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Assessing effects of soil fungal bioinocula on aboveground arthropod pests and beneficials in strawberry (*Fragaria × ananassa*) fields

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With 5 figures and 2 tables

Abstract: Strawberry plants are attacked by various arthropod herbivores, including insects and mites, causing damage to different parts of the plants during the season. Strawberry plantations also harbour beneficial arthropods such as predators, parasitoids and pollinators (e.g., predatory mites, lacewings, hoverflies,). Applications of beneficial fungi may enhance plant growth and decrease the incidence of specific arthropod pests, but their impact on entire arthropod communities is largely unknown. Two-season field trials were conducted in Denmark and Slovenia to study effects of the entomopathogenic *Metarhizium brunneum*, the mycoparasitic *Clonostachys rosea*, and arbuscular mycorrhizal biofertilizers, all fungi, on the main pest and beneficial arthropods in integrated (IPM) and organic (ORG) strawberry production systems. Soil-deployed bioinocula had limited impact on aboveground arthropod assemblages, but treatment with the *M. brunneum* bioinoculum significantly increased the number of predators in the trials in Slovenia, while reducing arthropod abundance and diversity in Denmark. Agricultural management strongly affected arthropod communities, with ORG trials harbouring higher arthropod abundance and diversity compared to IPM, suggesting potential benefits of sustainable farming practices. The nuanced relationships among herbivores, beneficials, and pest infestations invites further investigation to unravel the underlying ecological mechanisms shaping pest dynamics in diverse agricultural landscapes.

Keywords: agroecosystem; biological control; entomopathogenic fungi; integrated pest management (IPM); insect; organic production; sustainable agriculture; agroecology

1 Introduction

Reduced reliance on chemical pesticides is a key goal of the European Union's agricultural agenda (European Parliament 2009). Conventional pest management in strawberry faces major challenges, including pesticide resistance (Jakka et al. 2016), residues in food and feed (EFSA 2018), environmental risks (Devine & Furlong 2007), and human health concerns. Alternative approaches, particularly soil bioinocula-based strategies, are therefore of much interest. To address this, the EU project Excalibur (Exploiting the multifunctional potential of belowground biodiversity in horticultural farming; https://excaliburh2020.eu/en/) evaluated the potential of soil bioinocula to reduce pesticide and fertilizer inputs in horticultural crops, including strawberry (*Fragaria × ananassa* (Duchesne ex Weston) Duchesne ex Rozier) (Rosales: Rosaceae) (see Kowalska et al. 2020; Malusà et al. 2021).

Strawberries are susceptible to many pathogens (Maas 2004) and the plants are attacked by several arthropod pests (Lahiri et al. 2022) that damage various plant parts throughout the season. Major pests include aphids (Hemiptera: Aphididae), phytophagous thrips (Thysanoptera), true weevils (Coleoptera: Curculionidae), cutworms (Lepidoptera: Noctuidae), sap beetles (Coleoptera: Nitidulidae), phytophagous tarnished plant bugs (Hemiptera: Miridae), whiteflies (Hemiptera: Aleyrodidae), and spider mites (Acari: Tetranychidae). Consequently, conventionally produced strawberries often contain some of the highest pesticide

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residues among fruits and vegetables (EFSA 2018), posing risks to human health and the environment (Parker 2015). Biological control using plant-beneficial microbes, offers a sustainable alternative within integrated production systems.

Beneficial soil microbes such as arbuscular mycorrhizal fungi (AMF), plant growth promoting rhizobacteria (PGPR) and fungi (PGPF), are well-known for enhancing the growth of agricultural and horticultural crops (Gruden et al. 2020). Beyond growth promotion, several beneficial microbes also increase crop resilience to below- and aboveground pests and pathogens (Pieterse et al. 2014). Recent research has shown that microbe-induced plant defence responses, both direct and indirect, are highly context-dependent (Lee Díaz et al. 2021). The successful activation of these responses depends on multiple factors, including the identity of the beneficial microbe and plant cultivar, abiotic and biotic environmental conditions, and the composition of resident rhizosphere communities (Pieterse et al. 2014).

The present study investigated the potential of three fungal bioinoculum treatments to enhance strawberry plant growth and fruit yield under field conditions. The first was a formulation based on *Metarhizium brunneum* Petch (Hypocreales: Clavicipitaceae), an entomopathogenic fungus (EPF). Strains of *Metarhizium* and other EPF have shown efficacy in controlling strawberry pests in laboratory experiments, greenhouse pot experiments (Canassa et al. 2020a; 2020b), and field studies (Canassa et al. 2020b; Mantzoukas et al. 2022). Application of the EPF *Beauveria bassiana* (Bals.-Criv.) Vuill. and *Metarhizium robertsii* J.F. Bisch., S.A. Rehner & Humber generally showed no adverse effects on beneficial arthropods, including predatory mites and bumblebees (Canassa & Esteca et al. 2020; Leite et al. 2022). In addition to infecting insects and mites, many EPF such as *Metarhizium* spp. can also establish intimate relationships with plants as root colonizers or endophytes (Stone & Bidochka 2020).

Clonostachys rosea (Link) Schroers, Samuels, Seifert & W. Gams (Hypocreales: Bionectriaceae), the second bioinoculum tested in this study, became known as an aggressive mycoparasite that can destructively colonize mycelium of other fungi, including plant pathogens, mainly through activating cell wall-degrading enzymes (Chatterton & Pnja 2009). Additional mechanisms include the production of antibiotic compounds (Fatema et al. 2018) and tolerance to toxins produced by other fungi (Utermark & Karlovsky 2007), enabling *C. rosea* to compete effectively for nutrients and space and to suppress plant pathogens. Numerous studies have demonstrated its beneficial roles in agricultural systems, and several commercial biopesticides based on *C. rosea* are available (Funck Jensen et al. 2021). Moreover, the occasional associations with insects, nematodes, slugs, spiders, ticks, and mites (Zhao et al. 2023), suggest that *C. rosea* is a generalist with broad ecological adaptability (Piombo et al. 2023).

The third fungal bioinoculum tested contained a mixture of arbuscular mycorrhizal fungi (AMF), which act as plant biostimulants through symbiotic interactions with roots, enhancing nutrient and water uptake and tolerance to abiotic stress (Berruti et al. 2016). AMF colonize roots only in the presence of suitable host plants, extending their hyphal networks into the surrounding soil and thereby increasing the absorptive capacity of the root system (Berruti et al. 2016). Although AMF represent one of the best-studied plant-fungus symbioses, their use as growth-promoting agents in strawberry production remains relatively unexplored.

The objectives of this field study were to assess the effects of the three selected soil fungal bioinocula under two agricultural management practices on strawberry canopy arthropod communities when applied at two environmental conditions in Europe. In contrast to past field studies focusing on specific strawberry pests (e.g., mites (Canassa & D'Alessandro et al. 2020), aphids and thrips (Mantzoukas et al. 2022), or weevils (Ansari & Butt 2013; Klingen et al. 2015)), the novel aspect was to study the effects of soil fungal bioinocula on the broader arthropod assemblage of strawberry plant canopies. Thus, we assessed several groups of canopy pests and beneficial arthropods. We hypothesized that (1) treatment with different beneficial soil fungi will reduce the incidence of pests, whereas AMF and *C. rosea* will increase plant growth, (2) organic agricultural management practice will increase the overall abundance of arthropods, and (3) northern geographical location and pedo-climatic conditions will affect arthropod community composition and reduce the total abundance of aboveground arthropods.

2 Material and methods

2.1 Experiment description and locations

Four strawberry field trials were conducted in Slovenia and Denmark (2021–2023) as part of the Excalibur project.

2.1.1 Description of the trials

Slovenian field trials took place at Brdo pri Lukovici (300 m above sea level (asl), 25 km northeast of Ljubljana; 46.166205, 14.679168), in two fields: organic (ORG) and integrated (IPM), within the experimental orchard of the Agricultural Institute of Slovenia. The ORG trial was managed with minimal inputs, weeds were removed manually, and no fertilizers were added during the experiment. The IPM plots were treated with herbicide in 2021, before the start of the experiment, and with a fungicide in spring 2023 (Table S1). No fertilisation was needed in both fields, since they had previously been managed with cover crops and soil analyses in 2021 showed sufficient nutrient levels. In July 2021, the soil was tilled and four parallel elevated ridges were formed per field, covered with black foil with t-tape irrigation tube under the foil. The foil had pre-prepared holes for planting strawberries. On 27 July 2021, 1920 frigo plants (early fruiting cultivar 'Clery') were planted, spaced 50 cm between rows and 20 cm between plants. Both fields were covered by plastic tunnels from blooming (BBCH 60) until the end of the fruit-ripening stage (BBCH 89).

