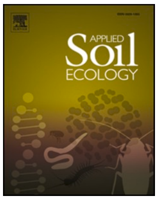
Applied Soil Ecology 188 (2023) 104897

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil



Dietary preferences of *Heteromurus nitidus* (Collembola) among wheat fungal communities: Implications for bioregulation of two widespread pathogens

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ARTICLE INFO

Keywords:
Springtail
Zymoseptoria tritici
Fusarium graminearum
Choice experiments
Biocontrol

ABSTRACT

Soil invertebrates play a key role in agrosystems as providers of several ecosystem services. In particular, they regulate fungal communities in soils and could contribute to mitigate the impact of phytopathogenic fungi overwintering in crop residues. In this study, we investigated the food preferences of *Heteromurus nitidus* (Collembola) between phytopathogenic and non-pathogenic (or beneficial) fungi present in crop soils and grown *in vitro*. First, two fungi responsible for the most important diseases of wheat worldwide *Zymoseptoria tritici* and *Fusarium graminearum*, and eleven fungi previously served on wheat plants were offered in pathogenic/non-pathogenic pairs to springtails. We showed that *Z. tritici* was preferred over seven out of the eleven non-pathogenic fungi offered while *F. graminearum* was only preferred over four of them. Second, we assessed the impact of long-term consumption of these two phytopathogenic fungi by springtails on their population development and assessed how the development of the fungi was affected by the springtails that fed on them. During this long-term experiment, springtails were more abundant in populations fed with phytopathogenic fungus than in control populations after ten weeks. At the end of the experiment, mycelium of both fungi was reduced by springtail activity. These *in vitro* results suggest a potential of *H. nitidus* to act as a biological control agent as populations grew when fed on either fungus while reducing fungal development. This point should be confirmed by testing the fungus grown on host plant tissues and with experiments involving interactions with soil and its communities. *Z. tritici* appears to be a better candidate for such experiments as it was preferred in choice experiments.

1. Introduction

Soils are complex systems made of mineral compounds and decaying organic matter, hosting a large diversity of organisms that are involved in crucial ecosystem services for both natural and managed environments. Most of the primary production eventually returns in soils (Wall et al., 2012), especially in conservation agriculture, and organic compounds are broken down into nutrients available to the primary producers by decomposer organisms. The decomposer guild is made of various species of bacteria, fungi and invertebrates that either disintegrate organic matter (primary decomposer) or facilitate the process (secondary decomposer). Their role is important in crops as they affect production (Swift and Anderson, 1994) and many of these organisms play a key role in recycling the matter derived from crop residues left after harvest, an ecotone between plant and soil (Kerdraon et al., 2019).

Among them, fungi living at the interface between the soil and decaying organic matter take a variety of different roles in crops. Several fungal species are beneficial to agriculture, for example by making nutrients available for plants, helping nutrient absorbance (*e.g.* in Owusu-Bennoah and Wild, 1979), or by protecting crops from abiotic and biotic stresses, including plant pests (Yadav et al., 2020). Several fungal species are, as phytopathogens, deleterious to the crops or have a negative

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https://doi.org/10.1016/j.apsoil.2023.104897
Received 7 September 2022; Received in revised form 20 March 2023; Accepted 22 March 2023

impact on crop yield (Deacon, 2013; Savary et al., 2019). Among these phytopathogens, *Zymoseptoria tritici* and the species complex *Fusarium spp.*, including *Fusarium graminearum*, are of major economic importance as they infect and cause recurrent damages on wheat, the most grown cereal worldwide (FAO.org, 2021).

Zymoseptoria tritici is the causal agent of the Septoria tritici blotch (STB), a foliar disease of wheat. Epidemics cause yield losses up to 50 % on susceptible cultivars not treated with fungicides (Fones and Gurr, 2015). Most of European conventional wheat fields are treated with fungicides to control STB when the disease pressure is high. However, their overuse has negative impacts on many organisms and leads to resistance against most of the active substances (Palumbi, 2001). The spread of fungicide resistance mutations within *Z. tritici* populations is favored by their high genetic variability (Linde et al., 2002), highlighting a need for alternative control methods.

Fusarium graminearum is one of the causal agents of the Fusarium head blight (FHB) on wheat, barley and maize. This worldwide distributed disease (Goswami and Kistler, 2004) causes yield losses up to 50 % and the sole 90's epidemic in the USA resulted in $2.6billion losses (McMullen et al., 1997). The fungus produces many toxic secondary metabolites such as deoxynivalenol (DON) (Miedaner, 1997) that reduces the quality of the remaining grains. Currently, FHB control relies on a combination of strategies including cultivar resistance and fungicides (Bai and Shaner, 2004) but the phytosanitary products still struggle to combine efficiency with food safety and economic issues (Jones, 2000).

Both species share a similar life cycle: after infecting a wheat crop, the fungi overwinter in wheat residues remaining on the soil. Leaving these residues on soils and the absence of tillage, both management practices promoted by conservation agriculture, could impact crops. On the one hand, they could have negative effects by promoting so-called “residue-borne” fungal diseases (Leplat et al., 2013; Suffert and Sache, 2011). On the other hand, they have a positive effect by favoring soil arthropods (Marasas et al., 2001), including epiedaphic springtails (Axelsen et al., 2022). The retention of residues at the soil surface creates a matrix that favors both phytopathogenic fungi and soil and litter dwelling arthropods, which could lead to increased mycophagy.

Collembola, also known as springtails, are apterygote hexapods that also belong to the decomposer guild and are present in the soils of almost every biotope, including agroecosystems. These soil arthropods are taking part, directly and indirectly, in multiple ecological processes such as litter decomposition, nutrient cycling and pedogenesis(Filser, 2002; McGonigle, 1995; Moore et al., 1988; Rusek, 1998; Siddiky et al., 2012). Springtails also have a direct impact on soil microbial communities, affecting biomass and composition. Indeed, analyses of the gut content of different collembolan species showed that some of them mostly feed on fungi (Bodvarsson, 1970; Poole, 1959), which is consistent with the finding of fungal spores in their feces (Poole, 1959). Moreover, although they usually are considered to be generalist feeders, collembolan species exhibit food preferences (*e.g.* in Jørgensen et al., 2003; Potapov et al., 2021; Staaden et al., 2011). They can be influenced by fungal secondary metabolites (Staaden et al., 2011), including pigments (Ponge, 1991; Xu et al., 2019). Given their alimentary habits, springtails can even be considered to shape microbial communities. Indeed, by preferentially feeding on certain species, they can regulate fungal populations (Friberg et al., 2005; Moore et al., 1988; Ponge and Charpentié, 1981; Tordoff et al., 2008; Wolfarth et al., 2013) or disperse fungal propagules (Becher et al., 2020; Lilleskov and Bruns, 2005; Seres et al., 2007), as well as stimulate fungal growth (Bengtsson and Rundgren, 1983). They can also impact microbial activity by stimulating or inhibiting it, depending on population size (Hanlon and Anderson, 1979).

