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RESEARCH

Influence of Cover Crops and Ground Beetles on the Invasive Slug *Deroceras invadens* and Soybean Damage Under Conservation Agriculture

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Abstract

Conservation agriculture provides valuable ecosystem services but can exacerbate slug pressure, particularly in temperate agroecosystems. This study investigated the impact of contrasting soil management and cover crop strategies on the invasive slug *Deroceras invadens* and predatory ground beetles in conservation agriculture. A two-year field trial in northern Italy compared conventional ploughing against no-till systems with different cover crops, i.e., rye, vetch, and a multi-species mixture. We assessed species activity-density using pitfall traps and evaluated slug-induced damage on soybean across phenological stages. *Deroceras invadens* was the dominant pest, while *Poecilus cupreus* and *Pterostichus melas* were the most abundant potential predators. Treatment-specific negative associations between ground beetle and slug activity-densities were observed. The two ground beetle species exhibited complementary temporal roles: *P. cupreus* was present throughout the sampling period, whereas *P. melas* showed stronger negative associations with slugs during the late sampling period. Soybean damage was positively correlated with slug density and significantly influenced by cover crop type, reaching its highest levels in rye plots and lowest in vetch plots. Notably, crop susceptibility peaked at the seed and unifoliolate stages, decreasing significantly by the trifoliolate stages. These findings indicate that cover crop identity and soil management drive slug damage risks, potentially exacerbated by early sowing if vulnerable crop stages align with peak pest activity. Therefore, in conservation agriculture, aligning biological control dynamics with crop phenology under different cover crop systems is crucial to maximize predation, mitigate slug pressure, reduce dependence on pesticides, and promote long-term sustainability.

Keywords Natural enemies · Phenology · Seedling period · No-till · Damage · Carabidae

Introduction

Agroecosystems face substantial threats from herbivores, which significantly reduce crop yield and compromise product quality worldwide. Globally, pre-harvest pests can cause high yield losses in the major crops, representing an important constraint to food security and sustainable agricultural production (Oerke 2006; Savary et al. 2019). Synthetic pesticides have historically sustained crop productivity by reducing pest-related yield losses. However, their negative impacts on biodiversity and agroecosystem resilience highlight the urgent need for integrated, sustainable pest management strategies (Geiger et al. 2010; Albaseer et al. 2024; Ullah et al. 2025).

Slugs (Mollusca: Gastropoda) represent significant agricultural pests, especially in temperate and humid climates where high soil moisture and mild temperatures promote their activity and population growth. They cause extensive damage to a wide range of plants, including field crops, horticultural crops, and ornamentals, by defoliating seedlings, hollowing grains, and impairing germination (South et al. 1992; Barker 2002; Douglas and Tooker 2012; Rowson

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et al. 2014). Invasive slug species such as *Deroceras invadens* Reise, Hutchinson, Schunack and Schlitt, 2011 (Stylommatophora: Agriolimacidae) and *Arion vulgaris* Moquin-Tandon, 1855 (Stylommatophora: Arionidae) further exacerbate the challenge of their management, as they exhibit high reproductive rates, broad ecological adaptability, and a remarkable ability to rapidly colonize disturbed or managed environments (Knop and Reusser 2012; Hutchinson et al. 2014; Rowson et al. 2014; Zając et al. 2017).

Slugs are of particular concern in organic and low-input farming such as in conservation agriculture, where minimum- or no-tillage, cover cropping, and permanent soil cover provide stable microhabitats that may favour their proliferation, while reduced tillage decreases disturbance of slugs and their eggs (Kromp and Meindl 1997; Rossi et al. 2019; Le Gall et al. 2022). On the other hand, conservation agriculture systems can enhance alternative pest management by supporting natural-enemy populations (Tooker et al. 2020; Mugala et al. 2023; Boeraeve and Hatt 2024). This effect is most pronounced early in the growing season and after a stabilisation period (Rowen et al. 2020; 2022; Scaccini et al. 2020), although some long-term exceptions have been reported (Rowen and Tooker 2021; Fiser et al. 2025).

Ground beetles (Coleoptera: Carabidae) are key natural enemies of slugs and can contribute to reducing pest populations and associated crop damage (Symondson 2004; Barua et al. 2021). As predominantly ground-dwelling generalist predators active at both larval and adult stages, several ground beetle species have demonstrated substantial predation on slugs, particularly under warmer conditions (Kromp 1999; Symondson 2004; Thomas et al. 2008; 2009; Barua et al. 2021). Their effectiveness in agroecosystems depends on prey availability, habitat structure, and environmental conditions (Symondson et al. 2006; Müller et al. 2022; Boeraeve and Hatt 2024; Sacco–Martret de Préville et al. 2024). Ground beetle assemblages are indeed shaped by crop type, rotation, and adjacent non-crop habitats that promote spillover and trophic interactions (Djoudi et al. 2019; Boetzl et al. 2024), where field margins can act as refuges, supporting dispersal into crops (Hatten et al. 2007; Rossi et al. 2019; Rowen and Tooker 2021; Knapp et al. 2022). Conservation agriculture practices enhance predator communities, whereas intensive tillage reduces beetle diversity and soil biodiversity (Landis et al. 2000; Tabaglio et al. 2008; 2009; Rowen et al. 2020; Fiorini et al. 2022; Müller et al. 2022; Neame and Galpern 2025).

The dynamics of slugs and their natural enemies under different agricultural practices require further investigation, particularly during early stages of spring crops in mild-climate areas, where slug activity can cause significant damage. Understanding these aspects is essential for developing sustainable pest management strategies that prioritize the conservation of natural enemies, thereby reducing reliance on synthetic pesticides for pest control. Despite extensive research on ground beetles as bioindicators of sustainable agriculture and their ecology in conservation agriculture, their potential role in pest suppression within conservation biological control remains largely underexplored in many regions (Barua et al. 2021), especially against invasive slug species.