The Danish trials were conducted in open field on commercial farms in the Sjælland Region, both located near the coast: the ORG trial was near Store Ladager (29 m asl, 8.7 km from the coast, 55.519671, 12.079487), while the IPM trial was near Skælskør (18 m asl, 8.4 km from the coast, 55.274700, 11.374771). In 2020, pumpkin was cultivated in the ORG trial and winter wheat in the IPM trial. The ORG trial followed low-input organic practises using organic manure, slug repellent, and mechanical weed removal, while the IPM trial used chemical inputs for weeds, insects and diseases control, along with synthetic fertilizers (Table S1). Both farms planted bare-root frigo plantlets (late-fruiting cultivar 'Faith') on 10–11 May 2021 (ORG) and 5–11 April 2021 (IPM), spaced 1 m between the rows and 30 cm between plants.

2.1.2 Common field trial design and description of treatments

The experiment included four treatments: three fungal bioinocula (*M. brunneum, C. rosea* and arbuscular mycorrhizal fungi) and one untreated control. Bioinocula were applied as solid-state formulations (see below) during transplanting in spring 2021 in Denmark (29 April in IPM and 20 May for ORG) and in summer in Slovenia (27 July). The prepared suspension was hand-applied directly into the planting holes before inserting the frigo plants, ensuring close contact between roots and inoculum. Treatments were repeated in spring 2023 (18 April [ORG] and 20 April [IPM] in DK and 21 April in SLO) by applying watery spore suspensions with a 100 ml syringe into the soil around the plants' stem base (further details in Table 1). Each field had six blocks, each with four plots (one per treatment). Each plot contained 40 plants in four rows of 10 plants (Fig. S1). The outer rows served as buffers, so only the 20 central plants were assessed in each plot.

2.1.3 Bioinocula production

The 2021 bioinocula were grown on potato dextrose agar (PDA) (BD Difco, USA; *M. brunneum*, strain 1868) or 1/3 strength PDA (*C. rosea*, strain 1881) for 18 days at 25 °C in darkness. Conidia were amended with 0.01% agar (*C. rosea*) or 0.01% Tween 80 (*M. brunneum*), filtered through four layers of cheesecloth and diluted to a concentration of 3×10^6 conidia ml^{-1} (*M. brunneum*) or 3.2×10^6 ml^{-1} (*C. rosea*). Aliquots of rye kernels (1.5 kg) were cooked (70 min in tap water), placed in mushroom bags (49 × 36 cm, with air vents), autoclaved (33 min, 120 °C), and inoculated in sterile conditions with 100 ml spore suspension. After sealing and mixing, incubation bags underwent aerobic solid-state fermentation for 37 days at 22 °C and then stored at 4 °C until further use. At planting, 5 g of fermented rye substratum with sporulating mycelium was used per plant. Dilution plating of suspended conidia revealed contamination free inoculum with ~5.0×10^8 (*M. brunneum*) or ~5.3×10^8 colony forming units (*C. rosea*) g^{-1}.

In 2023, liquid bioinocula were prepared by suspending conidia from PDA into 0.1% Tween 80 (for *M. brunneum*) or from oatmeal agar into distilled water (for *C. rosea*). Using a hemocytometer the spore suspensions were adjusted to a concentration of 1×10^7 conidia ml^{-1} and stored overnight at 4 °C before being used the next day. Spore viability was confirmed by plating and counting germinated spores after 24 h and was ≥ 95%. In the field, 10 ml of each suspension was diluted in 990 ml of tap water, thus each plant received 1×10^7 spores in 100 ml.

ASTERIA® (INOCULUM*plus*, Bretenière, France) is a granular AMF bioinoculum, with five fungal species (*Funneliformis geosporum* (T.H. Nicolson & Gerd.) C. Walker & A. Schüßler, *F. mosseae* (T.H. Nicolson & Gerd.) C. Walker & A. Schüßler, *Rhizoglomus intraradices* (N.C. Schenck & G.S. Sm.) Sieverd., G.A. Silva & Oehl, a species of *Glomus* Tul. & C. Tul. (all, Glomerales: Glomeraceae), and *Entrophospora claroidea* (N.C. Schenck & G.S. Sm.) Błaszk., Niezgoda, B.T. Goto & Magurno (Entrophosporales; Entrophosporaceae)) and ≥ 1000 infective propagules g^{-1} product. In 2021, 1 g was hand-placed near the roots during transplanting; in 2023, 1 g was diluted in 100 ml of water and applied on each plant by drenching.

Table 1. Description of the treatments and doses.

Treatment	Product provider	Main function of the fungus	Dose in 2021 (weight of rye-based formulation – dose* per plant)	Dose in 2023 (volume of liquid formulation – dose* per plant)
Metarhizium brunneum 1868	Agricultural Institute of Slovenia's mycological collection	Entomopathogen	5 g – 3.62×10^9	100 ml – 1×10^7
Clonostachys rosea 1881	Agricultural Institute of Slovenia's mycological collection	Antagonist of fungal plant pathogen	5 g – 2.83×10^9	100 ml – 1×10^7
Arbuscular Mycorrhizal Fungi (AMF, product Asteria)	INOCULUM*plus*	Nutrient enhancer	1 g – 1.74×10^9	100 ml –1.74×10^9
Control (untreated)	/	/	/	/

*number of conidia for *M. brunneum* and *C. rosea* but infective propagules for AMF.

2.2 Arthropod sampling protocol

Each plot of 20 plants was first visually inspected for beneficial flying pollinators, including hoverflies (f. Syrphidae), European honeybees (*Apis mellifera*), bumblebees (*Bombus* spp.), solitary wild bees (Anthophila, Apiformes clade), and others like f. Stratiomyidae. Arthropods were then shaken off from inflorescences or fruit buds of five randomly selected plants per plot into white trays (29 cm × 16 cm), with each blossom cluster shaken for three seconds. The arthropods were counted and grouped for each tray in the field, including pests (thrips, *Anthonomus* sp. and other Curculionidae, *Lygus* sp., Miridae, flea beetles) and beneficial arthropods such as predators (spiders/harvestmen, hoverfly larvae, ladybug larvae and adults, lacewings, predatory bugs), and parasitoids. Finally, the canopies of 20 plants per plot were visually examined for herbivorous mites, whitefly pupae and adults, aphids, and aphid mummies, and the previously mentioned taxa up to these specified taxonomic levels.

All taxa were counted in each plot (six plots per treatment and per field trial). For whiteflies, aphids and herbivorous mites, we recorded only presence/absence on the 20 plants/plot. Table S2 lists all monitored arthropods and their taxonomy. Specimens collected in the field were identified using a 15× magnifying glass if needed and assigned to a feeding guild or the required taxonomic level on-site. Small or morphologically challenging arthropods were identified in the lab with specialised taxonomic keys and other reference works (Blackman & Eastop 2008; Dvořák & Roberts 2006; Freude et al. 2004, 2012; Martin et al. 2000; Nedvěd 2020; Oosterbroek 2015; Parikka & Tuovinen 2014; Schuh & Slater 1996) using a stereo microscope (Leica M205 C, Germany). Mite samples were sent to specialists for identification to at least the family level. In 2022 and 2023, assessments were conducted three to four times per year at key crop stages: first open flower blossoms (BBCH 60–61), full bloom (BBCH 65), start of harvest (BBCH 81–85), during harvest (BBCH 87–89) and after harvest (BBCH 91–93). Assessments were carried out in sunny, cloudy or partly cloudy weather. Hygro-meteorological conditions (i.e., air temperature, humidity, rainfall, wind speed) were retrieved from World Weather Online as daily and monthly averages, minimums, maximums or totals.

