

# High insect pest damage increases faba bean (*Vicia faba*) yield components but only in the absence of insect pollination

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## Abstract

Identifying and quantifying crop stressors interactions in agroecosystems is necessary to guide sustainable crop management strategies. Over the last 50 years, faba bean cropping area has been declining, partly due to yield instabilities associated to uneven insect pollination and herbivory. Yet, interactions between pollinators and a key pest, *Bruchus rufimanus* (florivorous and seed predating herbivore), on faba bean yield have not been investigated. Using a factorial cage experiment in the field we investigated how interactions between two potential stressors, lack of pollination from *Bombus terrestris* and herbivory by *B. rufimanus*, affect faba bean yield. Lack of insect pollination reduced bean weight per plant by 15%. Effects of *B. rufimanus* herbivory differed between the individual plant and the plant-stand scale (i.e. when averaging individual plant scale responses), likely due to high variation in the level of herbivory among individual plants. At the individual plant scale, *B. rufimanus* herbivory increased yield but only in the absence of pollinators, possibly due to plant over-compensation and/or pollination by *B. rufimanus*. At the plant-stand scale, we found no effect of *B. rufimanus* on yield. However, there was a tendency for heavier individual bean weight with insect pollination, but only when *B. rufimanus* herbivory was absent, possibly due to a negative effect of *B. rufimanus* on the proportion of legitimate flower visits by *B. terrestris*. This is the first experimental evidence of interactive effects of *B. terrestris* and *B. rufimanus* on faba bean yield. Our preliminary findings of negative and indirect associations between *B. rufimanus* and individual bean weight call for a better acknowledgment of these interactions in the field in order to understand drivers of crop yield variability in faba bean. This study showed that herbivory can increase yield, but this effect is only detectable when investigated in combination with lack of pollination.

## Introduction

Stressors are biotic or abiotic variables that cause a negative response in a taxa or community (Barrett et al., 1976; Vinebrooke et al., 2004). For crop plants that benefit from insect pollination, insect herbivory and a lack of pollination can be referred to as biotic stressors if they negatively affect yield. Occasionally, compensatory responses may result in higher yields in herbivore-attacked plants compared to un-attacked plants (overcompensation, Poveda et al., 2010) and pollination benefits to yield may vary from negative to positive within and between cultivars (Bishop et al., 2020; Lundin & Raderschall, 2021). Therefore, the characterization of herbivory and lack of pollination as crop stressors is not clear cut, but rather a nuanced one that will depend on the frequency, timing and quantity of herbivory/pollination as well as modifiers such as nutrient availability and cultivar (Poveda et al., 2010). To characterize crop stressors it is thus important to explore such nuances (e.g. does herbivory or lack of pollination lead to yield overcompensation?) and investigate the potential for interactions among hypothesized stressors on crop yield (Peterson & Higley, 2000; Piggott et al., 2015). Stressors can interact in an additive, synergistic or antagonistic manner on plant growth and reproduction, making net effects on crop yield challenging to predict (Supplementary material, Fig. S1A). Empirically quantifying plant stressors and their interactions, particularly in agroecosystems, will help guide sustainable crop management strategies (Cote et al., 2016; Gagic et al., 2019; Saunders et al., 2016; Sutter & Albrecht, 2016).

Lack of insect pollination and insect herbivory may independently (additively), synergistically or antagonistically affect yield of pollinator-dependent crops. A synergistic effect between these stressors would result when the combined negative effect on yield, due to low insect pollination and herbivory, is higher than the sum of their individual effects. Alternatively, an antagonistic effect would result when yield loss due to lack of insect pollination and herbivory is lower than the sum of their individual effects. This may be the case if herbivore-induced plant overcompensation has the capacity to minimize the negative effect of lack of pollination (Järemo et al., 1999; Munguía-Rosas et al., 2015) or if the herbivore directly benefits plant reproduction by acting as a pollinator (i.e. some florivores, see: McCall & Irwin, 2006). Interactions between insect pollination and herbivory have recently been found to influence plant trait evolution (Ramos & Schiestl, 2019) and crop yield (Bartomeus et al., 2015; Gagic et al., 2019; Garibaldi et al., 2018; Lundin et al., 2013; Raderschall et al., 2021; Saunders et al., 2016; Sutter & Albrecht, 2016; Tamburini et al., 2019). Compensatory responses of crops to herbivory, and effects of florivorous herbivores on yield are important and under-investigated mechanisms as they can maintain or even increase yield of crops exposed to pests (Gagic et al., 2016; Poveda et al., 2018). A recent meta-analysis found that overcompensation for insect herbivory in plants is pervasive and can increase crop yield (Garcia & Eubanks, 2019). For example, flower abortion due to herbivory can lead damaged plants to grow larger fruits (Sanchez & Lacasa, 2008) or produce more flowers (Peschiutta et al., 2020) than plants without herbivory. Despite yield increases, overcompensation due to herbivory may decrease yield quality (Peschiutta et al., 2020) and reduce the marketable crop. These mechanisms in interaction with pollination services can be particularly important in crops with large compensatory potential to biotic and abiotic stressors, such as faba bean (*Vicia faba* L.) (Lopez-Bellido et al., 2005).