Springtails have even been evaluated as biological control agents against pathogenic fungi in numerous studies (reviewed in Friberg et al., 2005; Innocenti and Sabatini, 2018), for instance against *Fusarium culmorum*, a producer of the mycotoxin DON (reviewed in Schrader et al., 2013). However, their feeding habits in wheat fields and their potential ability to regulate fungal pathogens of this crop is little documented (Mehl, 1940). In a field experiment, Salmon et al. (2021) showed that abundance and species richness of Collembola slightly increased with the sensitivity of wheat cultivars to STB, highlighting the need to analytically study the relationship between springtails and *Z. tritici* in these crops. Furthermore, microcosm studies (Meyer-Wolfarth et al., 2017; Wolfarth et al., 2013) established the potential of the fungal-feeding collembola species *Folsomia candida* to limit the biomass of *Fusarium culmorum* (belonging as *F. graminearum* to the species complex causing FHB on wheat) in infected wheat straw, in line with the findings of Sabatini and Innocenti (2001). A recent meta-analysis from Goncharov et al. (2020) also showed that soil fauna growth increased when feeding on *Fusarium* species while negatively affecting fungal abundance.

In this study, we investigated potential fungus-springtail interactions in wheat crops using *Heteromurus nitidus* (Templeton, 1835), a cosmopolitan edaphic Collembola (Entomobryidae). This springtail species is frequently found in soils of forest and fields of cultivated area (Jørgensen et al., 2003; Ponge, 1993; Salmon et al., 2021). It is known to feed on fungi (Jørgensen et al., 2003; Staaden et al., 2011) and microalgae (Scheu and Folger, 2004), while it is also able to ingest fragments leaf litter and bacteria (Haubert et al., 2011). We investigated the dietary preferences of *H. nitidus* between one of the two aforementioned wheat fungal pathogens - *Z. tritici* and *F. graminearum* - and a non-pathogenic (or beneficial) fungal species that can be usually isolated from wheat crop soils or wheat plants. Eleven fungal species, including beneficial and potential biological control agents, were selected for the potential diversity of their lifestyle (epiphytic, endophytic, saprophytic), their phenotype (with different mycelium pigmentations) and their widespread presence in agrosystems. These species are supposed to be representative of wheat residues and soil microbiota. They may play a role in nutrient recycling or have a regulatory activity against wheat pathogens and were tested to check whether springtails could have a detrimental impact on the potential providers of ecosystem services. Therefore, they will be regrouped under the denomination “beneficial” as species with a potential positive impact on wheat crops. A choice experiment was based on offering *H. nitidus* each pair of pathogenic/beneficial fungal species grown on Petri dishes. We also studied the effect of long-term consumption of *Z. tritici* and *F. graminearum* by *H. nitidus* populations. To this end, we assessed the changes in size of springtail populations feeding on the two phytopathogenic fungi grown *in vitro* for ten weeks and the changes in the amount of fungal mycelium present on the medium surface after springtail grazing. With this study, the first to test *Z. tritici* and *F. graminearum* in two complementary experimental designs (choice test over several hours and long-term consumption experiment over several weeks), we intended to pave the way for a novel bioregulation approach by testing the following hypotheses in laboratory settings: (1) Springtails exhibit preferences by making choices between pairs of beneficial and detrimental fungi present in the wheat crop residues; (2) springtails feed on phytopathogenic fungi and grow and successfully reproduce; (3) springtail grazing have a negative impact on fungal development (coverage of the agar medium) of phytopathogenic fungi.

2. Materials and methods

2.1. Biological material

Springtails used for the experiments were taken from the culture stocks of MECADEV laboratory (Muséum national d'Histoire naturelle, Brunoy, France). They were kept in culture boxes (diameter 80 mm, height 52 mm) in the dark on a moistened Fontainebleau sand substrate (Sordalab) and were fed with tree algae (*Pleurococcus spp.*) and dry cow dung. Prior to the choice experiments, individuals were starved for seven days in culture boxes placed in climatic chambers (no light, 15 °C) containing moistened Fontainebleau sand. A seven-day starvation period allowed to stimulate the foraging of springtails and to empty their gut without any stress (Rohlfs et al., 2007; Staaden et al., 2011). One hour before the start of the experiment, starved individuals were taken out of the climatic chambers.

One strain of each of the eleven beneficial fungal species used for the experiments (*Acremonium strictum*, *Aspergillus nidulans*, *Aureobasidium pullulans*, *Cladosporium cladosporioides*, *Clonostachys rosea*, *Epicoccum nigrum*, *Mortierella alpina*, *Periconia macrospinosa*, *Trichoderma harzianum*, *Trichoderma hamatum*, *Trichoderma atroviride*; see details in Supplementary Table S1) and a strain of *F. graminearum* were obtained from the fungal culture collection of the Muséum national d'Histoire naturelle (Paris, France). *Z. tritici* was provided by INRAE BIOGER (Palaiseau, France; Supplementary Table S1). Three culture media were tested in preliminary experiments: potato dextrose agar, malt agar and Mandels medium (Mandels and Reese, 1957). The latter was selected as it was less consumed by springtails. All strains were thus grown in Petri dishes on Mandels medium (MM), prepared with the following composition: (in g l^{-1}): glucose, 10; $(NH_4)_2SO_4$, 1.4; KH_2 PO_4, 2; $CaCl_2$, $2H_2O$, 0.4; urea, 0.3; yeast extract, 0.25; agar, 20 and trace elements (in mg l^{-1}): $MgSO_4$ $4H_2O$, 300; $FeSO_4$ $7H_2O$, 5; $MnSO_4$ $4H_2O$, 1.6; $ZnSO_4$ $7H_2O$, 1.4; $CoCl_2$ $6H_2O$, 20. Spore suspensions were spread on the MM medium and Petri dishes were incubated for two weeks in climatic chambers at 25 °C for full colonization. Afterwards, all the Petri dishes were kept in the dark at 4 °C for a maximum of two weeks until subsequent experiments. The eleven fungal species (Supplementary Table S1) were paired with each of the two phytopathogenic fungi for a total of 22 trials and for each pair the fungi came from same age cultures.