2.3 Measurement of plant traits

In spring 2022 and 2023, plant canopy diameter was measured in two perpendicular directions and multiplied to estimate canopy surface (cm^2), on eight plants/plot in Denmark (11 and 13 April 2022, and 11 and 12 May 2023) and on 20 plants/plot in Slovenia (21 April 2022, and 9 June 2023).

Strawberries were harvested in summer 2022 and 2023 from the central 20 plants/plot. Fruits were classified as marketable or unmarketable (e.g., malformed, *Botrytis* infected), counted and weighted. Average marketable fruit weight was obtained by dividing marketable yield by the number of fruits per plants.

In summer 2023, fresh biomass was measured by sampling 10 plants/plot in Denmark (20 and 21 July 2023) and five plants/plot in Slovenia (11 July 2023). Plants were dug out and shaken to remove soil from the roots, then washed with tap water. Plants were air-dried on tissue paper in the sun for one hour and weighted (canopy + roots).

2.4 Statistical analysis

Analyses were performed using R software v. 4.3.1 (Wilson & Norden 2015) and the "RVAideMemoire" package and associated guideline document (Hervé 2023).

Data from 2022 and 2023 were summed per plot. Arthropods were grouped by feeding guilds: pollinators, parasitoids, predators, herbivores, competitors (i.e., ants, Formicidae that farm and protect aphids against enemies), but also as the proportion of infested-plants (i.e., by aphids, whiteflies and/or herbivorous mites) and as total arthropods (i.e., sum of the previous groups, without springtails and Formicidae as these groups were only quantified in Slovenia). These eight variables were analysed using either generalized linear models ("glm" function, Poisson family), generalized mixed models ("glmer" function, "lme4" package (Bates et al. 2015), Poisson family; "glmmPQL" function, "MASS" package (Venables & Ripley 2002), quasi-Poisson family), or linear models (lm) depending on whether the variables were following the Poisson or Gaussian distribution using histograms (details in Supplementary Tables). Models were validated when (1) independancy, (2) homocesdasticiy, (3) normality of the residues, (4) absence of overdispersion were respected for glm (1), glmer (4), and lm models (1, 2, 3), using "plotresid" or "overdisp.glmer" function of the "RVAideMemoire" package (Hervé 2023). Taxon richness was assessed as the number of arthropod taxa present. Pearson correlations were performed between the feeding guilds and between the feeding guilds and the hygro-meteorological conditions. Whenever applicable, a response variable (i.e., arthropods or plant traits) was analysed using one of the above models. Then, a type II analysis of variance tested the significance of the country (Slovenia and Denmark), year (2022 and 2023 for plant traits), production system (ORG and IPM), treatment (Control, AMF, *C. rosea, M. brunneum*), bi- and tri-partite interactions among these factors, and Block. When Block was significant, it was treated as a random factor; when not significant, it was removed from the model (details in Supplementary Tables). Lastly, pairwise comparisons were performed using the estimated marginal means, and p-values were corrected using the false discovery rate when a factor was significant.

The structure of arthropod communities was analysed using the summed data per plot and per year, then centred and log ratio-transformed ("clr" function, "Hotelling" package) (Curran & Hersh 2021) with a redundancy analysis (RDA) for each country ("rda" function, "vegan" package) (Oksanen et al. 2025). Their composition was visualized with an alluvial plot to assess the data distribution across the different experimental factors. The specific or shared arthropod taxa between conditions of each experimental factor were visualized using upset plots and Venn diagrams after summing data per condition and conversion into presence/absence.

Regarding plant traits, canopy surface, total plant biomass and harvest parameters were analysed using linear models or linear mixed models (“lmer” function, “lme4” package), depending on whether Block was significant. Models were validated as previously described for lm (1, 2, 3) and lmer (2, 3).

3 Results

Arthropod counts (assessments) in Slovenia revealed 4,705 specimens in 2022 (from three canopy observations) and 8,380 in 2023 (four observations), and in Denmark 512 specimens in 2022 (four observations) and 2,307 in 2023 (four observations). These counts exclude plants infested by whiteflies, aphids, or herbivorous mites (details in Table S2).

3.1 Arthropod richness and abundance in feeding guilds

Overall, a significantly higher taxon richness was observed in Slovenia, especially in 2023, while in Denmark, a higher taxon richness was observed in organic (ORG) compared to integrated (IPM) production system in 2022 (Fig. 1, Fig. S2, Table S3). Additionally, the total number of arthropod individuals (i.e., sum of pollinators, parasitoids, predators and herbivores) was significantly influenced by country, production system and their interaction (Table S3).

The number of pollinators (i.e., adult hoverflies, honeybees, solitary bees, bumblebees and soldier flies) was significantly influenced by the country, treatment and an interaction between country and production system (Fig. 2A, Table S3). The lowest number of pollinators was observed in the Danish and the highest in the Slovenian ORG system. Within the countries, pollinators were more abundant in IPM than ORG in Denmark, whereas the opposite was found in Slovenia. The pairwise comparisons between the treatments were not significant.

The number of parasitoids (i.e., aphid mummies and parasitoid wasps) was significantly influenced by country and production system, but Post-hoc comparisons revealed no significant pairwise differences, and the data showed a relatively high variability (Fig. 2A, Table S3).

The number of predators (i.e., predatory mites, spiders/harvestmen, ladybug adults and larvae, hoverfly larvae, lacewings, centipedes, ground, soldier and rove beetles, earwigs, robber flies, wasps, and predatory heteropterans) was significantly influenced by country, production system and their interactions with treatment (Fig. 2A, Table S3). Predator numbers were markedly higher in Slovenian than in Danish systems and significantly greater in ORG than IPM

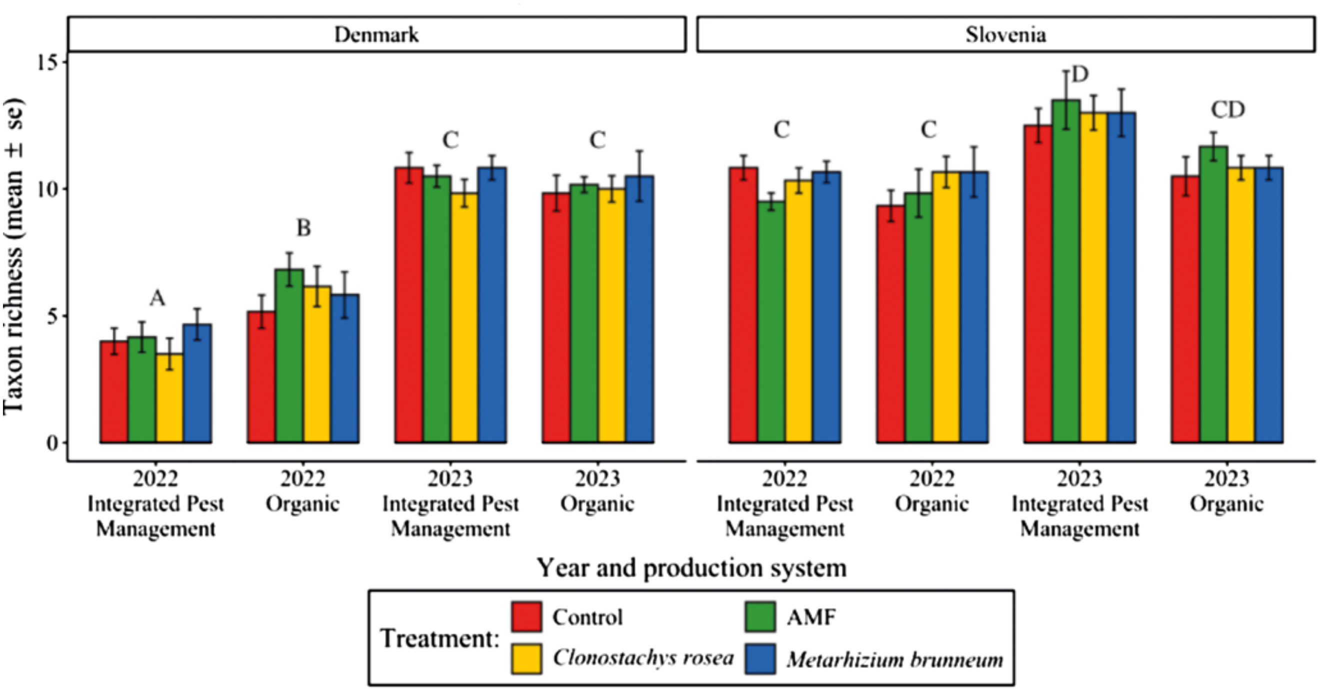

Fig. 1. Arthropod community richness (i.e., mean number ± standard error of taxa per plot) per year in experimental plots in Denmark and Slovenia. Different uppercase letters indicate significant differences between countries, years and production systems as the interaction between these factors was significant (n = 6 plots, each cumulates 7 or 8 observations). Statistical outputs are displayed in Table S3.