Faba bean is an important nitrogen-fixating legume crop grown worldwide (Jensen et al., 2010; Karkanis et al., 2018). Over the past 50 years, faba bean cropping area has been declining due to yield instabilities, associated to abiotic stress, pest and pathogen pressure (Karkanis et al., 2018), and possibly uneven insect pollination. Faba beans are partially dependent on insect pollinators (Bishop & Nakagawa, 2021). While insect pollination generally increases faba bean yield and yield stability (Suso & del Rio, 2015; Suso & Maalouf, 2010), pollination dependence within cultivars varies greatly, from -4 to 46% (loss in yield per plant without pollination)(Bishop et al., 2020). A recent study found that insect pollination benefit in faba bean, measured as the increase in bean weight per plant, lessened with aphid herbivory (Raderschall et al., 2021). This variability in pollination benefit underlines the importance to investigate interactions between pollinators and major pests if we want to understand factors affecting yield variability in faba beans.

A key pest in faba bean is *Bruchus rufimanus* (Boh.) (Segers et al., 2021). Adult beetles colonise the crop in spring to feed on pollen and nectar, and start laying eggs on developing pods (Segers et al., 2021). When the larvae hatch, they bore through the pods and develop and feed inside the beans. We use the term ‘herbivory’ to include both florivory by the *B. rufimanus* adults and seed predation by the larvae. Larval feeding reduces seed weight and quality (Epperlein, 1992; Roubinet, 2016; Segers et al., 2021). Adult beetles might have additional negative effects on yield if their feeding on pollen disrupts pollinator visitation (Ye et al., 2017), or, alternatively, positive effects if they pollinate (Krupnick & Weis, 1999; McCall & Irwin, 2006). Interactions between pollinators and *B. rufimanus* on faba bean growth and yield have so far not been investigated.

Here we evaluate the effect of herbivory by the pest *B. rufimanus* on faba bean yield components and ask how interactions between two hypothesized stressors, namely lack of pollination from bumblebees, and herbivory by *B. rufimanus*, affect above- and belowground plant traits and yield of faba bean. Specifically, we investigate whether flower visitation by pollinators changes with the inclusion of herbivores, and/or if there is over-compensatory growth of the plant in response to *B. rufimanus* damage in the presence of pollinators.

## Material and Methods

### *Field experiment set-up*

To assess the individual and interactive effects of the two stressors herbivory and lack of pollination on faba

bean, we conducted a cage experiment in 2020 in a faba bean field in Uppsala, Sweden (59deg50'29.12"N; 17deg42'02.44"E). We conducted a fully-crossed two-factor field experiment, with presence and absence of herbivores (H+/H-) and pollinators (P+/P-), where H+ and P- were the stressed level of each factor. Each H and P treatment combination had seven replicates (N=28 in total), arranged in seven blocks, with one treatment combination per block (Fig. S2). We used 2x2x2 m cages covered with a nylon net (mesh size: 0.6x0.6 mm) to control the access of the herbivores and pollinators to the crop. Faba beans seeds (cultivar: Tiffany, Scandinavian Seed) were planted in the field on the 24<sup>th</sup> of April (plant density per m<sup>2</sup>: mean+sd = 58.4+-8.5), and plants were treated with the fungicide Signum (0.5 kg.ha<sup>-1</sup>, BASF; 267 g.kg<sup>-1</sup>boscalid + 67 g.kg<sup>-1</sup>pyraclostrobin) on the 15<sup>th</sup> of June, before flowering (BBCH-51) and prior to bumblebee hive inclusion, to avoid negative impacts on pollinators (Fisher et al., 2021).

### *Herbivore inoculation*

*B. rufimanus* were collected over two weeks in early June from faba bean crops in the southern region of Vastergotland, where they had already colonised the earlier flowering fields. In the H+ treatment cages (N=14), 45 *B. rufimanus* individuals per m<sup>2</sup> (0.77 individuals per plant) were inoculated on the 16<sup>th</sup> of June, before crop bloom (BBCH-51:59). This pest density was chosen based on surveys of *B. rufimanus* conducted by the Swedish Board of Agriculture in 55 faba bean fields across Sweden between 2016-2019, which found that maximum naturally occurring pest incidences in commercial faba bean fields were 0.5-1 *B. rufimanus* per plant, depending on the region. To control for herbivores in the H- treatment (N=14), cages were checked for *B. rufimanus* and any individual was removed prior to pollinator supplementation. No other faba bean crop pests, such as aphids, were detected in the cages.

### *Pollinator supplementation and flower visitation*

To create a P+/P- treatment we supplemented P+ cages (N=14) with bumblebee hives (*Bombus terrestris* L., Natupol Seed, Koppert, <https://www.koppert.com/natupol-seeds/>) on the 22<sup>nd</sup> of June at the onset of flowering (BBCH-61). The hives contained approximately 2-5 workers foraging for pollen and nectar and 5-8 males collecting nectar. Hives were placed at 1 m above the ground facing east for the duration of crop flowering, until the 27<sup>th</sup> of July. At the end of the experiment, we found high variation in the abundance of bumblebees inside each hive (mean+sd = 13.6+-5.1), but there were no differences in bumblebee abundances between H+/H- treatments (t-test: p=0.4) and bumblebee abundances in the hives was not correlated with pollinator visitation rates (Pearson rho: -0.14).

