analyser and 8460 Sampler (FOSS Analytical, Hillerød, Denmark). The concentration of phosphorus (P), potassium (K), magnesium (Mg), sulphur (S), and calcium (Ca) in shoot biomass was analysed using a spectrophotometer (ICP-AES, ICP Spectro Flame, Spectro Analytical Instruments).

Statistical analysis

The data were analysed using the statistical software Stata version 14.2 (Stata, 2021). The unit of analysis throughout the study was the pot, with 5 pots per experimental group (and up to 20 plants per group). For the analyses of dry shoot biomass and shoot nutrient concentration, we used average measurements per plant within each pot to account for differences in germination, since variable plant numbers per pot would directly affect total biomass and nutrient values. This approach ensures that treatment effects reflect differences in plant performance, not just differences in germination. To complement the per-plant analysis, we also analysed total shoot biomass per pot to assess treatment effects at the pot level (Supplementary Figure S1).

Before analyses, the data were assessed for normality and homogeneity of variance using the Shapiro–Wilk and Levene tests, respectively. Normally distributed data were analysed using a one-way ANOVA, followed by Tukey's honest significant difference (HSD) test for pairwise comparisons when significant differences were identified ($p < 0.05$). For data that did not meet normality assumptions, the non-parametric Kruskal-Wallis test was used, with Dunn's test for pairwise comparisons when significant differences were observed ($p < 0.05$).

To compare the effects of frass and control treatments, a one-way ANOVA was applied. A two-way ANOVA was used to assess the impact of heat pre-treatment, application method, and their interaction. Since frass was not applied to control pots, the control group was excluded from the two-way ANOVA. Furthermore, a Pearson correlation analysis was used to evaluate the relationships between dry shoot biomass, height, and leaf chlorophyll content, using correlation coefficients (r) to quantify the strength and direction of the associations.

3 Results

The addition of *Acheta domesticus* frass as a soil amendment influenced multiple aspects of spring wheat growth. Furthermore, germination, plant height, shoot biomass, and plant nutrient concentration were all influenced by both heat pre-treatment and frass application method (Figure 1).

Germination

Heat pre-treatment affected germination differently depending on frass application method ($p = 0.023$) (Supplementary Tables S2–S4). Wheat that received heat-treated mixed application of frass and no-heat delayed application exhibited the highest percentage of germination (100 ± 0%), while heat-treated surface applied frass resulted in significantly reduced germination of the seeds (60 ± 13.7%) compared to all other treatments (Supplementary Tables S2–S4). No significant differences in germination were observed between the control and no-heat frass groups (Figure 1A, Supplementary Tables S2–S4); however, plants in the control group had significantly higher germination than plants with heat-treated, surface-applied frass ($p < 0.001$).

Height

Height of seedlings was significantly affected by both heat pre-treatment ($p = 0.013$) and application method ($p < 0.001$) of the frass (Supplementary Table S5–S7). Plants grown with no-heat frass were taller (27.05 ± 0.78 cm) than plants that received heat-treated frass (24.12 ± 0.78 cm). Wheat grown with no-heat frass mixed into the substrate before sowing produced the tallest plants (29.50 ± 1.31 cm), while surface application of heat-treated frass resulted in the shortest plants (20.48 ± 0.48 cm) (Figure 1B). No significant differences in plant height were observed between the control and no-heat frass groups; however, plants in the control group were significantly taller than those receiving heat-treated, surface-applied frass ($p = 0.001$).

Shoot biomass

Shoot biomass was significantly influenced by frass application method ($p = 0.004$), with surface application producing the highest biomass per plant across all treatments (5.82 ± 1.21 g) (Figure 1C, Supplementary Tables S8–S10). Neither pre-treatment of the frass, nor the interaction between pre-treatment and application method had any significant effects on the shoot biomass produced by the plants (Figure 1C). Furthermore, plants in the control group produced significantly