Our study investigates slug populations and ground beetles as their natural enemies, under contrasting agricultural practices. Specifically, we aimed to: (i) determine whether ground beetle activity-density predicts reductions in slug density under different management systems—conventional plough-based farming versus conservation agriculture with no-tillage and different cover cropping; and (ii) assess the effects of these practices on slug-induced damage to soybean across phenological stages. Our findings aim to inform sustainable pest management strategies that enhance biodiversity and strengthen the role of biological control agents within conservation agriculture systems.

Material and Methods

Study Site and Experimental Design

The field trial was established at the CERZOO Experimental Farm (45.006075°N, 9.707520°E, 70 m a.s.l.) in San Bonico, Piacenza, northern Italy. Here, we conducted a field trial comparing plots managed under conventional agriculture (ploughed with bare soil between cash crops) to plots under conservation agriculture (no-tillage with cover cropping). The field setup was established in 2011 and has been maintained until today with the same scheme, as a long-term test. A three-year crop rotation of maize (*Zea mays* L.) hybrid "Pioneer P0837", soybean (*Glycine max* (L.) Merr.) cultivar "Pr91m10", and winter wheat (*Triticum aestivum* sub. *aestivum* L.) cultivar "Bologna" was implemented consistently. The trial was laid out as a randomized complete block design with four replication and four treatments comprising 16 plots, each 22 m wide and 65 m long. Each plot was bordered by a 5 m-wide strip of mowed grass. Four soil management treatments were compared: (i) conventional agriculture, ploughed and with bare soil between cash crops (hereafter "Plough"); (ii) conservation agriculture no-till based with rye (*Secale cereale* L.) as a cover crop ("Rye"); (iii) conservation agriculture no-till based with hairy vetch (*Vicia villosa* Roth.) as a cover crop ("Vetch"); and (iv) conservation agriculture with 6-species (rye, hairy vetch, Italian ryegrass, *Lolium multiflorum* var. *italicum* Lam., crimson clover, *Trifolium incarnatum* L., phacelia, *Phacelia tanacetifolia* Benth., and radish, *Raphanus raphanistrum sativus* (L.) Domin.) mixture ("Mix") as a cover crop. Further details on main farm operations, including pesticide and fertilizer application are reported in Fiorini et al. (2020) for "Site 1". No phytosanitary treatments targeting slugs were applied in the plot area during the two study years.

In each plot, two beer-baited pitfall traps (200 mL volume), partially covered with plastic dishes to prevent rainfall from filling the traps and to reduce evaporation, were installed along the midline (11 m from each lateral border), and spaced at least 15 m apart. The traps were checked and replenished weekly, and they were installed one week before the first sampling. Slugs and main insects found in pitfall traps were counted and identified (see below). Pitfall trap slug and insect counts represent the "activity-density", which estimates the abundance of each species based on its activity during the sampling period and the population density within the sampled field, rather than providing a direct estimate of absolute population density (Curtis 1980; Thomas et al. 1998). Pitfall trapping was deemed the most appropriate monitoring method for our experimental conditions. Although the plots were remarkably large for an agronomic trial (22 × 65 m), they formed a mosaic of adjacent conditions within the experimental design. By focusing data collection on specific areas within these large plots, the traps effectively localized the assessments and minimized potential cross-contamination between neighbouring plots. Surveys were conducted over two growing seasons, with a focus on the early-season period. Field sampling targeted this initial phase, when slugs and ground beetles co-occurred and the crop was most vulnerable to slug attack. Slug and ground beetle populations were not assessed prior to the experiment. However, slug pressure was considered high based on previous observations of severe damage to maize seedlings shortly after emergence (V. Tabaglio, pers. obs.). Sampling occurred from March 26th to June 15th, 2015 (11 sampling events) and from March 3rd to June 1st, 2016 (14 sampling events). The surveyed cash crops were soybean in 2015 and winter wheat in 2016 (sown in October 2015). In 2015, weekly sampling was temporarily interrupted from May 7th to 14th to allow termination of the cover crop with glyphosate (Roundup® Platinum, 3 L ha^{-1}) and subsequent soybean sowing. Pitfall traps were replaced on May 14th before sampling resumed.

Slug-mediated crop damage was evaluated by comparing the four treatments described above. In the first sampling season soybean damage was assessed in four surveys aligned with crop phenology, identified following the BBCH scale (Meyer 2018): soybean seed stage (BBCH 06, May 20th), cotyledon/unifoliolate stage (BBCH 10/11, May 25th), first/second trifoliolate stage (BBCH 12/13, June 3rd), and fifth/sixth trifoliolate stage (BBCH 16/17, June 15th). Specifically, damage was assessed through visual inspections, recording the number of damaged seeds in four 40-seed rows per plot (BBCH 06; Figure S1A–C), or the number of damaged plants in four 40-plant rows per plot for subsequent stages (BBCH 10 to BBCH 17; Figure S1D–F). Damaged soybean was defined as seeds or plants showing visible signs of feeding damage caused by slugs (Figure S1). In 2016, winter wheat was intended to be evaluated for slug damage (Figure S2), following the approach used the previous year for soybean. However, possibly due to low slug infestation levels, no damage was observed, thus the damage evaluation was not conducted.

Slug and Ground Beetle Species Identification

Slugs were identified to the specific level when possible, using identification keys evaluating external features and, if necessary, genitalia of dissected specimens (Wiktor 2000; Reise et al. 2011; Rowson et al. 2014). Identification was also checked on some randomly selected specimens by mtDNA analysis (cytochrome c oxidase subunit I gene), using ~2 mm^3 of slug foot tissue portion as detailed by Scaccini et al. (2020). Ground beetles were identified to species based on external morphological characters of adults, following the keys by Hůrka (1996) and Facchini (2001).

