



Simultaneous top-down and bottom-up control of cereal aphids by predation, companion planting and host-plant diversity

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Abstract

Aphids are among the most economically significant pests in cereal crops worldwide. Despite high interest in the natural control of aphids by applying natural enemies, intercropping and companion planting, the concurrent effects of the combinations of these methods due to their synergistic or antagonistic interactions remain largely unknown for both aphids and their host crops. Here we identify the relative effectiveness of simultaneous bottom-up and top-down factors in controlling one of the most economically important species of cereal aphids, the bird cherry-oat aphid *Rhopalosiphum padi* L. For this, we conducted microcosm experiments using a full-factorial design of three aphid-control treatments including predator presence (i.e., lacewing larvae of *Chrysoperla carnea*), host-plant intercropping (i.e., barley alone vs barley in combination with wheat and rye) and companion planting with an aphid-repellent plant (garlic), and estimated their direct, indirect and interactive effects on aphid density. Our results show strong simultaneous top-down control of the aphid population by predation and bottom-up control by both host-plant biomass and companion planting with garlic. The use of garlic as a companion plant for cereal crops in our study neither altered crop biomass nor suppressed the efficiency of aphid predator. Our findings suggest that the simultaneous application of aphid predator and companion planting with garlic holds promise as a potential strategy for the natural control of cereal aphid populations on grain crops, without generating related agroecosystem disservices, such as loss in crop production and deterioration of the natural enemies of pests. However, given the controlled lab conditions and limited timeframe of our study, further research is needed to confirm its effectiveness in field conditions to ensure its broader applicability in sustainable agricultural practices.

KEYWORDS

aphid, biocontrol, biological control, insect-plant interactions, integrated pest management, predators

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1 | INTRODUCTION

The continuing growth of the global population predicts demand for an estimated 70% increase in food production over the next few decades (World Resources Institute, 2014), with the production of cereals as the foundation of world food security (FAO, 2016). This triggers a need to control herbivore pests, as they cause on average an estimated loss of 15% in global crop yield annually (Shavit et al., 2018), with aphids (Hemiptera: Aphididae) found as the most economically significant pests of cereal crops (Culliney, 2014; Shavit et al., 2018). However, the intensive use of insecticides for agricultural pest control comes at a high cost to biodiversity and ecosystem functioning (Buzhdygan & Petermann, 2023). This highlights the urgent need for alternative, ecologically-based pest control methods, for example, utilizing natural enemies of pests, intercropping among target crops (pest hosts) or implementing companion planting (a form of intercropping with non-host insect-detering or insect-repellent plants) (Ben-Issa et al., 2017; Lopes et al., 2016). Previous studies repeatedly call for the combined use of these different methods not only to manage plant pests effectively (Bueno-Pallero et al., 2018; Gurr et al., 2003) but also to maximize crop productivity and to harness other ecosystem functions and agricultural services, such as improving soil health (Bommarco et al., 2013; Buzhdygan & Petermann, 2023). However, we still lack understanding of the mechanisms by which host-plant neighbours of different species, their non-host companions and the natural enemies of the pests may interact to produce simultaneous direct and indirect effects on pestilent herbivores (Letourneau et al., 2011). In fact, the existing evidence on the directions and strengths of such interactive bottom-up and top-down effects is still contradictory (Karp et al., 2018).

While top-down effects, such as pest control by their natural enemies, have been extensively studied and integrated into agricultural practices, bottom-up effects have received comparatively less attention within the framework of integrated pest management (Han et al., 2022). Intercropping is among the most important bottom-up drivers in crop-arthropod and pest-natural enemy multitrophic interactions. However, little is known about the mechanisms underlying intercropping effects on pests and their enemies, likely due to the limited ability to track arthropod activities under field conditions (Han et al., 2022). Intercropping may involve diversification of the host crops of pests or companion planting with the non-host disruptive or trap crop. Previous studies suggest that the effects of plant diversity on herbivore arthropods are predominantly indirect, mediated via host-plant density or productivity (Otway et al., 2005; Root, 1973). For example, the *resource concentration hypothesis* predicts that herbivores attain higher abundance and loads (i.e., the number of individuals per host-plant biomass) in monocultures where their host plants are concentrated due to higher densities (Root, 1973). Although not universal, there is a growing evidence that increased host diversity can reduce herbivory rates of arthropods (Lopes et al., 2016; Otway et al., 2005; Petermann, Müller, Weigelt, et al., 2010) due to a *resource dilution effect*, that is, when more diverse plant assemblies contain a larger number of less preferable for pests plant species, which “dilute”

the reproductive and dispersal ability of pests. On the other hand, host-plant diversification may also affect food quality (e.g., C:N) and habitat for herbivores (Letourneau et al., 2011; Root, 1973; Utsumi et al., 2011). Therefore, discrepancies exist concerning the directions and strengths of these effects (Ben-Issa et al., 2017; Underwood, 2009) due to different mechanisms involved (for details, see Table S1). Furthermore, while companion planting of insect-detering or insect-repellent plants can be an effective measure for controlling pests (for the underlying mechanisms, see Table S1), there can be negative effects of these plants on neighbouring target crops (Ben-Issa et al., 2017; Hambäck et al., 2014; Moreno & Racelis, 2015). For example, companion planting can reduce productivity of target crops (Letourneau et al., 2011; Lopes et al., 2016) and their nutritional quality (Xiao et al., 2013). The current body of evidence regarding the optimal companion planting species for efficient pest control with minimized agroecosystem disservices is limited (Bommarco et al., 2013; Buzhdygan & Petermann, 2023).