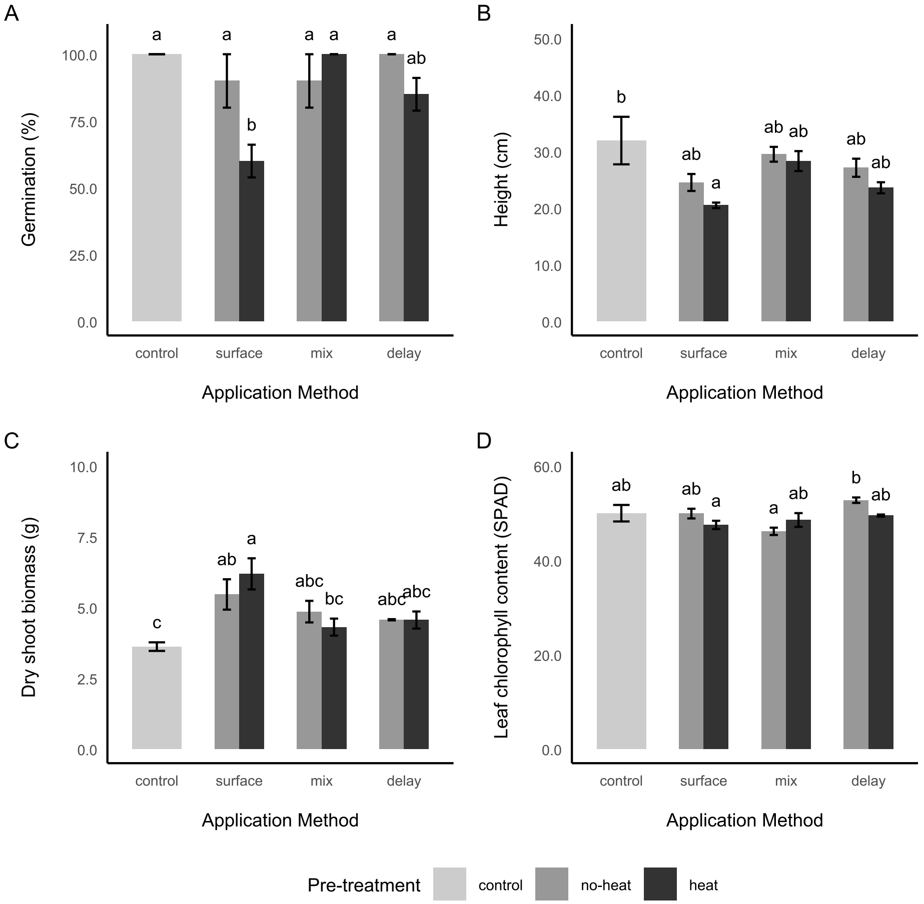

FIGURE 1 (A) seed germination (%), (B) plant height (cm), (C) dry shoot biomass (g) and (D) leaf chlorophyll content (SPAD) of young spring wheat plants pot-grown in a greenhouse at week 8 across treatments with no frass added (control), frass that is untreated (no-heat), and heat-treated frass (70 °C for 1 h) applied to the soil on the surface (surface), mixed into the soil before sowing (mix), or applied to the soil on the surface with a 2-week delay (delay). Each bar represents the mean of 5 pots per treatment, with error bars showing mean ± SE. Different lowercase letters above bars indicate statistically significant differences among treatments (Tukey HSD post-hoc test, $p < 0.05$).

less shoot biomass compared to those in surface-applied treatments, both with no-heat frass ($p = 0.007$) and heat-treated frass ($p = 0.001$) groups, but no significant differences were observed between the control and other application methods, regardless of the pre-treatment (Supplementary Tables S8–S10). A complementary analysis of total shoot biomass per pot showed a similar overall treatment effect ($p = 0.021$), though no pairwise differences were statistically significant (Supplementary Figure S1).