Data Analysis

The relationship between ground beetle and slug activity-density was analysed for each treatment (i.e., Plough, Rye, Vetch, and Mix) and by year using linear mixed-effects models (LMMs). Slug activity-density was used as the response variable, and ground beetle activity-density as predictor. Data were $\log_{10}(x+1)$-transformed to meet model assumptions. Analyses focused on the two most abundant ground beetle species. For the unique species present throughout the entire sampling period, models included ground beetle activity-density as a single predictor. Additive and interaction models including treatment were compared using likelihood ratio tests, and the best-supported model was retained. When interaction models were selected, pairwise comparisons of slopes among treatments were performed using estimated marginal trends (emtrends, package emmeans), and differences among slopes were assessed using Tukey-adjusted contrasts ($\alpha = 0.05$). During the second part of the surveyed period, when both ground beetle species were consistently present, to account for their concurrent presence the two were included as fixed predictors in linear mixed-effects models. Sampling date and block were included as random intercepts to account for repeated measures and spatial grouping. Models were fitted using maximum likelihood, and significance of fixed effects was assessed using Type III F-tests with Satterthwaite's approximation for degrees of freedom. Outliers in slug activity-density were removed using the 1.5 × interquartile range criterion.

Moreover, for the first growing season, slug-mediated damage to soybean seeds and plants (rate) was analysed using a generalized linear mixed model (GLMM) with a beta error distribution and logit link function, implemented in the glmmTMB package. The proportion of damaged seeds or plants was used as the dependent variable. Because beta regression requires values strictly between 0 and 1, proportional data were adjusted following Smithson and Verkuilen (2006). The model included slug activity-density, sampling date (corresponding to specific soybean BBCH growth stages) and treatment (i.e., Plough, Rye, Vetch, and Mix). Block was included as a random intercept to account for the experimental design structure. Significance of fixed effects was assessed using Type III Wald χ^2 tests ($\alpha = 0.05$). Pairwise comparisons among treatments were performed using Tukey-adjusted estimated marginal means implemented in the emmeans package. Model fit and assumptions were evaluated using simulated residual diagnostics in the DHARMa package, including tests for dispersion and zero inflation. Predicted marginal effects were estimated using the ggeffects package and visualized with 95% confidence intervals.

All analyses were conducted in R, ver. 4.2.1 (R Core Team 2022) using RStudio (RStudio Team 2016), with the packages lme4 (Bates et al. 2015), lmerTest (Kuznetsova et al. 2017), emmeans (Lenth 2023), ggplot2 (Villanueva and Chen 2019), dplyr (Wickham et al. 2021), patchwork (Pedersen 2025), glmmTMB (McGillycuddy et al. 2025), DHARMa (Hartig 2025), and ggeffects (Lüdecke 2018).

Results

During the two sampling periods, the most abundant slug species captured in pitfall traps was the invasive *D. invadens*, with 1796 individuals in the first growing season and 231 in the second one. Other slug taxa identified included a specimen of *Deroceras reticulatum* (Müller, 1774) (Stylommatophora: Agriolimacidae) and another of *Limax maximus* Linnaeus, 1758 (Stylommatophora: Limacidae) in the first season, while in the second we found 2 *Ambigolimax valentianus* (Férussac, 1821) (Stylommatophora: Limacidae), 1 *Arion* sp. (Stylommatophora: Arionidae), 12 *D. reticulatum*, and 27 *L. maximus*. Due to the low numbers of these other slug taxa, the analyses presented here focus exclusively on *D. invadens*.

Concerning ground beetle activity-density, the two main species on which we performed statistical analyses were *Poecilus cupreus* (Linnaeus, 1758) (Coleoptera: Carabidae), having 10,225 specimens collected in the first growing season and 12,804 in the second, and *Pterostichus melas* (Creutzer, 1799) (Coleoptera: Carabidae), with 119 and 821 specimens in the first and the second season, respectively. Other ground beetle taxa occasionally collected in pitfall traps during the sampling periods primarily belonged to the genera *Bembidion, Brachinus, Calosoma*, and *Harpalus*. These individuals represented 0.55% of the ground beetle fauna in the first sampling year and 2.45% in the second one.

The relationship between ground beetle activity-density and slug activity-density varied among treatments, years, and species. *Poecilus cupreus* was consistently present throughout the entire sampling period, whereas *P. melas* was recorded during the late part of the sampling season. Model selection revealed significant interactions between treatment and *P. cupreus* activity-density in some cases, indicating that the strength and direction of the association between ground beetles and slugs varied across treatments and between seasons. In the first growing season, treatment significantly influenced the relationship between *P. cupreus* and slug activity-density (likelihood ratio test: $\chi^2 = 12.61$, df = 3, $p = 0.006$). A significant overall effect of *P. cupreus* activity-density was detected ($F_{1, 138.7} = 5.21$, $p = 0.024$), with treatment ($F_{3, 147.1} = 4.64$, $p = 0.004$) and the interaction between treatment and *P. cupreus* activity-density also being significant ($F_{3, 146.6} = 4.38$, $p = 0.005$). Treatment-specific regression plots indicated negative relationships between *P. cupreus* and slug activity-density in the Plough and Vetch treatments, whereas relationships were weak or absent in Rye and Mix (Fig. 1a). Pairwise comparisons of regression slopes between treatments did not reveal statistically significant differences (Tukey-adjusted $p > 0.05$).

In the second growing season, treatment significantly affected the relationship between *P. cupreus* and slug activity-density ($\chi^2 = 9.47$, df = 3, $p = 0.024$). A significant main effect of *P. cupreus* activity-density was detected ($F_{1, 35.8} = 8.05$, $p = 0.007$), as well as for the interaction between treatment and *P. cupreus* activity-density ($F_{3, 174.8} = 3.24$, $p = 0.023$), whereas treatment alone did not have a significant effect ($F_{3, 174.3} = 1.89$, $p = 0.132$). Treatment-specific regression plots showed negative relationships in the Plough and Rye treatments, while slopes in Vetch and Mix were weaker and not statistically significant (Fig. 1b). Pairwise comparisons of slopes did not detect significant differences between treatments (Tukey-adjusted $p > 0.05$).