2.2. Experiments

2.2.1. Choice experiment

The choice experiment consisted of offering *H. nitidus* each pair of pathogenic/beneficial fungal species grown on Petri dishes. The experiment was conducted at 19 °C in Petri dishes (diameter 96.6 mm, height 13.9 mm) by adapting the setup of the choice experiment in Jørgensen et al. (2003). Twelve replicates were made for each pair of fungal species. Petri dishes were filled with humid sand substrate (25 g of Fontainebleau sand and 5 mL of tap water) to ensure proper humidity. Fungal plugs (10 mm diameter of MM medium colonized by the fungus, 3 mm height; see Fig. 1) were taken from two- to four-week-old colonized Petri dishes using a cork-borer and placed 75 mm apart on the sandy substrate, at 10 mm from the edge of the dishes (Fig. 1). Afterwards, 10 adults or sub-adults *H. nitidus* were placed in the middle of each Petri dish, equidistant from the plug of each fungal species using a funnel. Their position was picked up every ten minutes for thirty minutes and then every thirty minutes for three hours. Individuals were marked as either on the beneficial fungus plug, the pathogenic fungus plug or on the substrate. Their final choice at 210 min was used in the analyses.

2.2.2. Long-term consumption experiment

The long-term consumption experiment consisted in quantifying the feeding of springtails on the two phytopathogenic fungi by assessing the changes in the size of the springtail populations and their grazing effects on fungal development after up to ten weeks. Three conditions were tested for each pathogenic fungus with ten replicates each. Thirty springtails, adults or sub adults, were placed in presence of either: (i) the fungus grown on MM medium, (ii) uncolonized MM medium or (iii) sandy substrate alone (culture medium of *H. nitidus* without food resources). Conditions (ii) and (iii) were made to ensure that growth and reproduction were the result of the diet and not of potential reserves made prior to the start of the experiment and that egg-laying was not the result of environmental stress.

A specific experimental design was made for each of the two fungi and was justified by the fact that *Z. tritici*, unlike *F. graminearum*, has a yeast-like development. In consequence *Z. tritici* colonies do not cover homogeneously all of the MM medium. Thus, square plugs were taken in parts of the culture where the cover of the MM medium by *Z. tritici* was the densest. This allowed to offer approximately the same amount of fungi to springtails in all replicates. A setup using square plugs could not be used for *F. graminearum* as the fungus was grazed by springtails and replaced by opportunistic fungi during preliminary experiments.

For *F. graminearum*, a replicate was made of a Petri dish (diameter 96.6 mm, height 13.9 mm) filled with 10 mm of MM medium colonized (i) or not (ii) by *F. graminearum*, or with moistened sand (iii; 25 g of Fontainebleau sand and 5 mL of tap water; Fig. 2a).

For *Z. tritici*, circular culture boxes (diameter 80 mm, height 52 mm) were filled with moistened sand for the control (iii; 97 g of Fontainebleau sand and 21 mL of tap water, covered with a cellulose paper; Fig. 2b). A square plug of MM medium, colonized (i) or uncolonized (ii) by *Z. tritici* (dimensions 30 × 30 mm), was added on the cellulose paper for the other two box conditions. Fungal plugs were replaced every three weeks (just after springtail population measurements in week 3, 6 and 9) to ensure that fungal mycelium was always available in excess for all *H. nitidus* individuals.

For each fungus, control conditions without springtails consisted of the fungus grown on MM medium and uncolonized MM medium. For each control, ten replicates were made in order to ensure that there was no contamination by fungi or bacteria. The springtails were placed on the same day in all the Petri dishes and the boxes, which were then left in

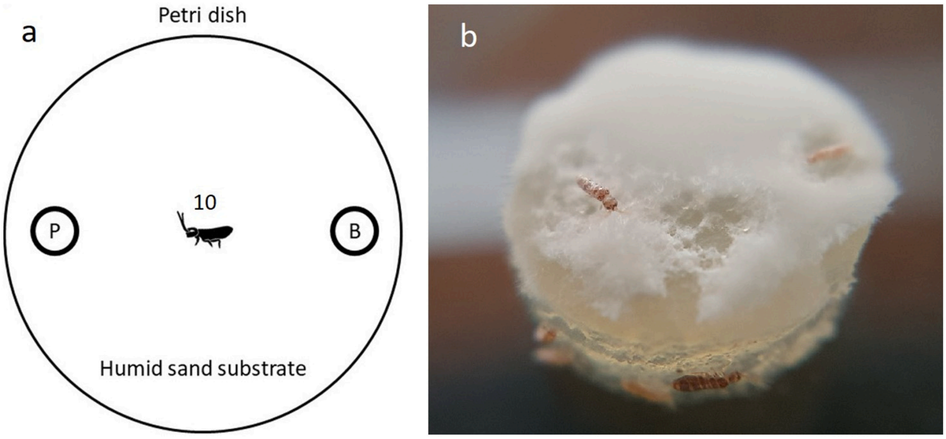

Fig. 1. Experimental design for the choice experiments. (1a) The circled P represents the MM medium plug colonized by the phytopathogenic fungus and the circled B represents the plug colonized by the beneficial fungus, 75 mm away. The springtails were positioned in the middle and a choice was deemed to be made when they arrived on one of the two plugs. (1b) Interaction between *H. nitidus* and *F. graminearum* on a plug from which his choice has been made.

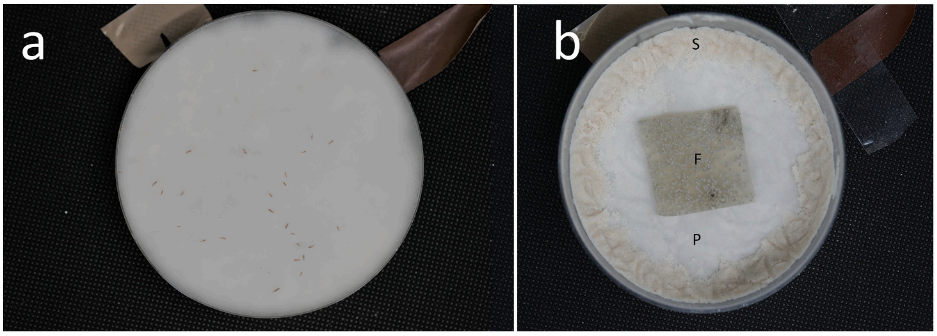

Fig. 2. Experimental design for the long-term consumption experiment (2a) for *F. graminearum* with completely colonized MM medium in a Petri dish and (2b) for *Z. tritici* with a square plug (30 × 30 mm) of colonized MM medium (F) positioned on the filter cellulose paper (P) above the sandy substrate (S) in the middle of the culture box.

the dark in climatic chambers at 15 °C for ten weeks.

H. nitidus adults/subadults, juveniles and eggs were counted each week three times, by the same observer, using a binocular magnifier. Dead individuals and exuviae were also counted and removed weekly. Additionally, a picture of the mycelium coverage on the MM medium was taken weekly for 10 weeks for *F. graminearum* and for the three first weeks – the time during which the first plug was offered - for *Z. tritici*. The mycelium coverage, *i.e.* the MM medium areas still covered by a white aerial mycelium, was measured using ImageJ (Schneider et al., 2012). This software allowed to count pixels to distinguish these areas from grazed ones using their color difference.