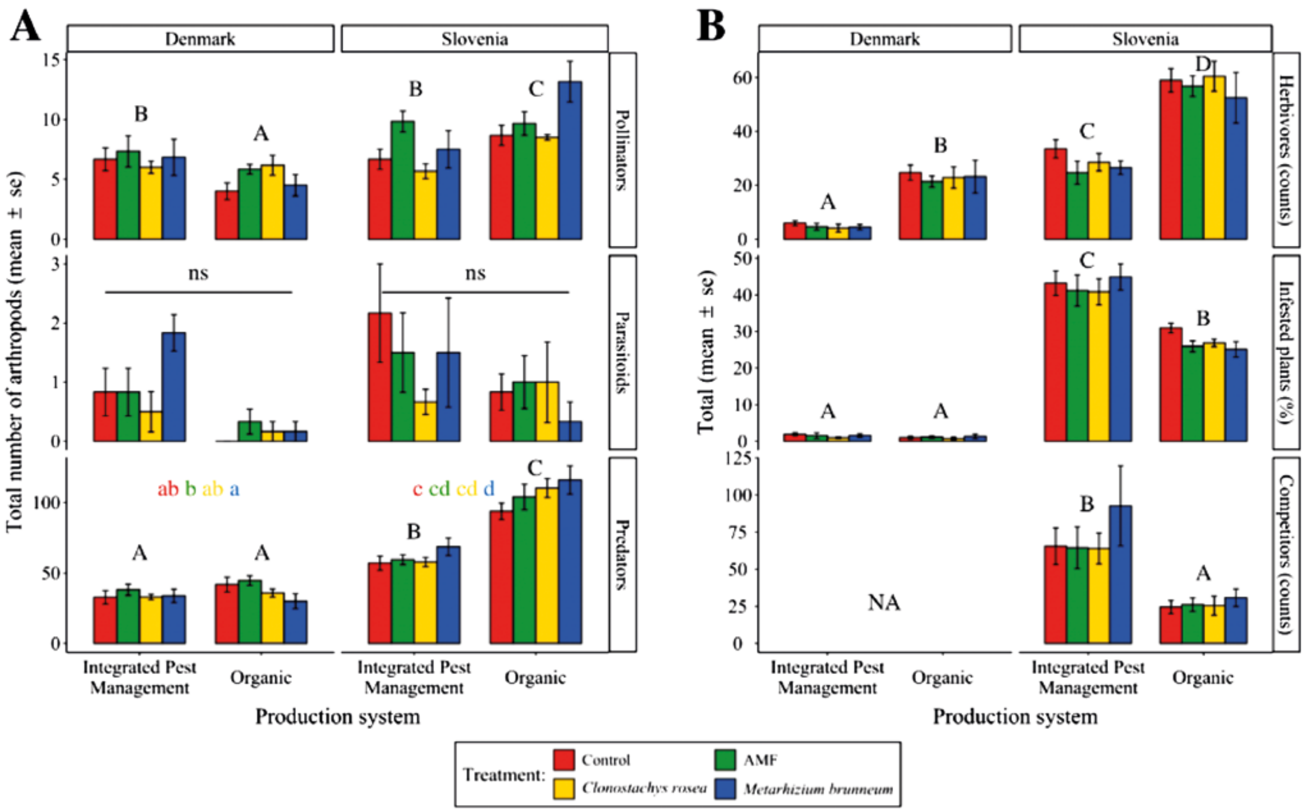

Fig. 2. Total abundance of beneficial (A) and pest (B) arthropods monitored in 2022 and 2023. 'Infested plants (%)' refers to the proportion of strawberry plant canopies infested with herbivorous mites, aphids and/or whiteflies. Uppercase black letters indicate significant differences between the countries (Denmark, Slovenia) and production system (integrated pest management, organic). In panel (A), lowercase coloured letters indicate significant differences between the two-way interaction 'country and treatment', for merged data sets of production system and are therefore not displayed above respective coloured bars ("ns", not significant while "NA", not acquired; n = 6 plots, each cumulates 7 or 8 observations) Detailed statistical outputs are displayed in Table S3.

in Slovenia. A contrasting pattern was observed in the ORG system: predators tended to be less abundant in the *M. brunneum* treatment in Denmark but significantly more abundant in Slovenia than in the control treatment. When analysed individually, however, predatory taxa (i.e., predatory mites, Araneae, and predatory Heteroptera) in Slovenia were not significantly influenced by the treatment (Table S4).

The number of herbivores (i.e., weevils, thrips, caterpillars, sap beetles, froghoppers, and phytophagous heteropterans) was significantly influenced by country, production system, and their interaction (Fig. 2B, Table S3). More herbivores were counted in Slovenia than in Denmark, with a higher number in ORG compared to IPM in both countries.

The proportion of plants infested with aphids, whiteflies, and herbivorous mites was influenced by country, production system and their interaction (Fig. 2B, Table S3). There were more infested plants in IPM than in ORG in Slovenia, and significantly less in both Danish systems than in Slovenia.

The number of competitors (i.e., Formicidae) was significantly higher in IPM than in ORG in Slovenia (Fig. 2B, Table S3).

3.2 Composition of the arthropod communities

There were significantly more arthropods observed in Slovenia than Denmark, and more in the ORG than in the IPM production system (Fig. 3, Table S3). In Slovenia, arthropod abundance was similar in both years and at the different monitoring times, while most arthropods in Denmark were observed in 2023 and after fruit harvesting. Overall, a prominent dominance of predatory mites, weevils and ants were observed in decreasing order in Slovenia, while in Denmark caterpillars and spiders, followed by thrips and lacewings, were dominant (Fig. 3A). Notable differences in the sampled arthropod communities were observed between sampling years, production system, and country (Fig. 3B, Fig. S3). In Slovenia, predatory mites and weevils were significantly more abundant in ORG in both years, while Formicidae were more abundant in IPM only in 2023 (Table S4). In Denmark, Lepidopteran caterpillars and thrips were consistently higher in ORG, whereas lacewings were unaffected by production system or treatment. Araneae were influenced by both factors in 2022, showing lower abundance in IPM and *M. brunneum* treatment, and only by factor treatment in 2023, being