To investigate effects of herbivores on pollinators we carried out pollinator visitation observations in each P+ cage in both herbivory treatments (N=14). Between the 23<sup>rd</sup> of June and the 10<sup>th</sup> of July, pollinators in P+ cages were surveyed 15 times. Surveys were carried out under good weather conditions (>15degC and no rain) between 1-6 pm. After each survey, the number of open flowers were counted, initially on 10 plants and from the 7<sup>th</sup> of July, when flowering was decreasing (survey round 7), in a 1 m<sup>2</sup> quadrat (1/4 of the cage). The same plants and quadrat were observed in every survey round. Pollinator visitation rate per flower and foraging behaviour were recorded for a duration of 10 min, initially on the 10 plants, where the number of flowers had been counted and later in the 1 m<sup>2</sup> quadrat. For each visit, we noted whether pollinators were legitimately visiting flowers by inserting their proboscis through the front of the flower opening, visiting extra floral nectaries (EFN) located underneath the stipules, or robbing nectar by inserting their proboscis through a hole at the base of the flower tube (Tasei, 1976). Because of low nectar reserves in all the hives due to spillage during transportation, pollinator behaviour might have been affected in the first half of the experiment, with more nectar robbing behaviour than would have been the case if hives had not been sugar-starved. From the 7<sup>th</sup> of July, each colony was supplemented with sugar-water. The timing of sugar-water supplementation was included as a factor in the analyses of pollinator visitation and foraging behaviour.

### *Plant measurements*

We estimated plant density by counting the number of plants within a 0.25 m<sup>2</sup> quadrat randomly placed in each cage. When pods reached maturity (BBCH-89), on 10<sup>th</sup> of September, 20 plants (stem, leaves, pods

and roots) were collected per cage. On each plant, we counted the number of pods, number of beans per pod, proportion of damaged beans (beans with *B. rufimanus* emergence holes), plant height and tap-root length. Pods were classified into three categories: mature, immature (small and green) and unfertilized (without beans inside). Roots were washed with water. Aboveground plant (stems and leaves) and root biomass and bean weight for each plant were dried at 65degC for 48 hours and subsequently weighed. Beans per pod was averaged per plant prior to statistical analyses, beans per plant was calculated by summing the number of beans across pods per plant and individual bean weight was calculated by dividing bean weight per plant with number of beans per plant. Yield in  $\text{kg}\cdot\text{ha}^{-1}$  was calculated for each cage by multiplying average bean weight per plant with plant density.

### Data analyses

We used generalised linear mixed-effects models to test the interactive effects of herbivory and pollination treatments on: (a) proportion damaged beans per plant (beans with *B. rufimanus* emergence holes) (b) faba bean yield components (individual bean weight, total bean weight per plant, number of beans per pod, number of beans per plant, number of pods (mature, immature and unfertilized) per plant, proportion of mature pods per plant, and yield ( $\text{kg}\cdot\text{ha}^{-1}$ ), and (c) plant growth components (plant height and aboveground biomass, root length and biomass). Normal distributions were used except for number of pods and beans per plant, where a Poisson distribution was used or a negative binomial when data was overdispersed, and for proportion of damaged beans and mature pods per plant where a binomial distribution was used (see Table 1 for model structures). The explanatory variables in all models included the H+/H- and P+/P- treatments and their interaction term. Despite the care taken to remove *B. rufimanus* from the H- cages at the beginning of the experiment, beans with emergence holes were also found in these cages, and there was a large variation in damage between plants within each H+/H- cage (Fig. S3). We therefore, in addition to the main H+/H- treatment effect (i.e. plant-stand scale, measured by averaging individual plant scale responses in each cage), investigated the effect of herbivory damage at the plant scale, measured as percentage of damaged beans per plant within cage (% Damage). Proportion of damaged beans did not vary with pollination treatment levels (Table 1,  $p=0.09$ ). We tested all plant yield and growth variables, and used P+/P- treatment and % Damage per plant and their interaction term as explanatory variables. The random structure in all models included cage identity (N=28) nested within block (N=7), except for yield ( $\text{kg}\cdot\text{ha}^{-1}$ ) per cage where only block was included. If significant interactions were found, post-hoc tests using the “emmeans” package were carried out to investigate the direction of the effect.

To test the effects of herbivory on observed pollinator behaviour (proportion of legitimate, robbing and EFN visits) and on pollinator visitation rate (visits per flower per time unit) we used a generalized mixed-effects model with a binomial and a normal distribution respectively. The explanatory variables included H+/H- treatment and the number of open flowers per  $\text{m}^2$  and their interaction term. To account for addition of sugar-water to the pollinators on the 7<sup>th</sup> of July a binary factor (sugar-water: yes/no) was included as well as its interaction with number of open flowers per  $\text{m}^2$  and herbivory treatment. The interaction between herbivory treatment and sugar-water was never significant and did not improve the models as determined by the Akaike Information Criterion (AIC), indicating that the effect of herbivory on pollinator behaviour did not change after the addition of the sugar-water. This interaction was therefore excluded. To investigate the effect of herbivores on number of open flowers per  $\text{m}^2$  in cages with pollinators, we used a generalized mixed-effects model with H+/H- treatment as explanatory variable. The random structure for all models incorporated the sampling round (N=15) nested within cage identity and block.

The residuals of all models were visually inspected to validate the model assumptions and additionally, generalized linear models were checked for overdispersion using “DHARMa” (Hartig & Lohse, 2020). Multicollinearity was checked for all models (variation inflation factor <2). All analyses were conducted in R version 3.6.3, using packages “nlme” (Pinheiro & Bates, 2020), “lme4” (Bates et al., 2020), “emmeans” (Lenth et al., 2021) and “ggplot2” (Wickham et al., 2020) to plot data.