2.3. *Statistical analysis*

All statistical analyses were conducted on the software R v 4.1.1 (R Core Team, 2021). For the choice experiments, the choices of the springtails in the Petri dishes at 210 min were used as basic data units to build the following matrix. The proportion of individuals choosing a fungal plug was analyzed as the response variable using the matrix of the number of individuals choosing one fungal plug and the number of individuals not choosing this fungal plug (*i.e.* a matrix [individuals on a plug_i; individuals on the other plug_i + individuals not on the plugs_i] with i = number of replicates). The fungus on the plug (pathogenic or beneficial fungus) was used as a fixed effect categorical variable. Analyses were conducted using generalized linear mixed effect models (GLMM) following Bolker et al. (2009) with the package *lme4* (Bates et al., 2007). The identification number of the Petri dish was included to the model as a random factor, and the likelihood approximation was done using an adaptative Gauss-Hermite quadrature. Data were analyzed assuming that the variables to explain follow a binomial distribution with a logit link function as they are proportion data (Bolker et al., 2009). All generalized linear models were checked with the package *DHARMa* (Hartig, 2017) to simulate scaled residuals and test for correct distribution, overdispersion and outliers.

For the long-term consumption experiments, six population indicators were analyzed after ten weeks: the number of adults, juveniles and both combined as well as the cumulative number of eggs, exuviae and dead individuals. These variables to explain were analyzed with the three different conditions with springtails (MM medium colonized with fungus, uncolonized MM medium or humid sand only) as an explanatory variable by building three different model types. Generalized linear models with a Poisson distribution and a log link function were built with the package *lme4* (Bates et al., 2007) as the six population indicators were count data. In case of overdispersion of the data, generalized linear models with a negative binomial distribution and a log link function were built with the package *MASS* (Ripley et al., 2013). Zero-inflated negative binomial models were also built to take into account a potential excess of zeros for the variable to explain with the package *pscl* (Jackman et al., 2015). For each response variable, the most appropriate of the three models was selected using Akaike Information Criterion (AIC) and pairwise comparisons between the three conditions were performed using estimated marginal means (EMMs) with the package *emmeans* (Lenth et al., 2019).

Mycelium coverage was analyzed as continuous proportion data (thus bounded to the interval [0,1]) using beta regressions with a logit link function (Douma and Weedon, 2019) using *betareg* (Zeileis et al., 2016) and *glmmTMB* (Magnusson et al., 2017) packages. A first model was made with the measurements of mycelial coverage taken for three weeks for *Z. tritici* ogtable 1r ten weeks for *F. graminearum*, *i.e.* the time each phytopathogenic fungus was exposed to the springtails. The presence/absence of springtails, the time and their interaction were used as fixed effect explanatory variables and the box identification label as a random variable. A second model was made using the measurements of the last week only (third week for *Z. tritici* and tenth week for *F. graminearum*) using the presence/absence of springtails as the fixed effect variable and the box identification label as a random variable. The average marginal effect (AME) was calculated to estimate surface changes of fungal mycelium with the *margins* package (Leeper et al., 2017).

3. Results

3.1. *Choice experiments*

A total of 2645 *H. nitidus* individuals were involved in the choice experiments. Over the 1322 used for the *Z. tritici* trials (Fig. 3), 1092 (82.6 %) were responsive *i.e.* they chose one of the two fungi offered at 210 min. For the *F. graminearum* trials (Fig. 4), 923 (69.7 %) out of the 1323 individuals used were responsive at 210 min. Over the 264 petri dishes tested, 5 contained an additional springtail (2 for *Z. tritici* tests, 3 for *F. graminearum* tests).

Z. tritici was preferred over *T. harzianum*, *C. rosea T. hamatum*, *T. atroviride*, *A. nidulans*, *M. alpina* and *E. nigrum* (Fig. 3). There was no preference between *Z. tritici* and *A. strictum*, *C. cladosporioides*, *P. macrospinosa* and *A. pullulans*. There was no pair where the beneficial fungus was preferred over *Z. tritici*.

F. graminearum was preferred over *T. harzianum*, *C. rosea*, *T. hamatum* and *T. atroviride* (Fig. 4). There was no preference between *F. graminearum* and *M. alpina* while the following beneficial fungi were preferred over *F.graminearum*: *A. nidulans*, *E. nigrum*, *A. strictum*, *C. cladosporioides*, *P. macrospinosa* and *A. pullulans*.

3.2. *Long-term consumption experiments*

3.2.1. *Development of springtail populations*

In the long-term consumption experiments, the food source had a significant effect on the number of springtails (individuals) at all their developmental stages (called developmental indicators; Table 1).

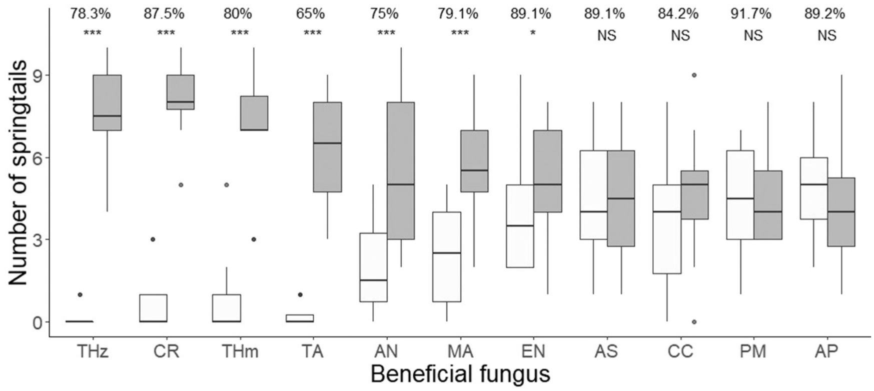

Fig. 3. *H. nitidus* choices between *Z. tritici* (grey boxes) and one of the eleven beneficial fungi (abbreviations in Supplementary Table S1, white boxes) 210 min after the beginning of the experiment. Boxes represent the first and third quartile, the black line the median number of springtails among ten. Whiskers represent maximum and minimum values within 1.5 times the interquartile value. Dots represent outliers. Percentages indicate the percentage of individuals that chose a fungus at 210 min. Fungal species were ranked from the least attractive to the most attractive species for *H. nitidus* compared to *Z. tritici*. Asterisks represent significance level of the corresponding GLMM (NS = not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$).