During the late-season period, both *P. cupreus* and *P. melas* were present and included simultaneously as predictors (first year: from May 20th; second year: from March 31st). The strength and significance of species-specific relationships differed among treatments for both years. Specifically, during the first sampling year in the Plough treatment, neither *P. cupreus* nor *P. melas* activity-density had a significant effect on slug activity-density (*P. cupreus*: $F_{1, 23} = 0.47$, $p = 0.501$; *P. melas*: $F_{1, 23} = 0.41$,

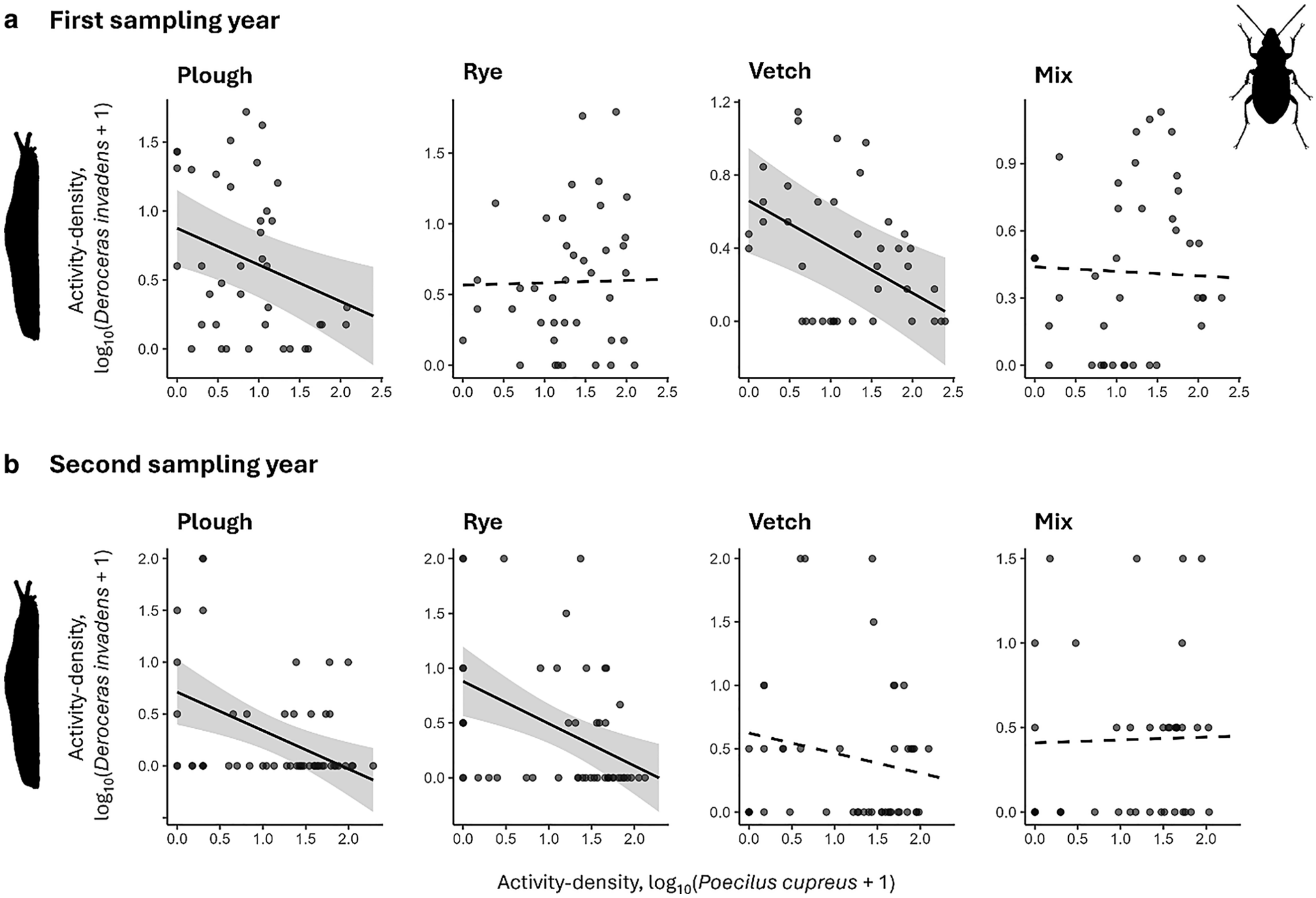

Fig. 1 Relationship between activity-density of *Deroceras invadens* (response variable) and *Poecilus cupreus* (predictor) across the four treatments (Plough, Rye, Vetch, and Mix) in the first (**a**) and second (**b**) sampling year. Points represent observed values. Predicted regression lines from the linear mixed-effects model are shown for each treatment, with solid lines that indicate statistically significant slopes ($p < 0.05$), whereas dashed lines that indicate non-significant slopes. Shaded areas represent 95% confidence intervals

$p = 0.530$; Fig. 2). In the Rye treatment, slug activity-density was significantly negatively associated with *P. melas* activity-density ($F_{1, 15.59} = 8.77$, $p = 0.009$), whereas the effect of *P. cupreus* was not significant ($F_{1, 16.50} = 1.27$, $p = 0.276$; Fig. 2). In the Vetch treatment, slug activity-density was negatively associated with *P. cupreus* activity-density ($F_{1, 16.07} = 11.89$, $p = 0.003$), whereas *P. melas* activity-density had no significant effect ($F_{1, 20.26} = 0.08$, $p = 0.787$; Fig. 2). In the Mix treatment, *D. invadens* activity-density was significantly negatively associated with *P. melas* activity-density ($F_{1, 19.67} = 6.21$, $p = 0.022$), while the effect of *P. cupreus* was marginal and not statistically significant ($F_{1, 20.85} = 3.74$, $p = 0.067$; Fig. 2).

Patterns observed in the second year were largely consistent with those of the first season, but significant effects were more frequent. In detail, in the Plough treatment *P. melas* activity-density had a significant negative effect on slug activity-density ($F_{1, 37} = 13.42$, $p < 0.001$), whereas *P. cupreus* was not significant ($F_{1, 37} = 0.99$, $p = 0.327$; Fig. 3). In the Rye treatment, both species showed significant negative relationships with slug activity-density (*P. cupreus*: $F_{1, 30} = 11.48$, $p = 0.002$; *P. melas*: $F_{1, 19} = 14.26$, $p = 0.001$; Fig. 3). In the Vetch treatment, slug activity-density was significantly negatively associated with *P. melas* ($F_{1, 23} = 4.75$, $p = 0.040$), but not with *P. cupreus* ($F_{1, 25} = 1.20$, $p = 0.283$), similarly to what was observed in the Mix treatment (*P. melas*: $F_{1, 20} = 9.98$, $p = 0.005$; *P. cupreus*: $F_{1, 22} = 2.67$, $p = 0.116$; Fig. 3).