## Results

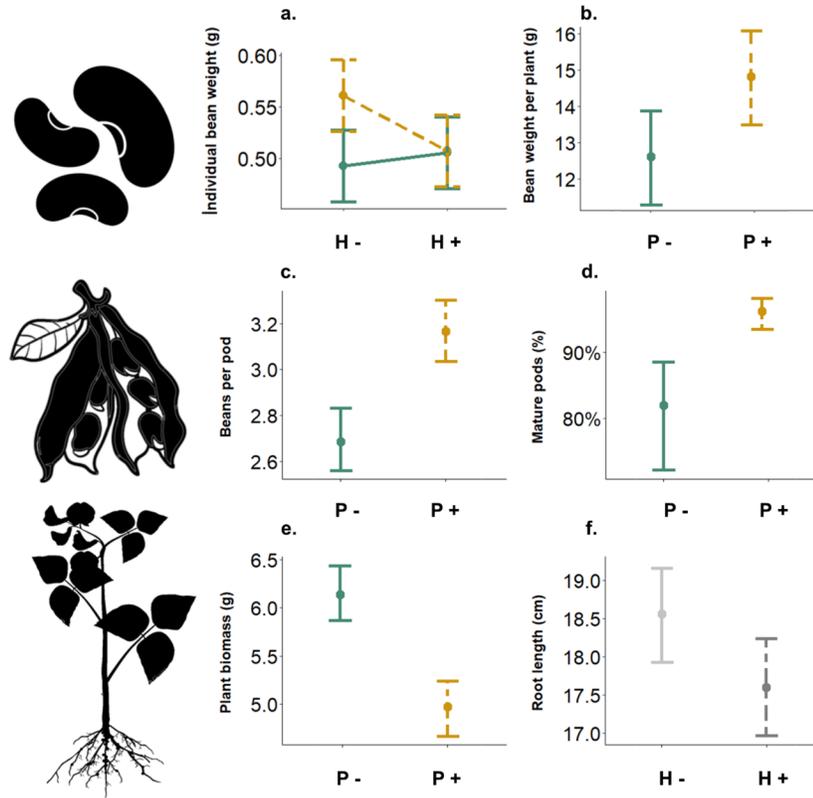
### *Yield and its components*

Lack of pollination (P-) decreased total bean weight per plant, mean number of beans per pod and total number of beans per plant, independently of the herbivory treatment (Table 1, Fig. 1b,c, Fig. S4). In the absence of insect pollination, bean weight and number of beans per plant decreased by 15% and 17%, respectively. There was a marginal ( $p=0.06$ ) interactive effect of pollination and herbivory on individual bean weight, with pollination increasing individual bean weight but only in the absence of herbivory (Table 1, Fig. 1a, Fig. S4). Herbivory increased percent damaged beans, with on average 39% damaged beans in the H+ treatment (Table 1, Fig. S3), which is over tenfold the economic injury threshold set for beans targeting human consumption and could lead to up to 78% economical losses (Bachmann et al., 2020; Roubinet, 2016). There was no effect of pollination nor herbivory treatments on yield ( $\text{kg}\cdot\text{ha}^{-1}$ ), or mature or total number of pods per plant, however, proportion of mature pods was lower with lack of pollination, due to higher numbers of unfertilized and immature pods (Table 1, Fig. 1d, Fig. S4).

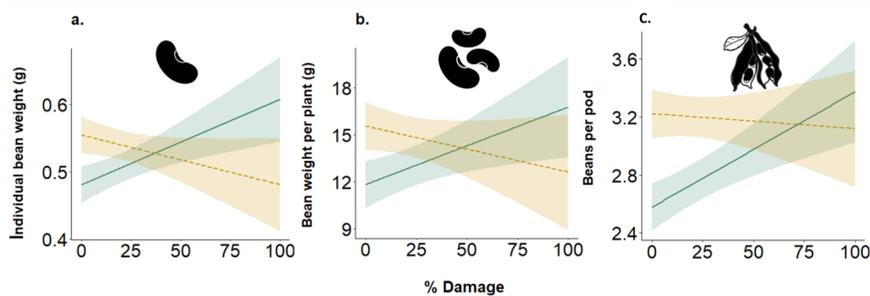
When herbivory damage on each plant was used as an explanatory variable (% Damage), there were interactive effects of pollination and herbivory damage on individual bean weight, total bean weight per plant, and number of beans per pod (Table 1, Fig. 2, Fig. S5). In the absence of pollination, there were positive relationships between yield and herbivory damage for several yield components (individual bean weight:  $\text{est}=0.001$ ,  $\text{se}=0.0004$ ,  $p<0.01$ ; total bean weight:  $\text{est}=0.06$ ,  $\text{se}=0.02$ ,  $p<0.01$ ; and number of beans per pod:  $\text{est}=0.007$ ,  $\text{se}=0.002$ ,  $p<0.01$ ) (Fig. 2, Fig. S5). In the presence of insect pollination, there were no relationships with herbivory damage. In addition, number of beans per plant increased with increasing herbivory damage independent of pollination treatment (Table 1). Number of pods per plant was not affected, but proportion of mature pods increased with herbivory damage due to a decrease in the number of unfertilized and immature pods (Table 1).

### *Plant growth*

Plant above-ground biomass and height were higher with lack of pollination (Table 1, Fig. 1e, Fig. S4). While there was no effect of pollination or herbivory on root biomass, root length was marginally ( $p=0.06$ ) shorter in the presence of herbivory (Table 1, Fig. 1f, Fig. S4), this effect became significant when using *B. rufimanus* % Damage as an explanatory variable (Table 1, Fig. S5). In addition, there was a negative relationship between herbivory damage and plant above-ground biomass and height (Table 1, Fig. S5).