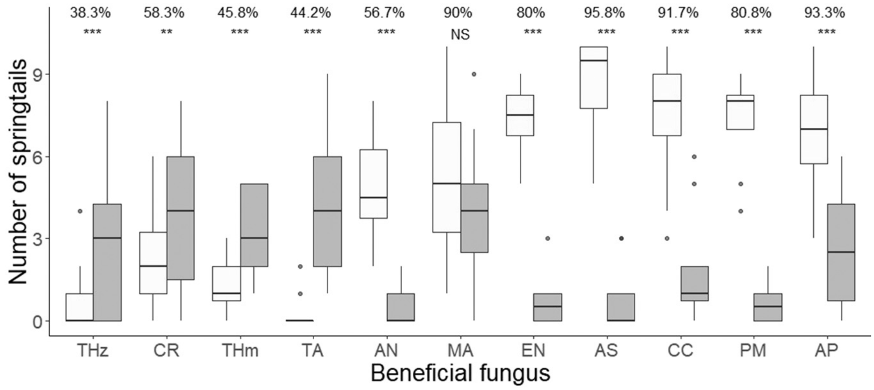

Fig. 4. *H. nitidus* choices between *F. graminearum* (grey boxes) and one of the eleven beneficial fungi (abbreviations in Supplementary Table S1, white boxes) 210 min after the beginning of the experiment. Boxes represent the first and third quartile, the black line the median number of springtails among ten. Whiskers represent maximum and minimum values within 1.5 times the interquartile value. Dots represent outliers. Percentages indicate the percentage of individuals that chose a fungus at 210 min. Fungal species were ranked from the least attractive to the most attractive species for *H. nitidus* compared to *Z. tritici* for better comparability with Fig. 3. Asterisks represent significance level of the corresponding GLMM (NS = not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$).

Populations grew over time and final populations were larger in presence of the fungi (Supplementary Fig. S1).

Significant differences between colonized and non-colonized MM medium conditions were observed for both pathogenic fungi (Table 2, 3) regarding the cumulated number of eggs after ten weeks. In both cases, more eggs were laid on the pathogenic fungi than on the uncolonized MM substrate. As there were no eggs on the sand substrate, no statistical comparison was possible with the two other substrates. Likewise, ratios were of the same order of magnitude for both fungi when comparing the cumulated number of exuviae removed after ten weeks, depending on the condition. The number of exuviae removed over the ten weeks was significantly higher in presence of the pathogenic fungus compared to the non-colonized MM medium and the sand alone, with the same indicator being significantly higher in presence of the non-colonized MM medium than with the sand only.

The number of juveniles counted after ten weeks was significantly higher on both pathogenic fungi compared to the other two conditions (uncolonized MM medium and sand only). There was no significant difference between these two conditions (MM-Sand; Table 2) for the setup used for *Z. tritici*. For the setup used for *F. graminearum*, juveniles were only observed in the dishes where the fungus was offered (Table 3). Their number was significantly different from zero in presence of *F. graminearum* but there was no significant difference between the three conditions. For both fungal species, the number of adults and the total number of individuals were significantly higher in presence of the fungus compared to the two conditions where it was absent. These indicators were significantly higher in presence of uncolonized MM medium than with the sand only in the *Z. tritici* setup while there was no

Table 2
Effect of the phytopathogenic fungus *Z. tritici* on developmental indicators of *H. nitidus* populations. Values are *p*-values. Fungus, MM and Sand are the three levels of the categorical variable food diet. NaN indicate when a population indicator only had zeros for a condition (NB: negative binomial model, ZINB: zero-inflated negative binomial model, EMMs: estimated marginal means).

					EMMs pairwise comparisons		
Developmental indicator	Model selected	Fungus (colonized medium) (Intercept)	MM (uncolonized medium)	Sand	Fungus-MM medium	Fungus-Sand	MM medium-Sand
Eggs	ZINB	$p < 0.001$	0.004	NaN	F > M	NaN	NaN
Juveniles	ZINB	$p < 0.001$	$p < 0.001$	$p < 0.001$	F > M	F > S	M = S
Exuviae	NB	$p < 0.001$	$p < 0.001$	$p < 0.001$	F > M	F > S	M > S
Adults	Poisson	$p < 0.001$	0.005	$p < 0.001$	F > M	F > S	M > S
Total living individuals	NB	$p < 0.001$	$p < 0.001$	$p < 0.001$	F > M	F > S	M > S
Dead individuals	NB	0.36	$p < 0.001$	$p < 0.001$	F < M	F < S	M < S

Table 3

Effect of the phytopathogenic fungus *F. graminearum* on developmental indicators of *H. nitidus* populations. Values are *p*-values. Fungus, MM and Sand are the three levels of the categorical variable food diet. NaN indicate when a population indicator only had zeros for a condition (NB: negative binomial model, ZINB: zero-inflated negative binomial model, EMMs: estimated marginal means).

					EMMs pairwise comparisons		
Developmental indicator	Model selected	Fungus (colonized medium) (Intercept)	MM (uncolonized medium)	Sand	Fungus-MM medium	Fungus-Sand	MM medium-Sand
Eggs	ZINB	$p < 0.001$	$p < 0.001$	NaN	F > M	NaN	NaN
Juveniles	NB	$p < 0.001$	$p > 0.99$	$p > 0.99$	F = M	F=S	M = S
Exuviae	ZINB	$p < 0.001$	$p < 0.001$	$p < 0.001$	F > M	F > S	M > S
Adults	ZINB	$p < 0.001$	0.01	0.34	F > M	F > S	M = S
Total living individuals	ZINB	$p < 0.001$	$p < 0.001$	0.03	F > M	F > S	M = S
Dead individuals	NB	$p < 0.001$	0.003	0.04	F < M	F=S	M = S

difference between these two conditions in the *F. graminearum* setup. The number of dead individuals removed after ten weeks was significantly lower in presence of *Z. tritici* than in its absence and the number of deaths was significantly lower on the uncolonized MM medium than on the sand only. The number of dead springtails removed in ten weeks was significantly lower in presence of *F. graminearum* than on uncolonized MM medium but there was no difference between the sand substrate and the two other conditions regarding dead individuals.

3.2.2. *Consumption of fungi by springtails*

For *Z. tritici* (Fig. 5), over the three weeks period, the beta regression model showed that the coverage of the MM medium by fungal mycelium significantly increased over time (Beta regression; $p < 2.2e\text{-}16$). *Z. tritici* initially takes the form of yeast-like colonies that did not cover the entire MM medium area at the start of the experiment and from which hyphae subsequently grew, leading to the development of aerial mycelium. The interaction between *H. nitidus* and time was significant (Beta regression; $p < 2.2e\text{-}16$) with the presence of springtails reducing mycelium surface over time. On the third week's data, the beta regression model (precision parameter $\phi = 7.326$, pseudo $R^2 = 0.608$) showed that the presence of springtails had a significant negative impact on *Z. tritici* ($p = 4.24e\text{-}12$) with a 55.1 % decrease of the area covered by aerial mycelium (AME; $p < 2.2e\text{-}16$, 95 % confidence interval: 43.1 %–67.1 %) in boxes with *H. nitidus* compared to control boxes.