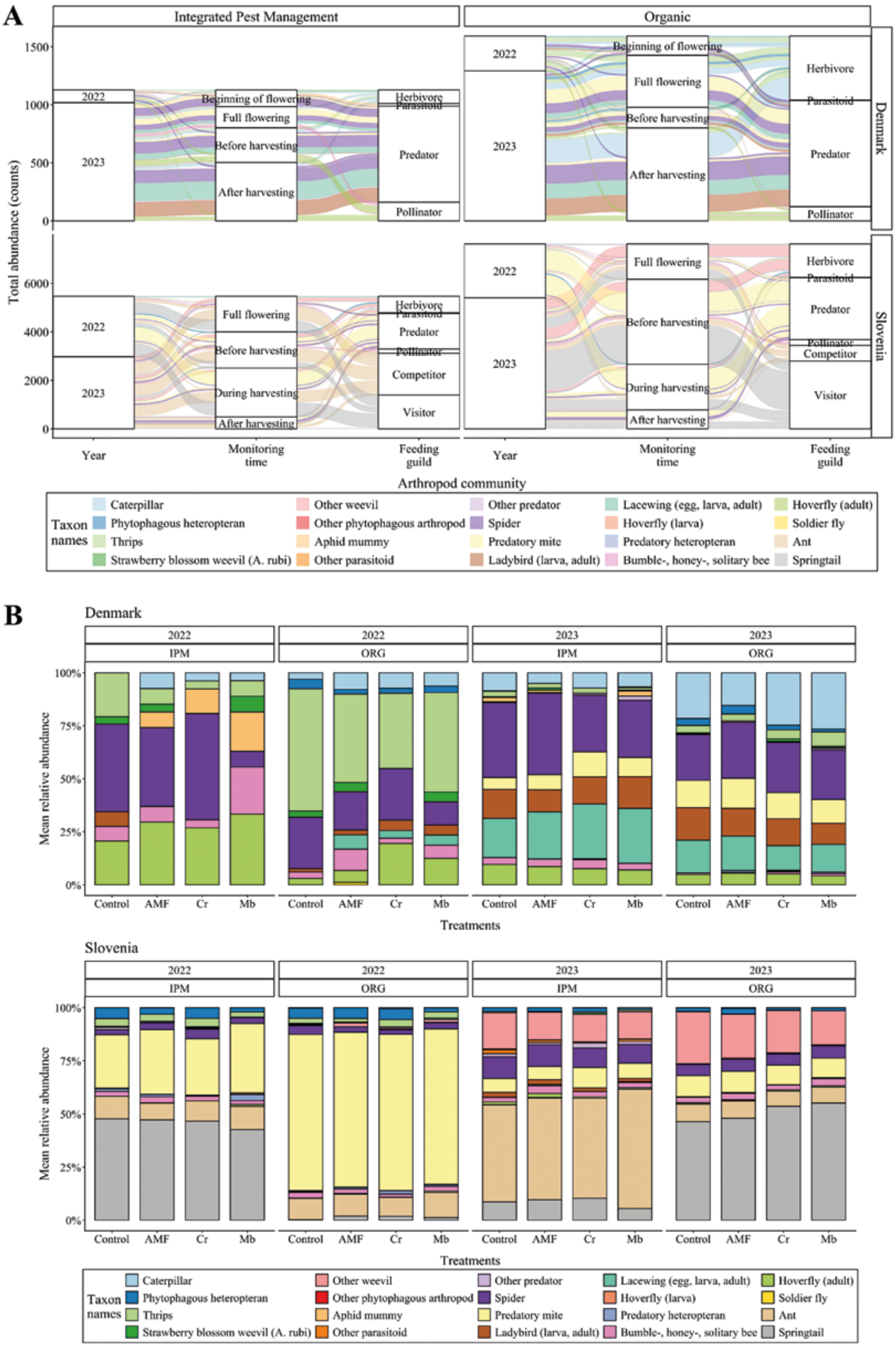

Fig. 3. Description of the arthropod communities observed over a 2-year field experiment in Denmark and in Slovenia. (A) The alluvial plot shows how the total abundance of arthropods is distributed in each field of each country for each factor. Total abundance corresponds to the sum of arthropod individuals observed in the 24 plots of the field. (B) The composition of arthropod communities in relation to the treatments is displayed in the stacked barplots. Order of "Other predator*": NA (see Table S2 for taxa), Dermaptera, Coleoptera, Diptera, Hymenoptera; Family of "Other predator*": Cantharidae, Staphylinidae, Asilidae, Vespidae, Carabidae, Forficulidae. "Other phytophagous arthropod" corresponds to beetle, bug, hopper, mite.

less abundant in *C. rosea* and *M. brunneum* than in AMF. However, no significant interactions occurred (Table S4).

RDA revealed that experimental factors explained 51.4% of the total variance in Danish arthropod communities, with year, production system, and their interaction significantly affecting community structure (Fig. 4A, Table S3). The treatment also had a significant effect but pairwise comparisons did not show any differences. Communities clustered in four

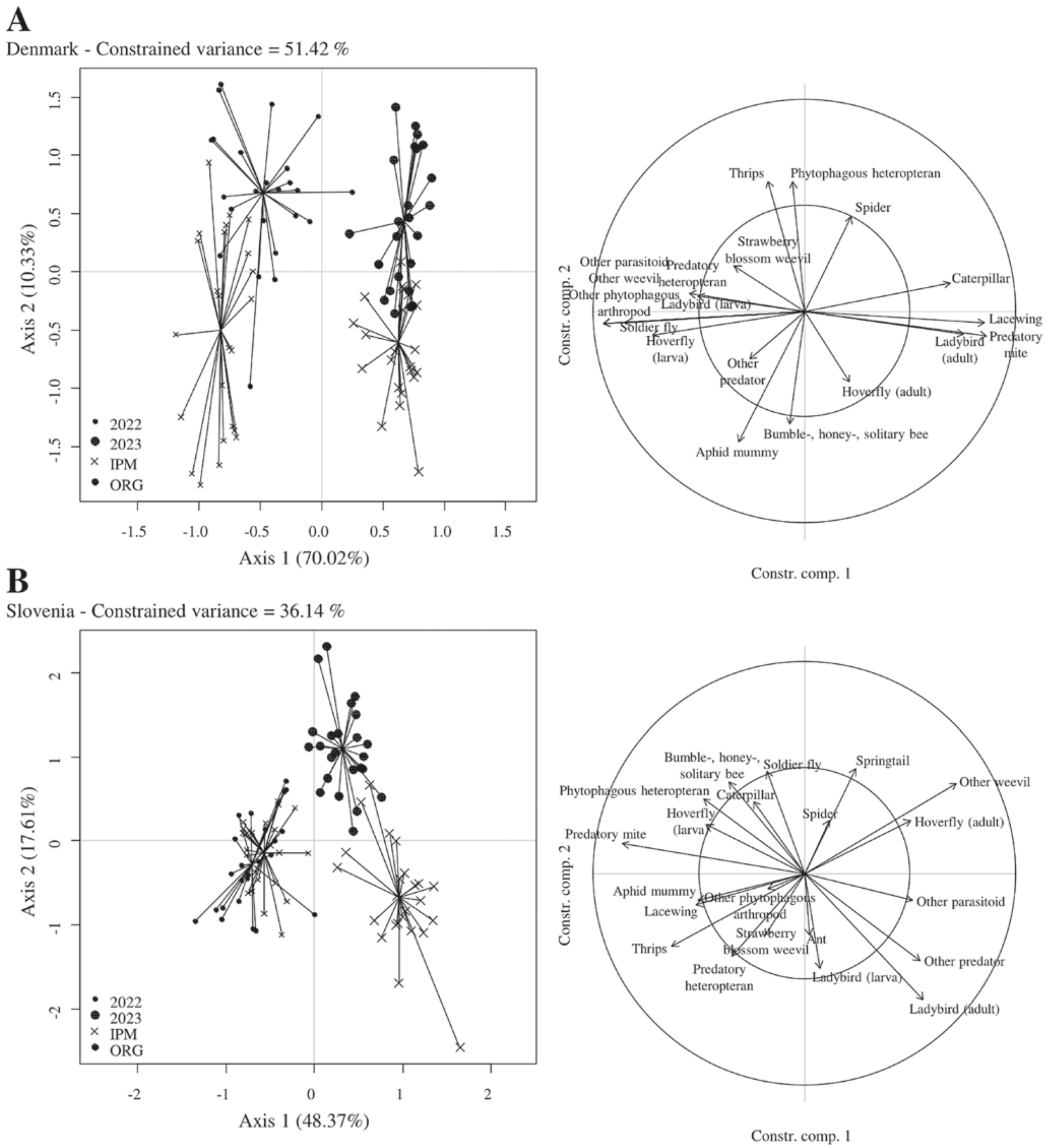

Fig. 4. Structure of the arthropod communities observed in 2022 and 2023 in Denmark (A) and in Slovenia (B) visualized with redundancy analysis (RDA). Score plots are on the left, correlation circles on the right. The variances explained by the RDA axes are given in parenthesis. IPM represents "Integrated Pest Management" and ORG "Organic" production systems (n = 24 plots per year and production system). "Other phytophagous arthropod" corresponds to beetles, bugs, hoppers, mites. Statistical outputs are displayed in Table S3.

groups: an IPM and an ORG cluster in both 2022 and 2023. The 2022 cluster was associated with soldier flies, hoverfly larvae, other weevils, parasitoids, and phytophagous arthropods, and the 2023 cluster associated with caterpillars, lacewings, predatory mites, and adult ladybirds.