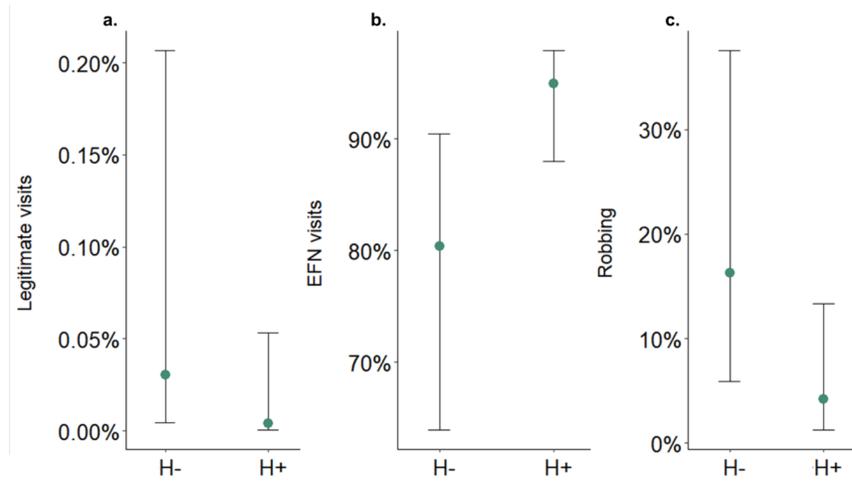
**Fig. 1** . Model prediction for faba bean yield and growth components in relation to herbivory (**H-** : *solid light grey line* ; and **H+** : *dashed dark grey line* ) and pollination (**P-** : *solid green line* ; and **P+** : *dashed yellow line*) levels: a. mean individual bean weight (g), b. bean weight per plant (g), c. number of beans per pod, d. percentage of mature pods per plant, e. aboveground plant dry biomass (g) and f. tap root length (cm) per plant. Whiskers represent 95% confidence intervals. Note that y-axes do not start at 0.



**Fig. 2** . Model predictions for faba bean yield components in relation to herbivory damage (% of beans with *B. rufimanuse* emergence holes per plant) and pollination levels (**P-** : *solid green line* ; and **P+** : *dashed yellow line*): a. individual bean weight (g), b. bean weight per plant (g) and (c) beans per pod. Bands represent 95% confidence intervals. Note that y-axes do not start at 0.

*Flower visitation*

Addition of sugar-water increased flower visitation rate ( $est=0.36$ ,  $se=0.11$ ,  $p=0.01$ ) and the proportion of legitimate visits ( $est=10.4$ ,  $se=2.6$ ,  $p<0.01$ ) as expected. Despite a low flower visitation rate (mean=0.03,  $sd=0.08$ , min=0, max=0.66 visits per flower per 10 min) and no effect of herbivory on visitation rate ( $est=-0.05$ ,  $se=0.04$ ,  $p=0.31$ ), there was a negative effect of herbivory on proportion of legitimate flower visits by *B. terrestris* (mean±se=0.006±0.005%,  $est=-2.03$ ,  $se=0.89$ ,  $p=0.022$ ,  $R^2_m=0.05$ ), due to higher proportions of EFN visits (mean±se=84±4.3%,  $est=1.34$ ,  $se=0.53$ ,  $p=0.011$ ,  $R^2_m=0.11$ ) but not robbing (mean±se=4.2±1.6%,  $est=-1.47$ ,  $se=0.81$ ,  $p=0.07$ ) (Fig. 3). While nectar robbing increased with the number of open flowers per m<sup>2</sup> ( $est=0.02$ ,  $se=0.01$ ,  $p=0.03$ , Fig. S6), visitation rate and proportion of legitimate visitation were negatively affected by the number of open flowers per m<sup>2</sup> but primarily after sugar-water was added (interaction term: visitation rate  $est=-0.004$ ,  $se=0.002$ ,  $p=0.073$ ,  $R^2_m=0.10$ ; proportion of legitimate visits  $est=-0.09$ ,  $se=0.04$ ,  $p=0.039$ ,  $R^2_m=0.42$ ) (Fig. S6). However, there was no effect of herbivory on number of open flowers per m<sup>2</sup> ( $est=-4.69$ ,  $se=5.55$ ,  $p=0.43$ ,  $R^2_m=0.01$ ).



**Fig. 3** . Model prediction for percent of a. legitimate flower visits, b. EFN visits and c. robbing by *B. terrestris* in relation to a. herbivory (H-/H+) levels. Whiskers represent 95% confidence intervals. Note that y-axis do not all start at 0.

**Table 1.** Model outputs for both plant-stand (cage) and plant scale analyses. Presented are the yield and plant growth components with respect to pollination treatment (P+) and herbivory treatment (H+) or herbivory damage (% of beans with *B. rufimanus* emergence holes per plant, % Damage) and their two-way interactions. Shown are mean estimates (Est) for the respective treatments, standard errors (se), p-values (p) and the adjusted marginal R<sup>2</sup>(R<sub>m</sub><sup>2</sup>) of the model. Significant results (p<0.05) are in **bold** . Plots for significant results and raw data are shown in Figs S4-S5.