F. graminearum (Fig. 6) significantly decreased in surface over the course of ten weeks (Beta regression; $p = 2.78e\text{-}03$) as, contrary to *Z. tritici,* the medium was fully colonized at the start of the experiment. The interaction between *H. nitidus* and time was significant (Beta regression; $p < 2.2e\text{-}16$) with a decrease of *F. graminearum* surface over time when springtails were present in the Petri dishes. The model built from the data of the tenth week (precision parameter $\phi = 2.4758$, pseudo $R^2 = 0.4263$) showed that the presence of springtails had a significant negative impact on *F. graminearum* ($p = 7.1e\text{-}4$) with a 36.4 % decrease of the area covered by aerial mycelium (AME; $p = 2e\text{-}4$, 95 % confidence interval: 17.1 %–55.8 %) in boxes with *H. nitidus* compared to control boxes. We also observed that mycelium coverage was not homogenous across the replicates. Petri dishes with a high coverage of aerial mycelium had a higher mortality and lower reproduction of *H. nitidus* after ten weeks (11.5 individuals *versus* 70.3).

4. Discussion

4.1. *Preferences of H. nitidus for phytopathogenic fungi*

Z. tritici was preferred over the beneficial fungi in seven out of the eleven choice tests (Fig. 3), while in the other cases there was no preference between the two fungi. *F. graminearum* was preferred in four choice tests (Fig. 4), but in most of the other cases the beneficial fungus was preferred. Overall, our first hypothesis was validated as springtails made choices, but *H. nitidus* behaved differently toward beneficial fungi depending on the phytopathogenic fungus they were paired with. However, the attractiveness ranking order of the beneficial fungi relative to the pathogen is consistent when testing with *Z. tritici* and *F. graminearum*.

Among the beneficial fungal species against which both phytopathogenic fungi were preferred, three belong to the *Trichoderma* genus, several species of which are considered potential biocontrol agents. It has already been shown that springtails avoid different species of this genus (Maraun et al., 2003; Ponge and Charpentié, 1981), suggesting that the relative repulsive effect of the different *Trichoderma* species could be the result of their strong chitinolytic activity. *T. harzianum*'s chitinase production during mycoparasitic interactions was widely

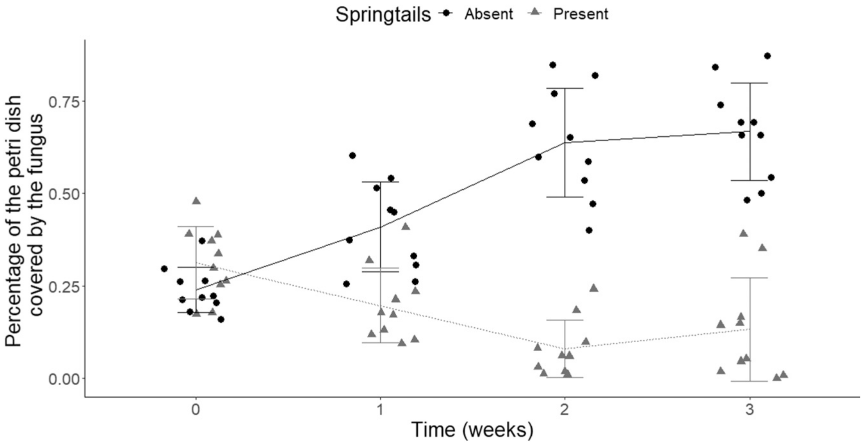

Fig. 5. Evolution of the proportion of MM medium area (square plug) covered by *Z. tritici* aerial mycelium over the first three weeks in the presence or absence of *H. nitidus*. Bars represent standard deviation and dots represent individual values.

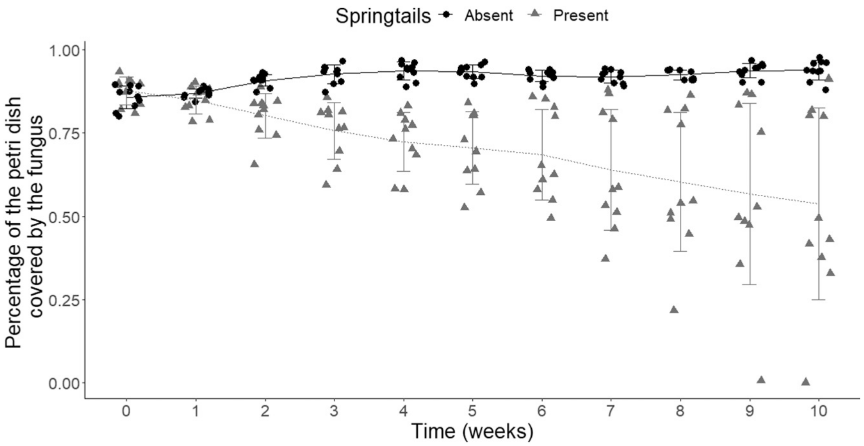

Fig. 6. Evolution of the proportion of MM medium area (Petri dish) covered by *F. graminearum* aerial mycelium over ten weeks in the presence or absence of *H. nitidus*. Bars represent standard deviation and dots represent individual values.

studied with different potential applications (reviewed in Stoykov et al., 2015) including the use of the fungus as a biological agent against chitin-producing fungi (Kubicek et al., 2001) or arthropods (Binod et al., 2007). Moreover, the consumption of *T. harzianum* by *Proisotoma minuta* and *Onychiurus encarpatus*, two springtail species, was followed by a higher mortality for both species (Lartey et al., 1989). *C. rosea*, the other fungus avoided by springtails when offered in pair with each of the two phytopathogenic fungi, was also evaluated as a potential biological control agent against numerous fungal phytopathogens, nematodes and insects, maybe because of its chitinase production (reviewed in Sun et al., 2020). Unlike *F. graminearum*, *Z. tritici* was preferred over *M. alpina*. The beneficial fungus has been shown to release chitinase into the medium in some cultures (Lähn et al., 2002), which may also explain its low attractivity compared to *Z. tritici* and suggesting that *F. graminearum* might not be palatable for *H. nitidus* or releases repulsive molecules (Xu et al., 2019). These five fungi, mostly avoided by *H. nitidus* in the current choice experiments, are known to produce chitinases in sufficient quantities to be used as a biological control agent. We thus may hypothesize that springtails, whose exoskeleton is made of chitin, avoid such fungi to increase their survival. This hypothesis is consistent with what is known about the impact of chitin and chitin-like compounds in plant-fungal interactions (Pusztahelyi, 2018).