In Slovenia, the experimental factors explained 36.14% of the total variance with year, production system and their interaction significantly influencing the structure of the arthropod communities (Fig. 4B, Table S3). Three clusters were identified: (i) 2022 both IPM and ORG were associated with thrips and predatory mites; (ii) 2023 IPM with adult ladybirds, parasitoids, and other predators; and (iii) 2023 ORG with adult hoverflies, springtails, and weevils.

Out of the 24 taxa monitored, 20 occurred in both countries (Table S5, Fig. S4A). In Denmark, only five taxonomic groups (representing spiders; springtails; *Anthonomus rubi*, the strawberry blossom weevil; bumble-, honey-, solitary bees; thrips) were consistently observed across all monitoring times over the two years, compared to nine taxa in Slovenia (representing spiders; predatory mites; springtails; other weevils; adult hoverflies; whiteflies; aphids; phytophagous heteropterans; ants (Table S5, Fig. S4B,C)), which were observed consistently in Slovenia. Most taxa were shared between the IPM and organic production systems within each country (i.e., 17 taxa in Denmark (Table S5, Fig. S4D) and 21 in Slovenia (Table S5, Fig. S4E)). A substantial overlap was also found across treatments, with 15 taxa shared in Denmark and 20 in Slovenia (Table S5, Fig. S4F,G). In Denmark, predatory heteropterans (comprising taxa from the Anthocoridae, Miridae, Nabidae, Pentatomidae) were shared among the three fungal treatments, but no taxa were common across the fungal treatments in Slovenia.

3.3 Correlations between arthropod feeding guilds and hygro-meteorological conditions

A significant positive correlation was observed between the number of natural enemies and herbivores (phytophagous arthropods), strongly influenced by the country, irrespective of the production system. In contrast, a significant negative correlation was observed between natural enemies and competitors (i.e., Formicidae) in Slovenia, strongly influenced by the production system (Fig. 5).

Considering influence of hygro-meteorological conditions, strong negative correlations were observed between ambient air temperature and the presence of competitors, and wind speed and all arthropod counts. Conversely, strong positive correlations were found between air temperature and predators, and air humidity and the occurrence of competitors (Fig. S5).

Arthropod monitoring was performed at earlier dates in Slovenia than in Denmark. At the different monitoring times, hygro-meteorological conditions were comparable in both countries, except for the higher temperature in Slovenia after harvest in 2023, and they were consistent across both years of the study (Fig. S6A). Monthly data indicated that Slovenia experienced higher summer and lower winter temperatures, as well as more rainfall, whereas Denmark was characterized by stronger winds and more stable air humidity (Fig. S6B).

3.4 Plant traits and strawberry yield

The canopy surface of strawberry plants was significantly influenced by country, year, and production system, as well as their interactions (Table S6). Plants were smaller in 2022 than in 2023. Plants from IPM were bigger than plants from ORG system in Denmark, while the opposite was observed in Slovenia (Table 2).

Marketable fruit yield was significantly influenced by country and production system, while the number of unmarketable fruits was significantly affected by country and year; both parameters showed significant interactions (Table S6). Overall, yield was higher and unmarketable fruit lower in 2022 than in 2023, and both values were greater in Slovenia than in Denmark. In Denmark, yield and unmarketable fruit were higher in IPM than ORG, whereas in Slovenia yield was higher in ORG (Table 2).

The number of marketable fruits was significantly influenced by country, year, and production system, as well as their interactions, and an interaction with treatment (Table S6). Marketable fruit numbers were lower in 2022 than in 2023 and lower in Denmark than in Slovenia. In Denmark more marketable fruits were harvested in the IPM than in the ORG trial, while the opposite was observed in Slovenia. In the Slovenian ORG system, plants inoculated with *M. brunneum* produced the highest number of marketable fruits, significantly more than other treatments (Table 2, Table S6).

The average marketable fruit weight was significantly influenced by country, year, and production system, as well as their interactions (Table S6). The average fruit weight was higher in 2022 than in 2023, and higher in Denmark than in Slovenia. In 2022, the fruit weight was higher in the IPM compared to the ORG trial in Denmark, while the ORG trial produced more than the IPM trial in Slovenia (Table 2).

The total plant biomass was significantly influenced by country, production system, and treatment, as well as their interactions (Table S6). In Denmark, IPM produced more plant biomass than the ORG system, and the treatments with *C. rosea* and *M. brunneum* showed reduced biomass compared to the control, while plants of the ORG system had more biomass compared to IPM in Slovenia, where no difference among the treatments was seen (Table 2, Table S6).

4 Discussion

Two three-year field experiments in Denmark and Slovenia tested effects of soil bioinocula on aboveground arthropods in strawberry. Arthropod abundance was higher in Slovenia, and greater under organic than integrated pest management (IPM) systems. Organic systems hosted more beneficial and pest species. Arthropod richness varied by year, system, and

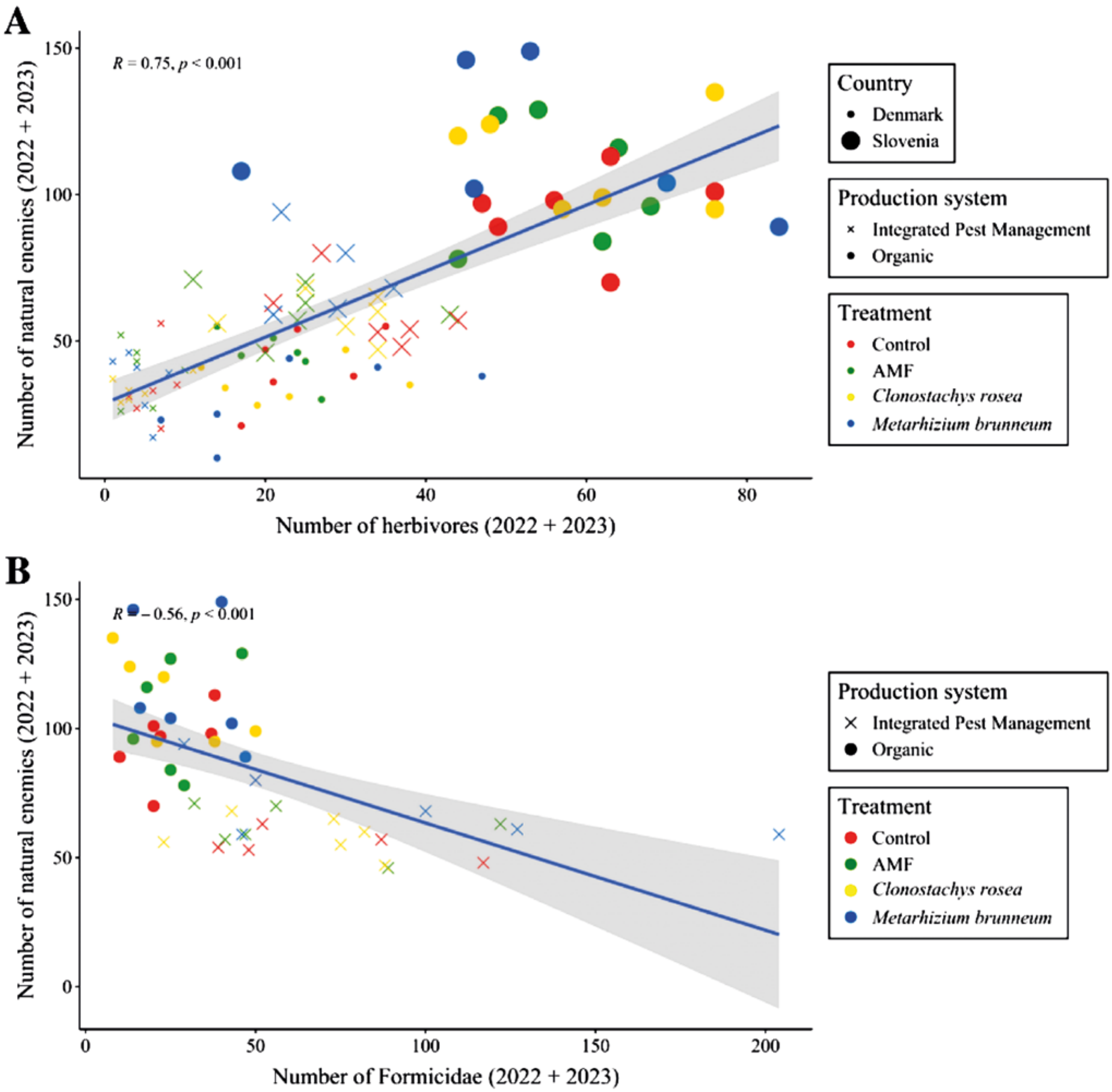

Fig. 5. Pearson correlation between natural enemies (parasitoids and predators) and herbivores in Slovenia and Denmark (A), and between competitors and natural enemies (i.e., Formicidae) in Slovenia (B) (n = 6 plots, each cumulates 7 or 8 observations).