	Variables	H+	P+	H*P	R <sub>m</sub> <sup>2</sup>	%DamageP+	%Damage
Bean	Proportion of damaged beans <sup>c</sup>	Est±se	3.85±0.64	-	0.98±0.93	0.59	
		p	< 0.01	0.09	0.29		
Bean	Individual bean weight (g) <sup>a</sup>	Est±se	0.01±0.02	0.06±0.02	-	0.03	0.001±0.0004
					0.06±0.03	0.07±0.01	-
							0.002±0.000

Variables		H+	P+	H*P	R <sub>m</sub> <sup>2</sup>	%DamageP+		%Damage	
Pods	Bean weight per plant (g) <sup>a</sup>	p Est±se	0.59 - 0.26±1.28	<b>0.01</b> 3.01±1.28	0.06 - 1.74±1.81	0.03	< <b>0.01</b> 0.05±0.01	< <b>0.01</b> 3.57±1.13	< <b>0.01</b> - 0.06±0.02
	Beans per pod <sup>a</sup>	p Est±se	0.83 0.1±0.14	<b>0.03</b> 0.57±0.14	0.34 - 0.2±0.2	0.07	< <b>0.01</b> 0.009±0.002	< <b>0.01</b> 2.65±0.12	<b>0.02</b> - 0.008±0.00
	Beans per plant <sup>b</sup>	p Est±se	0.48 - 0.009±0.1	< <b>0.01</b> 0.21±0.1	0.31 - 0.03±0.14	0.03	< <b>0.01</b> 0.004±0.000	< <b>0.01</b> 1.29±0.09	< <b>0.01</b> - 0.004±0.00
	Yield (kg/ha) <sup>a</sup>	p Est±se	0.92 - 413.8±679.4	<b>0.03</b> 1196.3±679.4	0.83 79.4 750.4±960.8	0.2	<b>0.01</b>	< <b>0.01</b>	0.10
	Proportion mature pods <sup>c</sup>	p Est±se	0.54 - 0.23±0.55	0.09 1.71±0.57	0.44 0.07±0.81	0.19	0.07±0.005	2.00±0.61	- 0.008±0.00
	Pods per plant <sup>b</sup>	p Est±se	0.67 - 0.02±0.06	< <b>0.01</b> -	0.92 0.01±0.09	<0.01	< <b>0.01</b> -	< <b>0.01</b> -	0.33 -
	Mature pods per plant <sup>b</sup>	p Est±se	0.67 - 0.07±0.11	0.66 0.16±0.1	0.85 0.04±0.15	0.03	0.13 0.007±0.002	0.79 2.36±0.11	0.96 - 0.007±0.00
	Immature pods per plant <sup>d</sup>	p Est±se	0.49 0.51±0.54	0.12 -	0.78 0.26±0.89	0.34	< <b>0.01</b> -	< <b>0.01</b> -	< <b>0.01</b> -
	Unfertilized pods per plant <sup>d</sup>	p Est±se	0.34 - 0.14±0.6	< <b>0.01</b> -	0.76 0.28±0.87	0.14	< <b>0.01</b> -	< <b>0.01</b> -	0.12 -
	Plant biomass (g) <sup>a</sup>	p Est±se	0.80 0.15±0.29	<b>0.02</b> -	0.74 -	0.06	< <b>0.01</b> -	0.07 -	0.057 0.005±0.00
	Plant height (cm) <sup>a</sup>	p Est±se	0.61 0.46±2.18	< <b>0.01</b> -	0.34 -	0.17	<b>0.01</b> -	< <b>0.01</b> -	0.48 0.09±0.04
		p	0.83	< <b>0.01</b>	0.57		< <b>0.01</b>	< <b>0.01</b>	0.052

Variables		H+	P+	H*P	R <sub>m</sub> <sup>2</sup>	%DamageP+		%Damage
Root biomass (g) <sup>a</sup>	Est±se	-	-	-	0.01	-	-	-
	p	0.14±0.15	0.20±0.15	0.03±0.21		0.003±0.003	0.21±0.14	0.0004±0.0004
Root length (cm) <sup>a</sup>	Est±se	0.36	0.19	0.88	0.01	0.29	0.14	0.92
	p	-	0.11±0.63	0.61±0.91		-	0.57±0.60	-
		1.29±0.66				0.02±0.01		0.008±0.01
	p	0.06	0.85	0.51		<b>0.02</b>	0.35	0.62

<sup>a</sup> Linear mixed model with normal distribution (“lme”)

<sup>b</sup> Generalized linear mixed model (glmm) with a negative binomial distribution (“glmer.nb”)

<sup>c</sup> Glmm with binomial distribution (“glmer”)

<sup>d</sup> Glmm with Poisson distribution (“glmer”)

## Discussion

We asked how interactions between two hypothesized faba bean stressors – herbivory and lack of insect pollination – affect yield components (Fig. S1B). While lack of insect pollination is a clear stressor of faba bean, as it related negatively to several yield components, effects of herbivory by *B. rufimanus* were less straightforward. *Bruchus rufimanus* effects changed depending on the scale investigated: individual plant or plant-stand scale, when averaging individual plant scale responses at the cage scale. While no interactions between lack of insect pollination and herbivory were observed at the plant-stand scale (Fig. S1B), at the plant scale interactions were antagonistic, with increasing *B. rufimanus* damage increasing yield components but only in the absence of pollinators. No negative effects of *B. rufimanus* on yield components were found at the plant-stand scale. Differences between the plant-stand and plant scale analyses in the effect on *B. rufimanus* are likely due to high variation in the level of herbivory damage among individual plants within cages (Fig. S3).