Slug-mediated damage to soybean was significantly affected by pest activity-density, BBCH stage, and treatment (Table 1). The beta GLMM revealed a positive relationship between slug activity-density and damage rate ($\chi^2 = 8.57$, df = 1, $p = 0.003$), indicating that damage increased with increasing slug abundance (Fig. 4a). Sampling date had a strong effect on damage ($\chi^2 = 334.63$, df = 3, $p < 0.001$); compared with the reference stage (BBCH 06), damage was significantly lower at later stages BBCH 12/13 and BBCH 16/17, whereas no significant difference was detected at BBCH 10/11 (Table 1; Fig. 4a). Treatment significantly influenced slug-mediated damage ($\chi^2 = 39.05$, df =

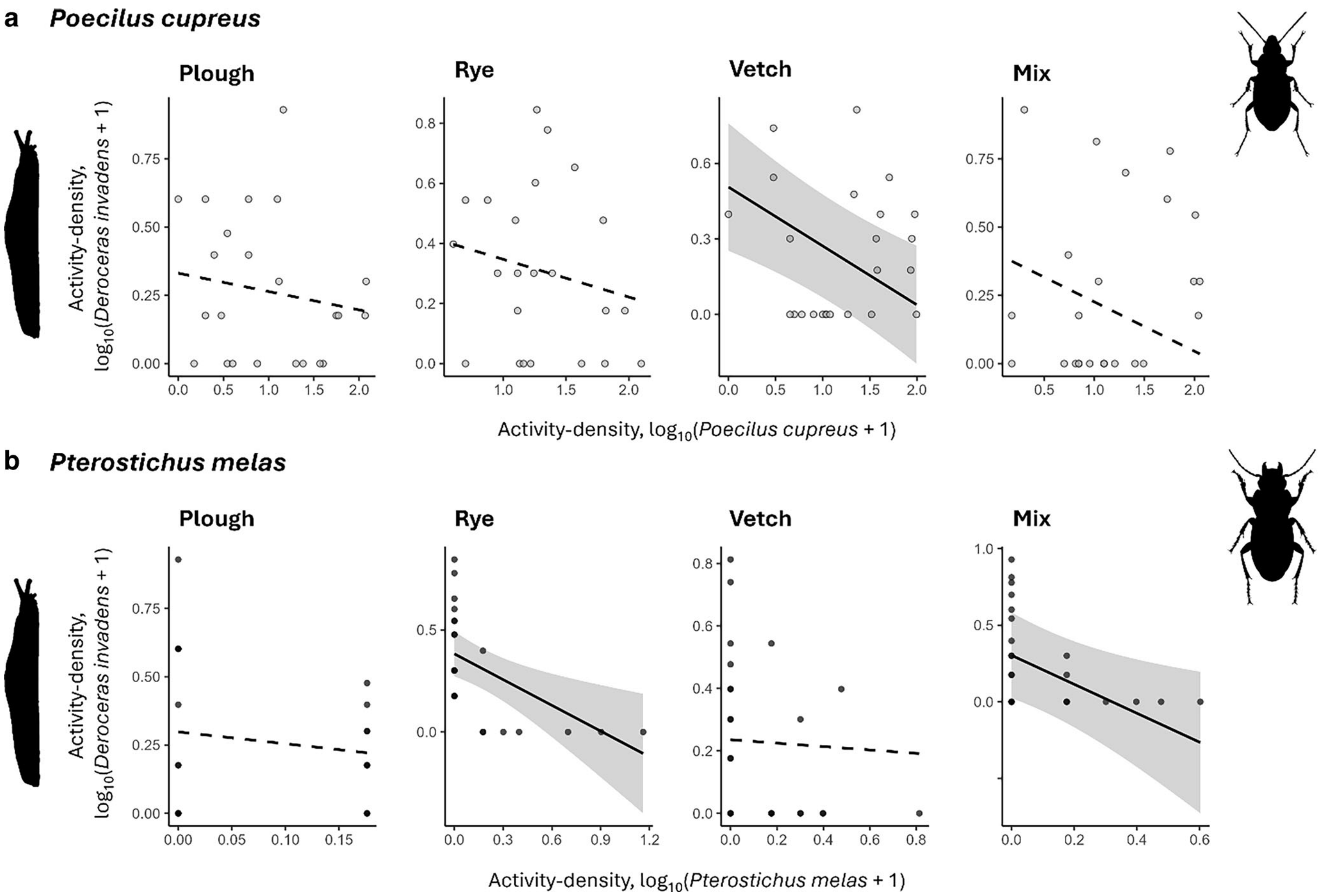

Fig. 2 Relationship between activity-density of *Deroceras invadens* (response variable) and activity-density of *Poecilus cupreus* (**a**) and *Pterostichus melas* (**b**) across treatments (Plough, Rye, Vetch, and Mix) from May 20th to June 15th during the first sampling year. Points represent observed values. Lines represent predictions from the linear mixed-effects model fitted separately for each treatment. Solid lines indicate statistically significant slopes ($p < 0.05$), whereas dashed lines indicate non-significant slopes. Shaded areas represent 95% confidence intervals

3, $p < 0.001$). Tukey-adjusted pairwise comparisons showed that damage was highest in Rye and differed significantly from all other treatments (all $p \leq 0.002$; Fig. 4b). Vetch showed the lowest damage, differing significantly from Rye ($p < 0.001$) and Mix ($p = 0.032$), but not from Plough ($p = 0.063$); moreover, Plough did not differ significantly from Mix ($p = 0.869$; Fig. 4b). Model diagnostics indicated no evidence of overdispersion (dispersion = 1.42, $p = 0.112$) and no zero-inflation issues, confirming an adequate model fit.