location, being higher in Slovenia. Distinct assemblages characterized each site: Slovenia had more predatory mites, weevils, and ants, while Denmark had more Lepidoptera, spiders/harvestmen, thrips, and lacewings. Production system and country explained most variation, while beneficial fungi had little effects overall. The only significant effect of soil bioinocula was an increase in arthropod predators and the number of marketable fruits in Slovenia. The long intervals between fungal application and arthropod monitoring (12 months after the first and 1–2 months after the second) may explain the lack of some expected effects discussed below, as interaction with established soil communities may reduce the efficacy of bioinocula over time (Klingen et al. 2015).

Most research studying effects of soil bioinocula on aboveground arthropods focuses on foliar and soil applications of entomopathogenic fungi (EPF). Brazilian field trials using root applications of *B. bassiana* and *M. robertsii* in strawberries showed no harm to predatory mites, indicating low non-target risk, and reduced *Tetranychus urticae* densities probably due to systemic plant defence (Canassa

Table 2. Plant growth and agronomical parameters monitored during the field trials in Denmark (DK) and in Slovenia (SLO) (mean ± standard error). Different upper-case letters denote significant differences between countries, years and production systems. Note: Detailed statistical outputs (e.g., bi- and tri-interactions between the aforementioned factors and fungal bioinocula) are displayed in Table S6.

Experiment	Treatment	Canopy surface (cm2)		Commercial yield per plant (g)		Commercial fruits per plant		Unmarketable fruits per plant		Commercial fruit weight (g)		Total plant biomass (g)	
DK 2022, IPM	Control	850.4 ± 42.9	C	569.9 ± 24.9	F	23.1 ± 0.8	C	4.6 ± 0.4	B	24.7 ± 0.9	E		
	AMF	901.2 ± 36.8		540.5 ± 16.5		22.4 ± 0.8		5.8 ± 0.8		24.2 ± 1.1			
	Cr	867.5 ± 48.3		582.2 ± 14.8		23.9 ± 0.7		5.6 ± 0.4		24.5 ± 0.8			
	Mb	923.4 ± 40.4		575.3 ± 35.7		23.2 ± 0.7		6.0 ± 0.7		24.7 ± 1.1			
DK 2022, ORG	Control	300.7 ± 21.6	A	353.5 ± 30.2	A	19.0 ± 1.5	B	7.2 ± 0.7	C	18.6 ± 0.9	D		
	AMF	322.9 ± 20.5		361.3 ± 41.5		19.4 ± 1.8		7.2 ± 0.7		18.5 ± 0.5			
	Cr	309.5 ± 18.5		309.7 ± 23.7		17.9 ± 1.2		9.3 ± 1.0		17.3 ± 0.6			
	Mb	309.5 ± 18.5		339.3 ± 54.4		17.9 ± 1.8		7.6 ± 0.6		18.4 ± 1.2			
DK 2023, IPM	Control	905.2 ± 44.9	C	506.0 ± 34.2	E	33.9 ± 1.1	F	12.1 ± 0.9	E	14.9 ± 0.7	BC	585.0 ± 24.4	C
	AMF	844.5 ± 47.9		454.5 ± 71.8		30.5 ± 3.3		11.3 ± 0.8		14.5 ± 1.1		553.0 ± 23.3	
	Cr	861.8 ± 44.7		500.6 ± 33.8		32.8 ± 1.4		10.9 ± 1.2		15.2 ± 0.6		543.8 ± 21.8	
	Mb	911.9 ± 42.7		540.5 ± 54.7		34.3 ± 2.6		10.5 ± 0.6		15.6 ± 0.7		501.0 ± 22.6	
DK 2023, ORG	Control	827.8 ± 37.6	B	202.3 ± 35.5	A	13.2 ± 1.7	A	8.5 ± 0.7	D	15.0 ± 1.1	B	344.1 ± 22.8	B
	AMF	792.8 ± 32.4		235.8 ± 42.7		14.8 ± 1.4		9.4 ± 0.8		15.4 ± 1.5		306.2 ± 19.1	
	Cr	768.5 ± 36.6		197.9 ± 32.7		13.9 ± 1.4		9.5 ± 0.7		13.9 ± 1.3		291.1 ± 21.5	
	Mb	714.2 ± 36.9		171.3 ± 34.4		12.4 ± 1.2		8.6 ± 1.2		13.3 ± 2.1		276.5 ± 21.0	
SLO 2022, IPM	Control	773.4 ± 21.9	B	412.5 ± 14.8	C	28.9 ± 0.7	D	0.4 ± 0.2	A	14.3 ± 0.3	B		
	AMF	791.2 ± 20.7		391.8 ± 17.1		27.4 ± 1.2		0.6 ± 0.2		14.3 ± 0.1			
	Cr	799.0 ± 24.7		371.0 ± 20.7		25.7 ± 0.9		0.7 ± 0.2		14.4 ± 0.4			
	Mb	783.8 ± 20.6		397.9 ± 15.3		27.7 ± 0.7		0.4 ± 0.1		14.4 ± 0.6			
SLO 2022, ORG	Control	1004.9 ± 24.4	D	465.2 ± 10.6	DE	28.8 ± 0.7	E	0.5 ± 0.1	A	16.2 ± 0.3	C		
	AMF	992.7 ± 22.5		470.5 ± 16.1		29.6 ± 1.2		0.5 ± 0.1		15.9 ± 0.3			
	Cr	1001.6 ± 25.4		472.1 ± 22.1		30.3 ± 0.9		0.7 ± 0.1		15.6 ± 0.6			
	Mb	1010.0 ± 26.1		487.8 ± 16.3		31.4 ± 1.2		0.4 ± 0.2		15.6 ± 0.3			
SLO 2023, IPM	Control	1131.3 ± 55.3	E	461.3 ± 12.3	D	45.7 ± 0.8	G	4.0 ± 0.3	B	10.1 ± 0.2	A	259.7 ± 18.8	A
	AMF	1176.3 ± 57.2		457.4 ± 14.9		43.4 ± 2.1		5.5 ± 0.4		10.6 ± 0.2		256.9 ± 16.3	
	Cr	1143.1 ± 57.3		454.9 ± 26.2		42.9 ± 2.1		4.8 ± 0.6		10.6 ± 0.2		247.1 ± 13.7	
	Mb	1152.4 ± 53.9		444.7 ± 16.4		43.4 ± 1.4		4.6 ± 0.7		10.2 ± 0.3		264.3 ± 16.6	
SLO 2023, ORG	Control	1608.0 ± 56.5	F	572.7 ± 27.2	F	53.2 ± 2.2	H	3.9 ± 0.4	B	10.8 ± 0.3	A	319.9 ± 16.4	B
	AMF	1573.4 ± 49.8		596.2 ± 27.9		58.4 ± 3.7		4.8 ± 0.6		10.3 ± 0.4		327.9 ± 16.8	
	Cr	1556.7 ± 53.7		582.0 ± 35.6		55.0 ± 1.9		4.6 ± 0.5		10.6 ± 0.4		341.1 ± 25.6	
	Mb	1559.2 ± 55.6		661.0 ± 30.6		66.2 ± 1.7		6.5 ± 0.6		10.0 ± 0.4		352.4 ± 22.1	

& Esteca et al. 2020). In our Slovenian trials, *M. brunneum* treatments increased predator numbers but did not reduce pest infestations, possibly due to poor rhizosphere and endophytic colonization (J. Razinger, personal observations).