Leaf chlorophyll content and plant nutrient concentrations

The leaf chlorophyll content in the plants was affected by the frass application method ($p < 0.001$), and delayed application of frass, regardless of pre-treatment, resulted in the highest SPAD values (51.11 ± 1.95) compared to surface (48.70 ± 2.38) and mix (47.34 ± 2.76) applications (Figure 1D). The heat pre-treatment caused higher SPAD values compared with the no-heat pre-treatment only in the mixed application, but lower SPAD values in the other two application methods (Figure 1D), a pattern reflected by a significant interaction between heat treatment and application method ($p = 0.01$) (Supplementary Table S11). The pre-treatment alone had no significant effect ($p = 0.155$). Furthermore, no significant differences in leaf chlorophyll content were observed between the control and frass treatments, regardless of pre-treatment (Supplementary Table S11).

Shoot nutrient concentrations at week 8 varied significantly across treatments (Figure 2). Surface application of heat-treated frass resulted in the highest nitrogen and potassium concentrations. The concentration of phosphorus was highest in shoots from the no-heat mix application, while magnesium concentration peaked with surface-applied heat-treated frass. Sulphur and calcium concentrations were not significantly affected by either application method or heat treatment (Supplementary Table S6). Control treatments generally exhibited lower levels of shoot nutrients compared to frass-amended treatments, although the extent of these differences varied depending on the nutrient, heat-pre-treatment, and application method (Supplementary Table S12).

The correlation analysis revealed that shoot biomass was not significantly correlated with neither shoot height ($p = 0.10$) nor leaf chlorophyll content ($p = 0.68$). However, there was a significant positive correlation between shoot height and leaf chlorophyll content ($p = 0.02$, $r = 0.36$).

4 Discussion

This study shows that frass from *Acheta domesticus*, when added to the soil, can affect the growth and nutrient concentration of young wheat (*Triticum aestivum*) plants. Effects were seen in many plant traits measured and varied depending on if the frass was heat treated before use and how the frass was applied to the soil. Similar patterns have been observed with frass from other edible insect species, where mealworm frass enhanced barley biomass and nutrient cycling (Houben *et al.*, 2020), and black soldier fly larvae frass increased shoot biomass and foliage nutrient content in cereals (Carroll *et al.*, 2023). While our results partially support the hypothesis that *Acheta domesticus* frass would enhance shoot biomass growth and nutrient concentration of young spring wheat plants (H1), they also confirm that heat pre-treatment (H2) and application method (H3) significantly influence the plant responses. To our knowledge, no previous studies have specifically investigated how frass application methods influence crop performance. Research on conventional fertilisers have demonstrated that application techniques can significantly affect nutrient availability and plant growth (Mehdi *et al.*, 2016), implying that tailored frass application strategies could enhance agronomic benefits of frass. Additionally, while a heat pre-treatment of 70 °C for at least 1 h is essential for pathogen control, it can reduce microbial activity (Van Looveren *et al.*, 2022; Praeg and Klammsteiner 2024) and impact growing conditions. Together, these findings highlight the potential of insect frass as a sustainable soil amendment while emphasising the importance of optimising frass management and application protocols.

In our study, mixed application of heat-treated frass and delayed application of no-heat frass exhibited the highest germination, whereas surface application of heat-treated frass significantly reduced germination. One potential mechanism for the observed reduction in germination rates with surface-applied heat-treated frass is the combined effect of heat pre-treatment and application method, leading to chemical and biological alterations – e.g. the release of phytotoxic compounds (Cui *et al.*, 2024) or reduction of beneficial microbes – that may have altered soil conditions near the seed, with surface application potentially concentrating these effects and exposing seeds to unfavourable conditions. This study did not assess phytotoxicity nor microbial dynamics, which could provide further insight into the underlying mechanisms. Additionally, this result may be more pronounced in controlled greenhouse conditions using potting mix and may differ in a field setting, where greater variability in soil structure and microbial activity could mitigate negative effects.