Despite high variation between faba bean cultivars in their dependency on pollinators (Bishop et al., 2020; Bishop & Nakagawa, 2021), lack of insect pollination generally leads to lower yield in faba bean crops (Cunningham & Le Feuvre, 2013; Free & Williams, 1976; Raderschall et al., 2021; Riedel & Wort, 1960; Suso et al., 1996; Suso & del Río, 2015). This study confirms that lack of pollination decreases several faba bean yield components and is in line with a recent cage experiment using the same cultivar (Tiffany), where bean weight per plant and beans per pod but not individual bean weight benefitted from insect pollination (Raderschall et al., 2021). In the absence of pollinators, bean weight and number of beans per plant decreased by 15% and 17%, respectively. Costs of lacking insect pollination were evident despite high frequencies of *B. terrestris* robbing, a common behaviour in this crop (Marzinzig et al., 2018), supporting the idea that robbing may benefit yield by increasing selfing in faba bean (Kendall & Smith, 1975). Counterintuitively, visitation rate and proportion of legitimate flower visits decreased with number of open flowers (after sugar-water addition), while proportion of nectar robbing increased (Fig. S6). This is likely due to nectar deprivation at the start of the study, which meant that *B. terrestris* shifted from robbing nectar to legitimate visit later in the season when there were less flowers open. The low frequency of legitimate flower visits could, explain why the decrease in bean weight per plant due to lack of pollination (15%) was modest when compared to results from a recent meta-analysis of faba bean pollinator dependency (37% on average, Bishop & Nakagawa, 2021) or an experiment using the same cultivar (Tiffany) and bumblebee hives (61%, Raderschall et al., 2021). In addition, a recent field study using the cultivar Tiffany, found no dependence on insect pollination (Lundin & Raderschall, 2021), indicating high variation in pollination benefit within this cultivar, likely mediated by environmental conditions. Finally, despite observed yield benefits with *B. terrestris* in this experiment, field studies have found that less frequent and more specialised pollinator species with long tongues, such as *B.*

*hortorum*, improve pollination and cross-fertilisation of faba bean compared to *B. terrestris* (Marzinzig et al., 2018). Further studies investigating pollination and herbivory interaction in faba bean should include a greater diversity of pollinator species varying in their behaviour.

The effect of the pest *B. rufimanus* on crop yield was inconclusive. While there was a higher proportion of damaged beans in the presence of *B. rufimanus*, which meant that the stand was non-marketable for human consumption due to aesthetic damage to the beans (> 3% damage threshold, Bachmann et al., 2020; Roubinet, 2016) (Fig. S3b), this did not translate to a lower total or individual bean weight, number of beans or pods per plant. This is in contrast to bean aphid herbivory, which reduced all yield components (Raderschall et al., 2021). However, we found a marginal interaction ( $p=0.06$ ) between pollination and *B. rufimanus* herbivory on individual bean weight, whereby individual bean weight was heavier with pollination, but only when *B. rufimanus* herbivory was absent. While we found no evidence that bumblebees legitimately visited flowers less frequently, proportion of legitimate flower visits decreased and EFN visits increased in the presence of *B. rufimanus*. Insect pollination has been shown to increase individual bean weight (Suso & del Río, 2015), therefore, reduced proportion of legitimate flower visits due to *B. rufimanus* direct interference with pollinators or indirect damage caused by feeding on pollen, could lead to lower individual bean weight. There is, to our knowledge, no literature investigating damage to flowers or pollen by *B. rufimanus* adults. This interaction was, however, not apparent on other yield components, such as number of beans per pod and per plant. This might be because the number of beans is primarily determined by ovule fertilisation (pollination), while individual bean weight might also be affected by plant resource allocation after fertilisation, which could have been adversely impacted by the presence of *B. rufimanus* (Patrick & Stoddard, 2010). Adverse herbivory effects of leaf chewers and sap feeders on bean weight have been found in *Fabacea* (Cuny et al., 2018; Raderschall et al., 2021). Therefore, resource allocation to developing beans might have been compromised by *B. rufimanus* and lead to lower individual bean weight when pollinators were present.

We detected a high variation in *B. rufimanus* damage between plants within cages (Fig. S3). When analysing the effect of *B. rufimanus*, at the individual plant scale we detected interactions and, generally, positive relationships between *B. rufimanus* herbivory damage and yield components, but only in the absence of pollination by *B. terrestris*. This indicates that the level of damage caused by *B. rufimanus* affects plant resource allocation, and that this response depends on the presence of pollinators. Two non-exclusive mechanisms, plant overcompensation and pollination by adult *B. rufimanus*, explaining these results are discussed below.

A biological process, which potentially underlies the differential response to herbivory depending on pollination treatment, is the capacity of faba bean plants to overcompensate for damage or stress (López-Bellido et al., 2005). Faba bean might overcompensate for early and high pod damage by *B. rufimanus* by increasing pod production or bean weight during their growth. This is because the growth of faba beans is indeterminate, and while pods are developing at the lower nodes, flower production continues at the upper ones. This leads to competition for resources within the plant between the first set of pods, the roots, bean growth, as well as with the developing pods further up the stem (Jaquierey & Keller, 1978; Smith, 1982). Roots were on average 5% shorter in the presence of *B. rufimanus* and root length correlated negatively with herbivory damage. This indicates alterations in resource allocation from roots to other plant parts in the presence of *B. rufimanus* (Heinze, 2020). Further studies quantifying faba bean root nodules in interaction with herbivory and lack of pollination would shed some light on plant resource acquisition and allocation in relation to biotic stress. Plants might have overcompensated for herbivory damage in the absence of pollinators, as several yield components in highly damaged plants were higher compared to undamaged plants (Fig. 2). Overcompensation in terms of seed-set in response to herbivory is common in other crops such as *Brassicaceae* (Gagic et al., 2016; Rusman et al., 2018). Increase in yield components with increasing *B. rufimanus* damage were only visible in the absence of pollinators, when plants were stressed by both a lack of pollination and high herbivory damage. Plant resource allocation is complex, especially so in plants with indeterminate growth. We found that in the absence of pollinators, faba bean plants had a higher above-ground biomass, likely to compensate for insufficient fertilisation (Raderschall et al., 2021). Higher plant biomass might enhance photosynthetic capacity and result in higher ability to overcompensate to *B. rufimanus* damage in the ab-

sence of pollination. However, very little is known about how plants optimize their resource allocation under multiple stressors.