Discussion

Slug captures across both growing seasons were dominated by *D. invadens* (2027 individuals), while other slug species were only sporadically recorded. This invasive alien species is widely associated with arable crops, woodlands, and grasslands and shows strong adaptation to human-disturbed environments, including gardens, greenhouses, waste sites, and polluted rural habitats (Hutchinson et al. 2014; Rowson et al. 2014). However, empirical data on its specific impact and natural control in field settings remain scarce, highlighting the significance of our findings regarding its dominance and interaction with native ground beetles.

Deroceras invadens was present from the earliest sampling dates but was notably less abundant in the second year. These seasonal and interannual fluctuations likely reflect variations in abiotic drivers, such as temperature and rainfall (Honek 1997; Kromp 1999; Mugala et al. 2023), alongside crop-related factors. For instance, the winter wheat grown in the second season was likely less favourable than protein-rich hosts like Fabaceae, which are generally preferred by slugs (Douglas and Tooker 2012; Jensen et al. 2013; Brooks et al. 2005; Brichler 2020).

Beyond the cash crop, cover crop identity and residue management significantly influence slug dynamics. While cover crops and intercropping generally support biological pest control by enhancing natural enemy abundance through the provision of shelter, alternative food, and favourable microclimates (e.g., Bugg and Waddington 1994; Landis et al.

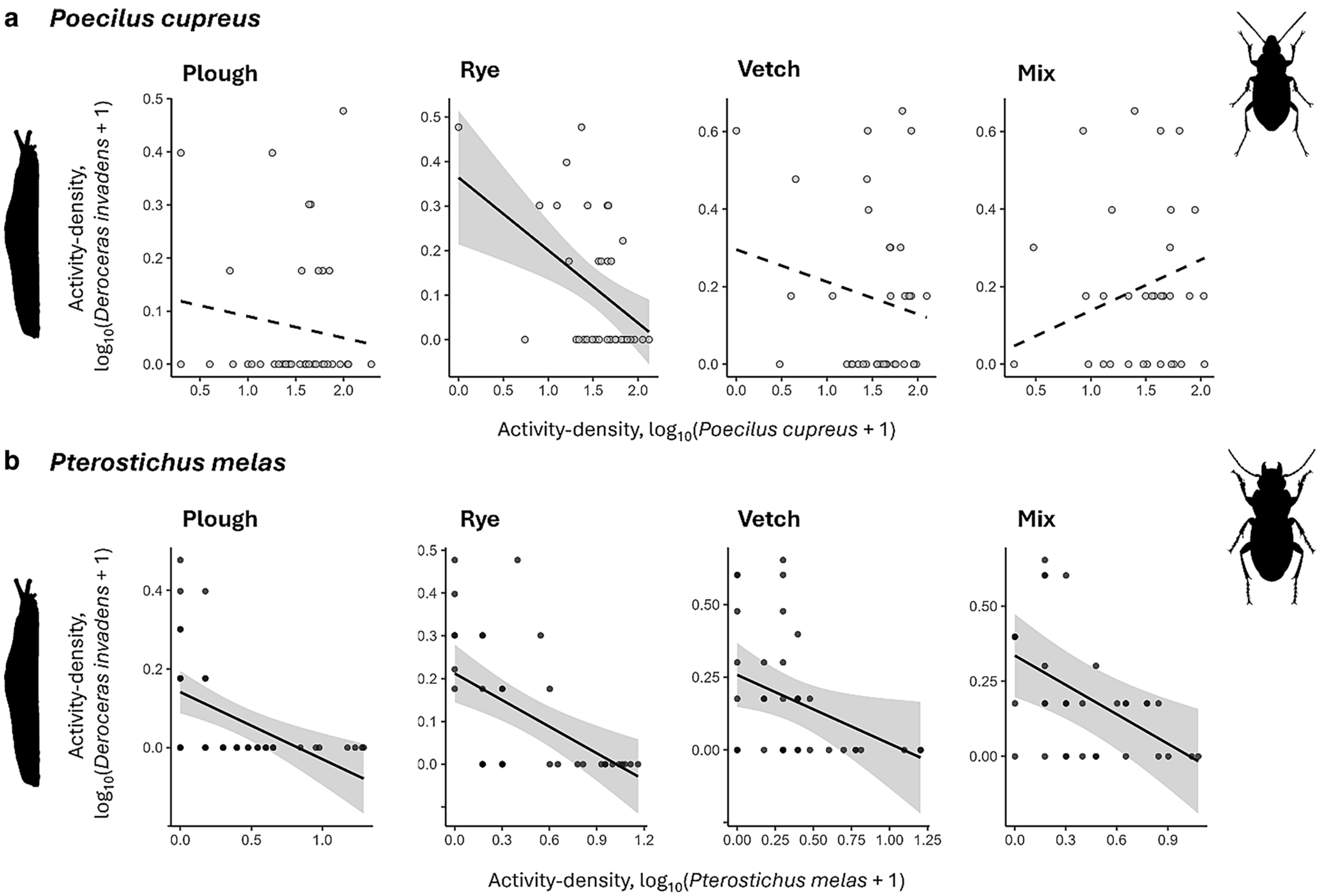

Fig. 3 Relationship between activity-density of *Deroceras invadens* (response variable) and activity-density of *Poecilus cupreus* (**a**) and *Pterostichus melas* (**b**) across treatments (Plough, Rye, Vetch, and Mix) from March 31st to June 1st during the second sampling year. Points represent observed values. Lines represent predictions from the linear mixed-effects model fitted separately for each treatment. Solid lines indicate statistically significant slopes ($p < 0.05$), whereas dashed lines indicate non-significant slopes. Shaded areas represent 95% confidence intervals

2000; Altieri and Nicholls 2004; Irvin et al. 2014; Blubaugh et al. 2016; Beaumelle et al. 2021; Judt et al. 2023; Mele et al. 2025; Sanchez et al. 2025), their net effect on slugs is complex. Some systems reduce slug pressure, whereas others create moist microhabitats that increase activity-density (Douglas and Tooker 2012; Scaccini et al. 2020; Le Gall et al. 2022; Rowen et al. 2022). Ground beetle responses are similarly variable and, although conservation practices generally benefit natural enemies, effective slug suppression remains highly site- and context-specific (Kromp 1999).