Beyond the results described above, it should be noted that springtails expressed some opposite preferences depending on the pathogenic fungus offered in the choice tests, highlighting that interactions (repulsion *vs.* palatability) are complex and more often relative than absolute. *Z. tritici* was thus preferred over *A. nidulans* and *E. nigrum* while these two fungal species were preferred over *F. graminearum*. On the one hand, it was shown that *A. nidulans* produces endochitinase ChiB known to induce autolysis of the fungus (Shin et al., 2009). This species also produces secondary metabolites that are perceived from a distance and avoided by different collembolan species (Rohlfs et al., 2007), including *H. nitidus* (Staaden et al., 2011). On the other hand, it was shown that *E. nigrum* is the preferred fungus of another springtail species (Bardgett et al., 1993) and can increase chitinolytic activity although it is not a chitinase producer (Sena et al., 2013). In both cases, the fungus has chitinolytic activity but it remains weak. Springtails could be able to perceive it and thus avoid it against a palatable fungus, but nevertheless would prefer it to one producing repulsive metabolites.

In our experiment there was no difference of preference between *Z. tritici* and any of the four beneficial fungi (*C. cladosporioides*, *A. strictum*, *P. macrospinosa*, *A. pullulans*) offered to the springtails while these four fungi were preferred over *F. graminearum*. *C. cladosporioides* was shown to be of high nutritional value for two collembolan species, *Folsomia candida* and *Protaphorura armata* (Scheu and Simmerling, 2004), and preferred over other fungi by several species of springtails (Maraun et al., 2003; Visser and Whittaker, 1977) including *H. nitidus* (Staaden et al., 2011). Thus, the preference for this fungus compared to *F. graminearum* is consistent with previous studies' findings. The absence of preference for *Z. tritici* when proposed to *H. nitidus* in pair with *C. cladosporioides* suggests that both fungi of this choice experiment are highly attractive. *A. strictum* does not seem to produce chitinase on an agar medium (Nigh et al., 1980) and to our knowledge, no study on *P. macrospinosa* showed chitinase production. None of these two fungi was previously tested with springtails. Our results show that both fungi are relatively attractive as they were preferred against *F. graminearum* and there was no preference against the attractive *Z. tritici*. *A. pullulans* is a potential postharvest biological control agent that also produces cell-breaking enzymes such as chitinases (Ippolito et al., 2000; Zhang et al., 2010). It was shown that this fungus, when offered to *Onychiurus sinensis*, another springtail species, was not preferred nor avoided compared to other fungi (Sadaka-Laulan et al., 1998). It was preferred over the less palatable phytopathogenic fungus in our study and there was no preference against the most palatable, suggesting it is quite attractive.

In our choice experiments, several preferred fungi were species with a dark pigmentation (*Z. tritici*, *P. macrospinosa*, *C. cladosporioides*, *A. nidulans*) but several darkly pigmented species (*T. harzianum*, *T. hamatum*, *T. atroviride*) were avoided by *H. nitidus*, suggesting that attraction or palatability is not driven by this criterion. Melanin is a pigment widely spread among fungi species (Belozerskaya et al., 2017) that affected springtail growth and reproduction but was not shown to influence springtail preferences (Scheu and Simmerling, 2004). Our results support this absence of effect of melanin on springtail choices, suggesting that the production of active secondary metabolites is not necessary accompanied by color expression, explaining the non-univocal link between preference and pigmentation. For one of the phytopathogenic fungi tested, *F. graminearum*, the production in high quantities of a nontoxic pigment was shown to be involved in its protection against springtail grazing (Xu et al., 2019). While our results suggest that pigmentation alone does not define springtail preferences, the aim of our study was not to investigate the impact of pigments and the validation of these hypotheses must be the focus of further specific experiments.

Overall, *Z. tritici* was preferred in a majority of the trials, making it an attractive fungus for *H. nitidus*. Springtails prefer to consume fungi that maximize their fitness (Klironomos et al., 1992; Scheu and Simmerling, 2004). We can thus infer that *Z. tritici* is likely of high nutritive value to compete with *C. cladosporioides* and should, *in vitro* at least, not excrete metabolites involved in defense against grazing mycophagous organisms (Böllmann et al., 2010). While out experimental setup did not allow direct comparisons, results regarding *F. graminearum* were more contrasted. The phytopathogenic fungus was only preferred over beneficial fungi that produce chitinolytic enzymes. A recent meta-analysis from Goncharov et al. (2020) showed that *Fusarium* species were preferred over other fungi by soil fauna, including six species of springtails, but *H. nitidus* showed no preference. These results are congruent with ours and could be explained by the production of mycotoxins (Chen et al., 2019; Hart et al., 1984; McMullen et al., 1997), the emission of nontoxic defense compounds (Xu et al., 2019) or/and a lower nutritional value.

Our results showed that *Z. tritici* was preferred over other fungi potentially associated with wheat crops but extrapolation to field conditions should be considered with caution as Bengtsson et al. (1988) showed that springtail preferences can switch between *in vitro* and *in situ* assays. Therefore, experiments on wheat, using living tissues or plant residues infected by a pathogenic fungus, should be conducted to confirm this differential attractiveness. These results should also entice similar studies using other springtails species as they coexist in fields with different dietary preferences (Jørgensen et al., 2003). Species with similar preferences could reinforce the effect of *H. nitidus* on *Z. tritici* while other species could prefer *F. graminearum* (Goncharov et al., 2020).

4.2. Springtail populations survival through feeding on fungus

Analysis of the complete *H. nitidus* cohort (eggs, juveniles, exuviae and adults) showed that this species population can grow and successfully reproduce when fed on *Z. tritici* or *F. graminearum* (Table 1), therefore validating our second hypothesis. While populations fare better with the Mandels medium (MM) than on the sand substrate, the differences with the presence of fungus, *Z. tritici* or *F. graminearum*, are great and significant, proving that although springtails fed on the MM medium, the development of their population was made possible by the consumption of the fungi. The total number of exuviae, usually used as an aggregative developmental indicator of springtail growth, was higher when *H. nitidus* fed on the pathogenic fungi than on uncolonized MM medium alone or on the sand substrate. The same trend was observed for the size of the population (total number of living individuals) depending on the condition. Populations of *H. nitidus* increased when fed on *Z. tritici* or *F. graminearum* while other populations decreased, meaning that both fungi were primary source food for this springtail species. However, the final number of juveniles born per adult initially exposed to each phytopathogenic fungus was lower than in a previous study with other fungi (Scheu and Folger, 2004), suggesting that the conditions that we tested were suboptimal. However, populations were maintaining themselves and growing with each of the pathogenic fungus, meaning that long-term consumption of the fungi would not be an impediment to the use of *H. nitidus* as a biological control agent. Nevertheless, our results suggest that optimal conditions could be achieved for springtails in wheat crops since they could supplement their diet based on *Z. tritici* with other attractive fungal species such as *C. cladosporioides*, *P. macrospinosa* and *A. strictum*. In fact, several studies highlighted that mixed diets, *i.e.* diets consisting of more than one food source, increased the fitness of collembolan species, including *H. nitidus* (Scheu and Folger, 2004; Scheu and Simmerling, 2004).