Another non-exclusive biotic process that can explain the observed increases in yield with increasing herbivory in the absence of bumblebee pollination is that of pollination by *B. rufimanus*. Indeed, florivorous herbivores potentially act as pollinators if they transfer pollen between (cross-pollination) or within (self-pollination) plants. For example, damage by the bud-clipping weevil *Anthonomus signatus* lead to an increase in self-pollination in strawberries (Penet & Collin, 2009). Faba bean plants that had greater level of herbivory damage might have had flowers that were visited more often by *B. rufimanus*, leading to positive associations between damage and pollination by *B. rufimanus* and increased yield components in highly damaged plants. The positive effects of *B. rufimanus* on yield were only visible in the absence of bumblebee pollination, an indication that when more efficient pollinators are present, *B. rufimanus* does not benefit faba bean pollination. While the net effect of bumblebees on yield components was positive, in the presence of both bumblebees and *B. rufimanus*, some plants likely received high numbers of visits and sustained more flower damage than what they could compensate for (Sáez et al., 2014), leading to lower bean weight per plant in the pollination treatment under high levels of herbivory damage. The fact that *B. terrestris* mainly robbed nectar instead of conducting legitimate visits could have influenced the results. Indeed we hypothesize that more legitimate visits would lead to higher rates of cross-pollination and higher yields in the presence of pollinators. In iris, a short-tongued bumblebee shifted to more nectar robbing and longer flower handling time during legitimate flower visits than long-tongued species because of increased competition with a florivorous sawfly (Ye et al., 2017). We did not find an effect of *B. rufimanus* on nectar robbing, but there was a negative effect on proportion of legitimate flower visits. While nectar robbing is a common foraging behaviour in the field (Marzinzig et al., 2018), further studies also with long-tongued bumblebee species present, which mainly conduct legitimate visits, are necessary to understand interactions between florivory and pollination in faba bean.

Differences in *B. rufimanus* effects at different scales (plant-stand versus individual plant level) are likely due to differences between plants in the amount of florivory, oviposition and pollination visits they received. At the plant-stand scale, taking into account variation in *B. rufimanus* herbivory damage, pollinators have a positive effect while *B. rufimanus* only have a tendency to interact with pollinators and negatively affect individual bean weight. On the other hand, at the individual plant scale, herbivory damage by *B. rufimanus* strongly and positively correlates with yield components but only in the absence of pollinators. Effects of *B. rufimanus* on yield components were only visible when high levels of pest damage per plant (>50%, see Fig. 2a,b) were included in the analysis – damage levels, which are not occurring at plant-stand-level means in the cages, which are below 50% (Fig. S3b). In the field, *B. rufimanus* damage is, to our knowledge, generally lower than 50% and so interactions with pollinators might be less relevant for commercial production. In addition, the scenario of pollinators being absent, which is where *B. rufimanus* benefitted yield components, is not, yet, realistic in the field. Therefore, under field conditions, it is unlikely that *B. rufimanus* directly affects faba bean crop yield. However, the negative and indirect effects of *B. rufimanus* on individual bean weight and proportion of legitimate visits by pollinators call for further studies of these interactions in the field.

In summary, we confirm an insect pollination benefit on several faba bean yield components despite low rates of legitimate pollination, whereas plant responses to *B. rufimanus* herbivory differed on the individual versus plant-stand scale. Interestingly, positive effects of *B. rufimanus* herbivory were found on faba bean yield components, but only in the absence of pollinators and under high levels of herbivory damage. Another interesting result is that of a tendency for higher individual bean weight due to pollination, but only in the absence of *B. rufimanus*. Further studies at the plant scale level to understand how the plant allocates its resources under varying levels of pollination and herbivory would be required to clarify the mechanisms driving these interactions. In addition, to disentangle the effects of pollen limitation from other factors, such as flower damage due to high visitation rates, it will be important to investigate effects of herbivory in hand pollinated plants. This is the first experimental evidence of interactive effects of *B. terrestris* and *B. rufimanus* on faba bean plants. While our results strengthen the case for management of pollinators to

maximize pollination benefits in faba bean, there is no evidence for direct yield losses, in terms of total bean weight and numbers, at infestation level of *B. rufimanus* that typically occur in the field despite high bean damage levels. Bean damage by the larvae will decrease faba bean saleability and germination and thus requires control. However, findings of a negative and indirect association between *B. rufimanus* and individual bean weight and proportion of legitimate visits by pollinators call for an improved understanding of these interactions in the field.

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### Authors' contributions

O.L. conceived the idea. L.R. conducted the experiment, analysed the data and wrote the manuscript. All co-authors planned the experiment and provided comments on the manuscript.

### Data availability statement

Data will be made available via the free Swedish National Data Service (<https://snd.gu.se/en>).

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