Consistent with this variability, we found that relationships between ground beetle and slug activity-density were highly species- and treatment-specific across sampling years. In several instances (specific treatments, years, or species), no significant relationships were recorded, highlighting the inherent variability of these field-based observations. *Poecilus cupreus* was collected throughout the season, maintaining a constant presence that suggests a potential for continuous, albeit variable, interaction with slug populations. In contrast, *P. melas* exhibited stronger and more consistent negative associations with slug activity-density, although it was recorded primarily during later sampling dates. *Poecilus cupreus* is a widespread generalist predator in European agricultural landscapes, active from spring to autumn (Honek 1997; Fusser et al. 2016; Gailis et al. 2017; Lemic et al. 2017; Scaccini et al. 2020; Guenay-Greunke et al. 2022; Sacco-Martret de Préville et al. 2024). It has demonstrated efficacy as a natural enemy of slugs, including *Deroceras* (Oberholzer and Frank 2003; Oberholzer et al. 2003; Barua et al. 2021; Guenay-Greunke et al. 2022; 2024). Conservation agriculture, particularly when combined with cover crops, may enhance *P. cupreus* activity-density, likely by increasing prey availability and improving microclimatic conditions via mulch retention (Langmaack et al. 2001; Gailis et al. 2017; Rossi et al. 2019; Scaccini et al. 2020). Detailed microclimatic features, such as soil surface temperature and moisture, were not assessed in the present study; incorporating these variables in future research will be useful to better disentangle environmental effects from biological interactions.

Table 1 Fixed-effect parameter estimates (logit scale) from the beta generalized linear mixed model (GLMM) analysing the proportion of slug-induced damage ($n = 64$). BBCH 06 stage and the Plough treatment were used as reference levels. Block was included as a random intercept.

Predictor	Estimate	SE	z	*p*-value
Intercept	–0.721	0.139	–5.18	< 0.001
Deroceras invadens activity-density	0.231	0.079	2.93	0.003
BBCH 10/11	–0.114	0.117	–0.98	0.329
BBCH 12/13	–1.944	0.152	–12.78	< 0.001
BBCH 16/17	–3.412	0.247	–13.79	< 0.001
Rye	0.523	0.133	3.92	< 0.001
Vetch	–0.372	0.150	–1.86	0.063
Mix	0.024	0.145	0.17	0.869

Moreover, during the first year of sampling, glyphosate application may have influenced weed dynamics and microhabitat structure, which can in turn affect invertebrate composition and behaviour (Sullivan and Sullivan 2003; Klátyik et al. 2023). While we cannot entirely rule out transient shifts, the activity-density data revealed no impacts of the herbicide application on the investigated taxa.

Alongside *P. cupreus, P. melas* is one of the most common ground beetles in organic and low-input farms across central and northern Italy (Rossi et al. 2019; Scaccini et al. 2020). *Pterostichus* species, particularly *Pterostichus melanarius* (Illiger, 1798) (Coleoptera: Carabidae), are well-documented predators of slugs (including Agriolimacidae), often aggregating in areas of high slug biomass to feed on eggs and juveniles (Symondson et al. 1996; Bohan et al. 2000; McKemey et al. 2001; Barua et al. 2021; Guenay-Greunke et al. 2024). For instance, laboratory studies indicate that *Pterostichus* species can consume larger slugs (up to 50 mg) compared to *P. cupreus*, whose impact is more variable (McKemey et al. 2001; Oberholzer and Frank 2003). In the field, these interactions are shaped by environmental conditions and habitat features, with *Pterostichus* likely utilizing olfactory cues to locate prey patches, thereby enhancing predation and potentially reducing crop damage (Kromp 1999; McKemey et al. 2003; Thomas et al. 2008; Douglas et al. 2015; Busch et al. 2021).

Although direct predation on *D. invadens* was not observed in this study and warrants further investigation, our findings suggest complementary temporal roles for these two predatory species under certain year and treatment combinations. In these cases, *P. cupreus* may exert regulatory pressure on slug populations during early crop establishment, whereas *P. melas* appears to contribute more substantially later in the season. These dynamics are likely modulated by treatment-specific environmental conditions that influence predator–prey interactions. Future research should explicitly explore these relationships in the context of *D. invadens*, which remains comparatively understudied relative to other European slug species. Slug occurrence and damage under no-till systems are inherently variable across years, being strongly driven by microclimatic conditions and the quantity and quality of surface residues or cover crops (Douglas and Tooker 2012). Such inter-annual variability is particularly pronounced in conservation agriculture, where residue retention can simultaneously provide favourable habitats and trophic resources for both slugs and their natural enemies (Kromp 1999; Rivers et al. 2017). Consequently, interactions between predatory ground beetles and slugs are expected to be context-dependent and highly variable across years and management systems. For this reason, treatment comparisons are more robust when conducted within the same growing season, whereas cross-year comparisons must be interpreted with caution unless microclimatic conditions are remarkably similar (Symondson et al. 2002; Douglas et al. 2015).

Slug-mediated damage to soybean was positively correlated with pest activity-density but varied significantly depending on field management and crop phenology. Specifically, soybean following a rye cover crop sustained the highest damage, while intermediate damage levels were observed in ploughed plots and those preceded by a 6-species mixture, and showing the lowest damage in vetch plots. This indicates that cover crop identity shapes damage risk beyond simple pest abundance. Specifically, rye mulch likely provided favourable shelter for slugs, while the resident ground beetle community may have failed to suppress them effectively, resulting in increased crop damage. In contrast, vetch residues appeared to mitigate damage, likely through enhanced slug suppression by ground beetles, consistent with previous local findings of lower slug densities in vetch compared to ploughed fields (Scaccini et al. 2020). Indeed, higher ground beetle densities were reported in vetch than in rye-covered fields (Rivers et al. 2018), and vetch cover has been associated with reduced crop damage in maize and soybean compared to rye (Brichler 2020), yet rye has been shown to reduce slug densities in other no-till maize systems (Beloghi and Bullock 2024). In ploughed plots, intermediate damage levels may be linked to the ability of *P. cupreus* to prey on slugs that are more exposed in the ab-