No significant predator increase was observed in *M. brunneum*-treated plants in Denmark, possibly because a different, late fruiting strawberry cultivar was used. Cultivar can influence the efficacy of root-inoculated EPF against target pests, arthropod communities, and microbial interactions (Canassa & D'Alessandro et al. 2020; Gong et al. 2018). A laboratory experiment with the same *M. brunneum* strain showed higher *T. urticae* populations on cultivar 'Faith' than 'Clery' (Xie et al. 2025).

Metarhizium brunneum did not affect pollinator or parasitoid numbers. Because bioinocula were applied to soil rather than foliage, flying arthropods were unlikely to come in contact with the fungus. Soil-dwelling or low-canopy arthropods (e.g., spiders, centipedes, ground, and rove beetles) were also unaffected despite possible exposure. Generalist predators like *Anthocoris nemorum* avoid *B. bassiana*-treated leaves, but not bioinoculum-treated soil (Meyling & Pell 2006). Aboveground herbivores may be attracted to *M. brunneum*-

inoculated roots, while their parasitoids are repelled (Cotes et al. 2020). The increase of predators, observed in Slovenia, remains unexplained.

Metarhizium brunneum did not significantly affect aphids or whiteflies, consistent with previous field studies using *M. robertsii* in Brazil (Canassa & Esteca et al. 2020) and *B. bassiana*/*M. brunneum* in the US (Clifton et al. 2018). This suggests that root-applied *Metarhizium* spp. have limited impact on these herbivores under the specific field and monitoring conditions.

Bioaugmentation can reduce plant growth or yield (Biere & Goverse 2016) and several *Metarhizium* isolates reduced strawberry leaf/root biomass or fruit yield (Biere & Goverse 2016), while no effect was observed by Canassa & D'Alessandro et al. (2020). Conversely, fungi like *Aspergillus niger* and *Purpureocillium lilacinum*, yearly applied, increased yields in a 3-year strawberry trial (Sas-Pasz et al. 2023). Our results mirror both scenarios: inoculation with these fungi reduced biomass in *C. rosea*- and *M. brunneum*-treated plants in Denmark but increased marketable fruits in *M. brunneum*-treated plants in Slovenia, suggesting resource allocation to reproductive organs.

Clonostachys rosea treatments did not alter arthropod communities, which may be due to extended time intervals between inoculation and monitoring, and possibly weak root colonization. Evidence for entomopathogenic activity in *Clonostachys* is scarce. Although isolates have been recovered from insect cadavers and shown to infect adult leafhoppers (Toledo et al. 2006), *C. rosea* is seldom found on living or dead insects. *Clonostachys rosea* reduced *Thrips tabaci* feeding on onion leaves but was not directly pathogenic to that insect (Muvea et al. 2014). When co-inoculated with *M. brunneum, C. rosea* suppressed *Fusarium culmorum* but reduced *M. brunneum*'s virulence toward *Tenebrio molitor* larvae (Keyser et al. 2016).

As a destructive mycoparasite, *C. rosea* was expected to reduce soil-borne phytopathogen pressure and improve plant fitness, potentially affecting arthropod communities. However, Danish trials showed reduced plant biomass, and Slovenian trials showed no significant effects. This lack of efficacy may stem from secondary metabolites in the fermentation substratum (Yafetto 2022), suboptimal inoculation timing (Tadesse Mawcha et al. 2025), environmental conditions, or their combination.

Previous studies showed that AMF effects are highly variable and depend on plant species or soil conditions. Foliar herbivory can decrease AMF root colonization in Asteraceae or increase it in common ragweed *Ambrosia artemisiifolia* (Xing et al. 2025). AMF can influence arthropod communities by altering plant nutrition (Wu et al. 2024). Typically, these effects are indirect, as arthropods respond to AMF-induced changes in plant growth. In addition, AMF symbiosis can enhance plant resistance to biotic stresses such as insect herbivores by activating phytohormone pathways to balance, e.g., insect herbivores (Khan et al. 2025). AMF can also have positive, negative, or no effects on plant growth and yield, and its influence on Lepidoptera herbivory varies in tomato (Orine et al. 2025). Herbivore responses to AMF may also shift from negative in low-nutrient soils to neutral in high-nutrient soils (Wang et al. 2023). AMF enhance nutrient uptake under low phosphorus availability (Berruti et al. 2016), which suggests that their benefits may be limited when soil nutrients are sufficient. Predator recruitment such as midges, lacewings, syrphids, and spiders, appears to be largely unaffected by AMF inoculation, as shown in milkweed field trials (Meier & Hunter 2021). There is no evidence that AMF influences pollinator or parasitoid abundance, although some studies have examined floral traits. The results from our field tests are therefore consistent with those reported in literature showing no effects on herbivores, parasitoids, pollinators, or predators. Adequate mineral nutrient levels in our fields may explain why there was no impact on yield, canopy surface, and plant biomass.

Organic strawberry fields in both countries had more arthropods, suggesting that organic practices can support sustainable farming with fewer pesticide inputs (EFSA 2018; Godfray et al. 2010). Reduced pesticide and fertilizer inputs likely explain the higher arthropod diversity observed in organic strawberry fields (Jacobsen et al. 2019). In Slovenia, organic fields had clearly more natural enemies (predatory mites, syrphid larvae, specialised parasitoids) and perhaps therefore also fewer aphid- or mite-infested plants than those with IPM, possibly due to natural enemies. (Jacobsen et al. 2019)

Arthropod communities are shaped by surrounding landscapes, which also aid plant colonisation in agricultural settings (Doehler et al. 2023). Danish fields were in intensively farmed landscapes with large arable crop fields, few hedges, and distant forests, limiting habitats for beneficial arthropods (Morandin et al. 2014). Slovenian fields, by contrast, were near diverse fruit crops, hedges, forests, and meadows, likely attracting more arthropod species (Morandin et al. 2014). Aphids and whiteflies thrive in protected environments (Stansly & Natwick 2009), explaining their higher abundance in Slovenia's tunnels compared to Denmark's open fields.

Total arthropod numbers were higher in the second year, rising by nearly 50% in Slovenia and 75% in Denmark, as established fields generally support arthropod abundance and diversity due to local pest and natural enemy population buildup (Sigsgaard et al. 2014).

In multitrophic agroecosystems, more herbivores usually attract more predators and parasitoids (Abdala-Roberts et al. 2019), and this is corroborated by our results. Ants disrupt this by protecting honeydew-producing hemipterans and deterring predators and parasitoids through aggressive behaviour or chemical signals (Zhang et al. 2012). They also compete for sugar sources like honeydew, reducing parasitoid reproduction and survival, and excluding generalist predators (Anjos et al. 2022). Interference by ants can therefore weaken biological control and increase the probability of pest outbreaks (Anjos et al. 2022). The negative correlation between ants and natural enemies reflects these patterns in the Slovenian trials. Increased understanding of ant-predator interactions in strawberries could improve pest management.

Fruit yield in Denmark declined significantly in the second year across all treatments and systems, as expected (Conti et al. 2014). In Slovenia, yields increased in the second year, likely due to influence of the Mediterranean climate as Mediterranean regions often see higher second-year yields despite lower fruit market value (Shokaeva 2008).

In Denmark, plants had smaller canopies but higher biomass, whereas Slovenia showed the opposite, likely due to varietal differences. Climate and biogeography can explain the disparities in arthropod numbers (Thomson et al. 2010): Slovenia is warmer, wetter and sunnier but less windy and humid than Denmark (https://www.worlddata.info/), with the field sites at 300 m (Slovenia) and 24 m (Denmark) elevation. Predator numbers rose with air temperature and total arthropods declined with wind, consistent with prior research (de Groot & Kogoj 2015). Strong windiness in Denmark may have affected arthropod movement, species interactions, and microclimates.

Conclusions. The impact of soil-applied bioinocula on aboveground arthropods was limited in both countries, indicating that the effects of field application of beneficial microbes may not be straightforward. Higher arthropod abundance and diversity in organic fields suggest benefits of sustainable farming for biodiversity and pest regulation. Differences in arthropod communities between Slovenian and Danish strawberry fields and between management systems illustrate complex ecological interactions in diverse landscapes. Further research on context-dependent microbial effects is needed to enhance strawberry production.

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Fig. S1–S6, Table S1–S6.