Conflicting results exist regarding the link between food preference and fitness of springtail species (Böllmann et al., 2010; Menta et al., 2019; Scheu and Simmerling, 2004), which could explain that only *Z. tritici* appears as a preferred fungus while *F. graminearum* also allows *H. nitidus* population growth without being attractive. Böllmann et al. (2010) showed that the production of metabolites involved in defense against grazing by mycophagous organisms is the main factor influencing preferences and that other traits such as palatability or an increase of fitness have a lower impact on springtail choices. Therefore, our results suggest that *F. graminearum* is not as low in nutrition as suggested by the choice experiment results and that its lack of attractiveness may be due the production of repulsive compounds.

4.3. Reduction of fungal mycelium due to springtail grazing

Our results validate our third hypothesis and show that *H. nitidus* can reduce coverage of aerial mycelium of both phytopathogenic fungi grown *in vitro*. This result paves the way for further *in situ* experiments with *H. nitidus* as a promising candidate for biocontrol or bioregulation against fungal wheat pathogens which carry out part of their life cycle on living or decaying pieces of plants in contact with the soil. The significant impact of the presence of *H. nitidus* on the fungal coverage was significant for both *Z. tritici* (decrease of 55.1 % after three weeks) and *F. graminearum* (decrease of 36.4 % after ten weeks) compared to the controls. Springtails were observed grazing on the hyphae of both fungi.

For *F. graminearum*, our results confirm the influence of *H. nitidus* on the fungus showed in Mehl (1940). However, there were discrepancies between boxes containing springtails: the fungal development in four Petri dishes was important and close to the control while in the six remaining Petri dishes fungal cover was low to nonexistent. We observed that the replicates with a high coverage of aerial mycelium were the ones with higher mortality and low reproduction of *H. nitidus* after ten weeks (11.5 individuals *versus* 70.3). Moreover, the initial quantity of *Z. tritici* exposed to *H. nitidus* at the beginning of the experiment was lower than those of *F. graminearum* (30 × 30 mm square plug *versus* a whole Petri dish) and the final quantity was less variable (Fig. 5). Previous studies also showed that fungal growth could be reduced or stimulated by springtail grazing (Bengtsson and Rundgren, 1983; Hanlon and Anderson, 1979; Van der Drift and Jansen, 1977) depending on their density. While our results show an overall reduction in *F. graminearum* coverage (Fig. 6), having two groups following opposite trends could mean that the initial population is barely enough to reduce aerial mycelium.

Additionally, if the area covered by the fungi decreased with the presence of *H. nitidus*, spores can pass the digestive system of springtails and be found in feces, leading to the dissemination of spores. Therefore, density and spore dispersion should be considered for further experiments to test the regulation capacity of *H. nitidus* against these two phytopathogenic fungi. Future studies should complexify experimental setup as organic amendments reduce infection by *F. graminearum* (Goncharov et al., 2021) and could therefore impact the effect of *H. nitidus* on phytopathogenic fungi. Overall, our study gives promising

Table 1
Developmental indicators of *H. nitidus* populations after ten weeks on MM medium colonized with the phytopathogenic fungus *Z. tritici* or *F. graminearum* (fungus), uncolonized MM medium (MM) or sandy substrate only (sand). Mean values are given with associated standard errors.

	Zymoseptoria tritici			*Fusarium graminearum*		
Developmental indicator	Fungus (colonized medium)	MM (uncolonized medium)	Sand	Fungus (colonized medium)	MM (uncolonized medium)	Sand
Eggs	35.7 ± 7.2	0.4 ± 0.4	0.0 ± 0.0	66.7 ± 11.3	0.3 ± 0.3	0.0 ± 0.0
Juveniles	67.6 ± 16.9	1.4 ± 0.9	0.1 ± 0.1	28.6 ± 21.2	0.0 ± 0.0	0.0 ± 0.0
Exuviae	145.5 ± 7.6	19.1 ± 4.5	2.5 ± 0.7	165.3 ± 7.2	77.1 ± 12.1	5.5 ± 1.9
Adults	28.0 ± 0.7	21.7 ± 1.2	10.6 ± 1.4	18.2 ± 3.1	8.1 ± 1.9	4.0 ± 2.1
Total living individuals	95.6 ± 16.8	23.1 ± 1.6	10.7 ± 1.5	46.8 ± 23.3	8.1 ± 1.9	4.0 ± 2.1
Dead individuals	0.7 ± 0.4	6.3 ± 1.2	15.6 ± 1.9	9.8 ± 2.5	20.4 ± 2.54	16.2 ± 2.4

results toward the potential ability of *H. nitidus* to limit the amount of primary inoculum of phytopathogenic fungi, thus appearing as a new biotechnical lever in integrated pest management.

4.4. Conclusion

This study, the first to our knowledge on the feeding choices of *H. nitidus* among fungi found in European wheat crops using a large set of species, showed promising results regarding its ability to regulate two widespread important fungal pathogens present in living wheat plants but also on their residues. Both fungi appeared to be suitable food sources for *H. nitidus* and their biomass, approximated by the mycelial coverage on Petri dishes, was reduced by springtails in long-term consumption experiments. This highlighted the potential ability of springtails to regulate the growth of both phytopathogenic fungi by moderate grazing. *H. nitidus* might be a promising biocontrol agent against *Z. tritici* and, to a lesser extent, against *F. graminearum*: the first species was among the preferred fungi in the choice experiments while the second one was preferred only against some beneficial fungal species maybe due to repulsive metabolites. Understanding how these metabolites governing springtail preferences could help predict the food-web interactions in crop soils and improve ecosystem services of springtails, especially the regulation of plant pathogens. These results should be confirmed with the fungus grown on wheat tissues to assess the actual impact of *H. nitidus* on fungal development. Future studies should also complexify the setup and use microcosms including soil matrix and its communities to get closer to crop conditions before *in situ* experiments.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2023.104897.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

We acknowledge the financial support of the AVIV department of the Muséum national d'Histoire naturelle through Fédérateur projects. Thank you to Dr. Marjorie Roscian for her advice and technical support on the software ImageJ and to Monique Van Dorssen for proofreading this manuscript.

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