Along with the reduced germination observed with surface-applied heat-treated frass, the plants generated by this heat pre-treatment exhibited the highest shoot biomass per plant. This pattern may be due to either reduced competition among fewer germinated seedlings (i.e. providing more nutrients per individual plant) and/or differences in shoot (tiller) number across treatments, as plants with fewer tillers tend to grow taller, while more tillers can result in shorter shoots but greater biomass. Additionally, application method played a critical role in determining plant height and shoot biomass, with mixing frass into the soil producing the tallest plants and surface application resulting in the greatest biomass per plant. In terms of nutrient concentration, delayed frass application, regardless of heat pre-treatment, produced the highest leaf chlorophyll content (SPAD) values, while shoot nutrient analysis revealed that surface-applied heat-treated frass led to

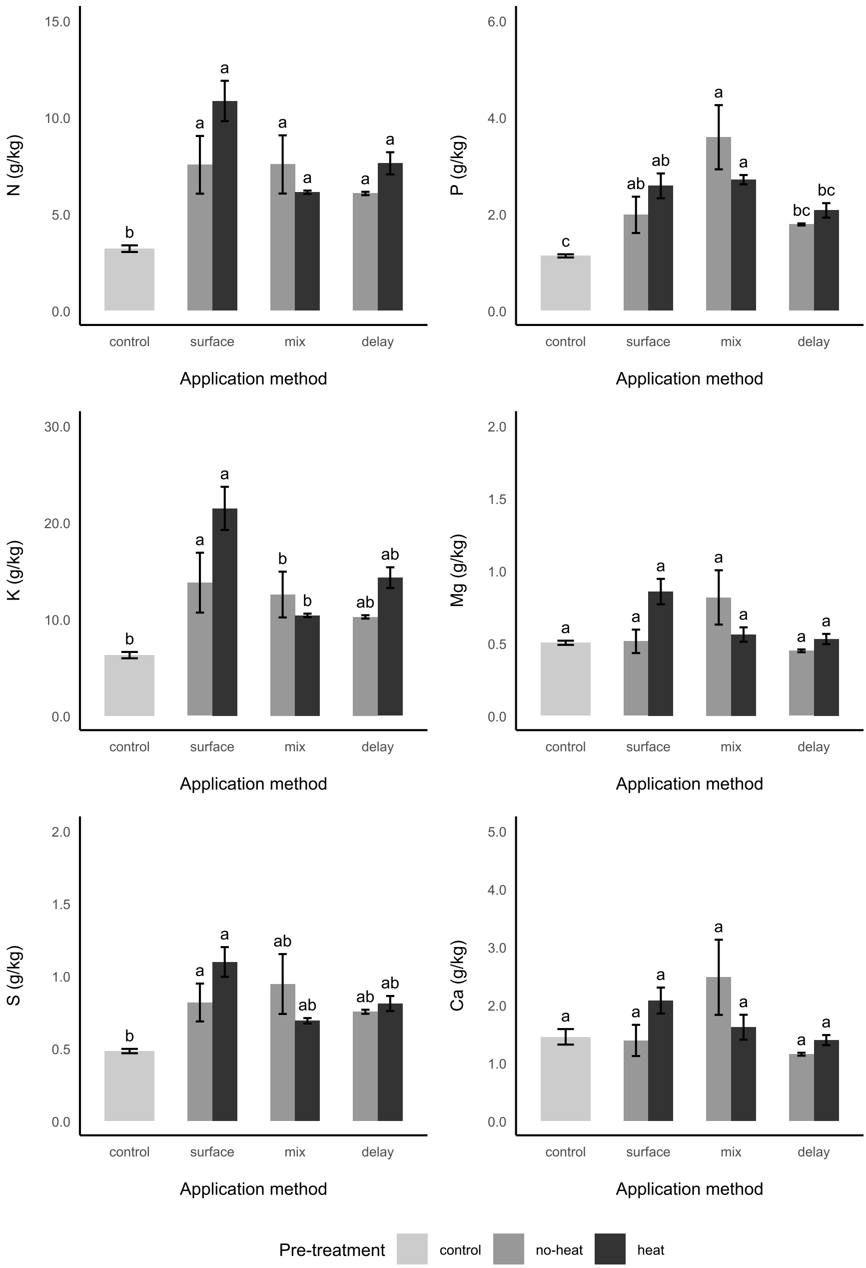

FIGURE 2 Nutrient concentrations (g/kg) of N, P, K, Mg and S in the shoots of 8-week-old spring wheat plants pot-grown in a greenhouse across treatments with no frass added (control), frass that is untreated (no-heat), and heat-treated frass (70 °C for 1 h) applied to the soil on the surface (surface), mixed into the soil before sowing (mix), or applied to the soil on the surface with a 2-week delay. Each bar represents the mean of 5 pots per treatment, with error bars showing mean ± SE. Different lowercase letters above bars indicate statistically significant differences among treatments (Dunn's post-hoc test, $p < 0.05$).

the highest shoot nitrogen and potassium concentrations.