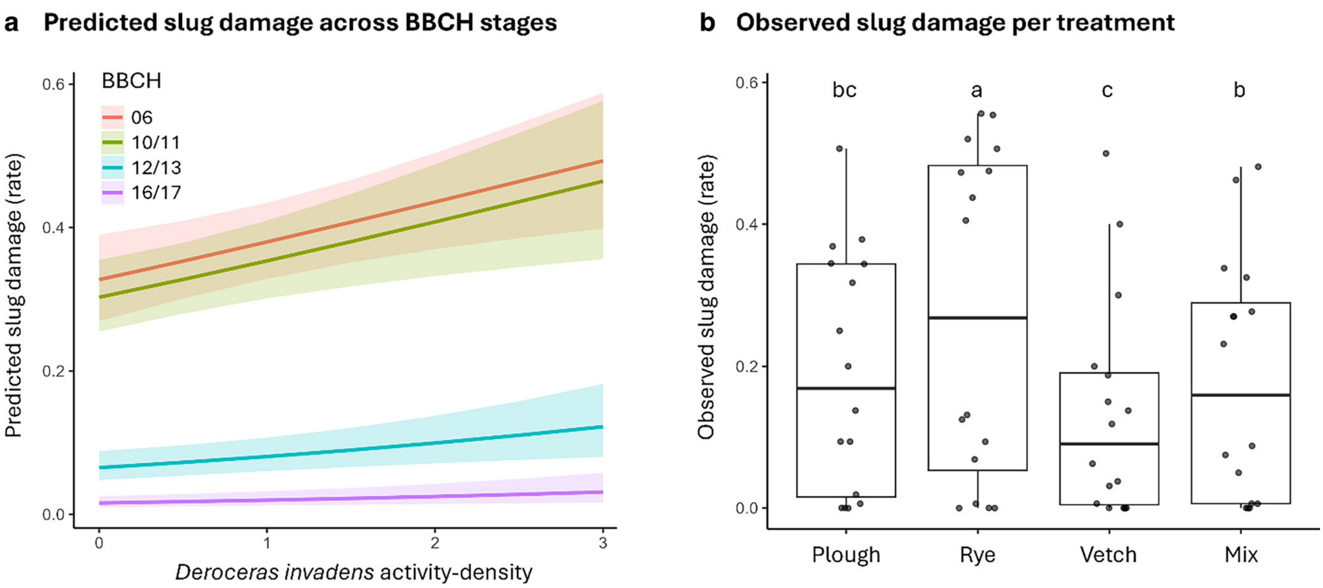

Fig. 4 Model prediction from a beta generalized linear mixed model (GLMM) of slug-mediated soybean damage. **a** Relationship between activity-density of *Deroceras invadens* (predictor) and predicted damage rate (response) across BBCH stages. Lines represent model predictions; shaded areas indicate 95% confidence intervals. **b** Estimated marginal means (± SE) of predicted slug damage for each treatment. Different letters indicate significant differences among treatments (Tukey-adjusted $p < 0.05$)

sence of surface residues, although this hypothesis warrants further investigation.

Crop susceptibility is strongly driven by phenology, with early growth stages being the most vulnerable to slug damage (Ester and Huiting 2005; Douglas and Tooker 2012). In soybean, the unifoliolate stage is particularly sensitive to injury (Hammond 2000), especially under reduced plant densities (Barratt et al. 1994). Conversely, if seedlings survive this initial bottleneck, soybean plants can generally tolerate substantial defoliation at later stages without significant yield penalties (Hammond 2000; Douglas and Tooker 2012). This compensatory ability has been similarly observed in other crops, such as maize, provided early damage remains limited (Tooker et al. 2025). Consistent with these patterns, we observed the highest damage frequencies during the earliest phenological stages, affecting approximately 30–50% of seeds and 15–50% of plants at the cotyledon and unifoliolate stages. Notably, this severe damage occurred even though *D. invadens* populations were lower than their early-season peaks, highlighting the disproportionate impact of slugs on vulnerable soybean seedlings. In contrast, damage recorded from the first and second trifoliolate stages onwards appeared to have only a marginal impact on crop performance, even when slug activity-density increases. While the temporal and spatial co-occurrence of ground beetles and slugs suggests a potential for natural pest regulation, our study did not directly measure predation rates or the impact of carabid abundance on slug-induced crop damage. Therefore, direct evidence of biocontrol efficacy in this system remains to be explicitly demonstrated.

Mitigation strategies against slug damage include advancing sowing dates, which is often proposed to decouple susceptible growth stages from peak slug activity (Rivers et al. 2020). However, our findings suggest that under specific pedoclimatic conditions like those we studied, this strategy might inadvertently increase risk by synchronizing the most vulnerable crop stages with periods of significant slug activity. Therefore, while these results are instructive, they are not universally generalizable and require site-specific evaluation, underscoring the importance of integrating cover crop selection and local features data when scheduling agronomic operations. For these concerns, continued long-term monitoring, particularly in the context of climate change, remains essential to further refine sustainable management strategies for the soybean–slug–ground beetle system.

Conclusions

Our findings identify the invasive species *D. invadens* as the dominant slug pest in the investigated system. The study highlights the potential for conservation biological control provided by ground beetles, suggesting that *P. cupreus* and *P. melas* may fulfil complementary temporal roles in suppressing slug populations across the growing season, particularly under specific agronomic management systems. However, direct empirical evidence quantifying this regulatory effect specifically against *D. invadens* remains a critical priority for future research. Crucially, soybean susceptibility was greatest during early phenological stages, indicating that management strategies—such as anticipating sowing dates—must be carefully calibrated to avoid synchronizing the critical window of seedling vulnerability with peak slug activity. Ultimately, sustainable management of *D. invadens* requires a holistic approach that integrates cover crop selection to further improve slug suppression by enhancing native natural enemies, reducing reliance on pesticides and promoting sustainable agricultural practices.

Supplementary Information The online version of this article (https://doi.org/10.1007/s10343-026-01373-3) contains supplementary material, which is available to authorized users.

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Declarations

Competing interests The authors declare no competing interests.

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