An interesting finding of this study is the discrepancy between the effects of frass on height and biomass. While shoot biomass was not significantly correlated with height or leaf chlorophyll content (SPAD), which is in contrast to other studies on wheat (Hamnér *et al.*, 2017), plant height increased significantly with leaf chlorophyll content. This suggests that frass influenced shoot height and biomass in different ways, potentially affected by the number of plants (through germination rate), the number of tillers (shoots) produced per plant, and the specific wheat variety used. Moreover, vegetative growth may not necessarily translate into increased grain yield at harvest. While traits such as plant height and biomass are often used as proxies for productivity in controlled studies (Weiner, 2004), grain yield is determined by additional factors, such as the allocation of resources to reproductive structures during the grain-filling stage. Thus, under certain environmental conditions, greater plant biomass has even been reported to be associated with reduced yield (Thapa *et al.*, 2020). These dynamics can also differ between greenhouse and field settings, where nutrient availability, stressors, and competition are more variable (Asplund *et al.*, 2016). Future research should investigate how frass pre-treatments impact both vegetative growth and harvestable grain yield and quality under field conditions, addressing current gaps in understanding the direct effects of frass on crop productivity and grain quality.

Beyond the observed physiological effects on plant growth and nutrient concentrations, the practical feasibility of frass as a crop fertiliser must be considered. While frass demonstrates significant potential in crop production, today, its use as a fertiliser for large-scale field applications may be constrained by limited supply or high transaction costs, as the edible insect industry is still in its early stages. Frass may therefore be best used as a supplement to conventional fertilisers or as a targeted soil amendment (e.g. biostimulant) for specific stages of crop growth. Furthermore, while the use of a single crop species and one frass type limits the scope of our study, the simplified and controlled experimental design allowed us to clearly isolate treatment effects – an important step given the limited research on *Acheta domesticus* frass as a fertiliser. Future research should build upon these findings by evaluating different frass types across diverse cropping systems and investigating longer-term impacts of frass on soil health, nutrient cycling, and microbial communities in the field.

5 Conclusion

Overall, *Acheta domesticus* frass shows promise as a soil amendment for the vegetative growth and nutrient concentration of spring wheat. However, there are nuances to its use. Heat pre-treatment and application method are critical factors influencing the effectiveness of frass, with mixed and delayed applications improving germination, no-heat mixed application promoting greater plant height, and surface application of heat-treated frass increasing shoot biomass. In terms of nutrient concentrations, delayed application produced the highest leaf chlorophyll content and surface-applied heat-treated frass resulted in the highest shoot concentrations of nitrogen and potassium. By demonstrating how frass management and application strategies can impact plant growth and nutrient dynamics, this study contributes to the broader understanding of insect frass as a soil amendment.

Supplementary materials

Data is available on https://doi.org/10.1163/23524588-bja10245 under Supplementary Materials.

Conflict of interest

The authors declare no conflict of interest.

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House crickets (*Acheta domesticus*) contribute to circular food systems by converting organic residual streams into protein and frass. This thesis investigates how crickets and their frass influence system sustainability. Using cricket performance trials, plant bioassays, and microbial analysis, I assess how crop residue diets affect cricket growth and survival, frass quantity and quality, and how different frass treatments influence wheat growth, nutrient uptake, and aphid population growth. I show that both diet and frass handling shape these outcomes, with frass microbes affecting plant performance and rhizosphere communities.

Sara Capitán received a PhD education from the Department of Ecology, Swedish University of Agricultural Sciences (SLU) in Uppsala, and obtained a Master of Science in Agronomy from the University of Wyoming.

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