Bottom-up control measures for herbivore pests can also affect their natural enemies, thereby potentially altering the effectiveness of top-down control measures (Han et al., 2022). For example, the *enemies hypothesis* suggests that variations in the diversity or density of the plant community can lead to differential predation pressure on plant pests (Andow, 1991; Root, 1973; Russell, 1989). Natural enemies are expected to be more effective in suppressing pests in polycultures because of the increased availability of suitable microhabitats for predators in diversified plant communities (Root, 1973). The efficiency of natural enemies may also be enhanced by chemical cues from associated plants (Letourneau, 1990). On the contrary, the insect-repellant effects of companion plants may negatively affect the efficiency of pest natural enemies (Gols et al., 2005; Lai et al., 2011; Letourneau et al., 2011; Lin et al., 2003; Risch et al., 1982; Singh et al., 2019; Zhou et al., 2013). Furthermore, higher plant density or biomass may reduce enemy searching effectiveness due to the greater difficulty of encountering prey in more dense vegetation (Clark & Messina, 1998; Gols et al., 2005; Risch et al., 1982). The variety of potential mechanisms underlying the positive and negative effects of plant diversity and intercropping on the efficiency of herbivore natural enemies have been widely reviewed (Andow, 1991; Letourneau, 1990; Letourneau et al., 2011; Russell, 1989; Sheehan, 1986; see also Table S1). While some supporting evidence was found for the *enemies hypothesis* (Andow, 1991; Song et al., 2012; Letourneau, 1990; Letourneau et al., 2011; Lin et al., 2003; Lai et al., 2017; Russell, 1989; Utsumi et al., 2011; Zhou, 2012; Zhou et al., 2016), the consistency of the effects across different studies remains unclear (Karp et al., 2018; Lopes et al., 2016; Moreno & Racelis, 2015; Otway et al., 2005; Petermann, Müller, Weigelt, et al., 2010; Risch, 1981; Root, 1973).

Here we explore the potentially synergistic relationship between host-plant intercropping (barley alone vs barley intercropped with wheat and rye), companion planting with unpalatable pest-repelling plant (garlic) and predation (by lacewing larvae) when applied simultaneously to improve the efficiency of the management of cereal aphid. We use one of the most economically important species of cereal

aphids, the bird cherry-oat aphid *Rhopalosiphum padi* L., which is relatively abundant and is one of the most efficient in transmitting viruses—a further risk to the crop besides direct phloem-feeding, across a host range of over a hundred plant species (van Emden & Harrington, 2017).

Specifically, we address the following questions:

- Does intercropping among host plants affect aphid density directly or indirectly via altered host-plant biomass?
- Is there a tradeoff among the effects of companion planting with garlic on the target cereal crops, that is, garlic suppresses aphid density but reduces the biomass of the target crops?
- Is the top-down control of the aphid population by predation altered by changes in the host-plant community and with the use of garlic as a companion plant?

2 | MATERIALS AND METHODS

2.1 | Experimental design

We performed a controlled lab experiment using microcosm systems to test the drivers controlling aphid population density. In our experiment, we used a fully crossed design of the following three factors (Figure 1) with two levels each: (1) host-plant intercropping (barley monoculture vs barley intercropped with wheat and rye), (2) companion planting with repellent non-host plant (absence vs presence of garlic), and (3) predator presence (absence vs presence of lacewing

larvae). Each of the eight treatments was replicated over five microcosms, resulting in 40 microcosms in total.

Bird cherry-oat aphid *Rhopalosiphum padi* L. (Hemiptera, Aphididae) was used as our model crop-pest species in all treatments. There is strong evidence that *R. padi* is a generalist pest of cereals and grasses that infests a range of cereal crops including barley, wheat and rye (Wiktelius et al., 1990). Barley (*Hordeum vulgare* L., Yukatan variety, Ukraine) was chosen as the focal host-plant species, therefore appearing in all microcosms of all treatments. To investigate the effects of host-plant intercropping, we used wheat (*Triticum aestivum* L., Struna Myronivska variety, Ukraine) and rye (*Secale cereale* L., Zabava variety, Ukraine) planted in combination with barley. To test the effects of companion planting, we used garlic (*Allium sativum* L.), which is not a host to cereal aphids and has strong aphid-repelling effects (Zhou et al., 2013, 2016).

Barley, wheat and rye were grown from seeds, and garlic was grown from cloves. Seeds of barley, wheat and rye were received from the Bukovyna State Agricultural Experimental Station of the National Academy of Agrarian Sciences of Ukraine (Chernivtsi, Ukraine). Garlic was ordered from a commercial supplier (Agromarket50, Zmiiv, Ukraine). All seeds were sterilized and stratified for 5 days at 5°C temperature. All plants were grown for 21 days in monocultures under stable laboratory conditions at a temperature of 22°C, a humidity of 40% and a 16:8 h light/dark cycle. On the twenty-first day of growth, plants were transferred to experimental microcosms, each consisting of a pot (10 cm height and 10 cm diameter) enclosed with a transparent plastic cylinder (20.3 cm height and 11.4 cm circular diameter) with fine-meshed windows for ventilation.

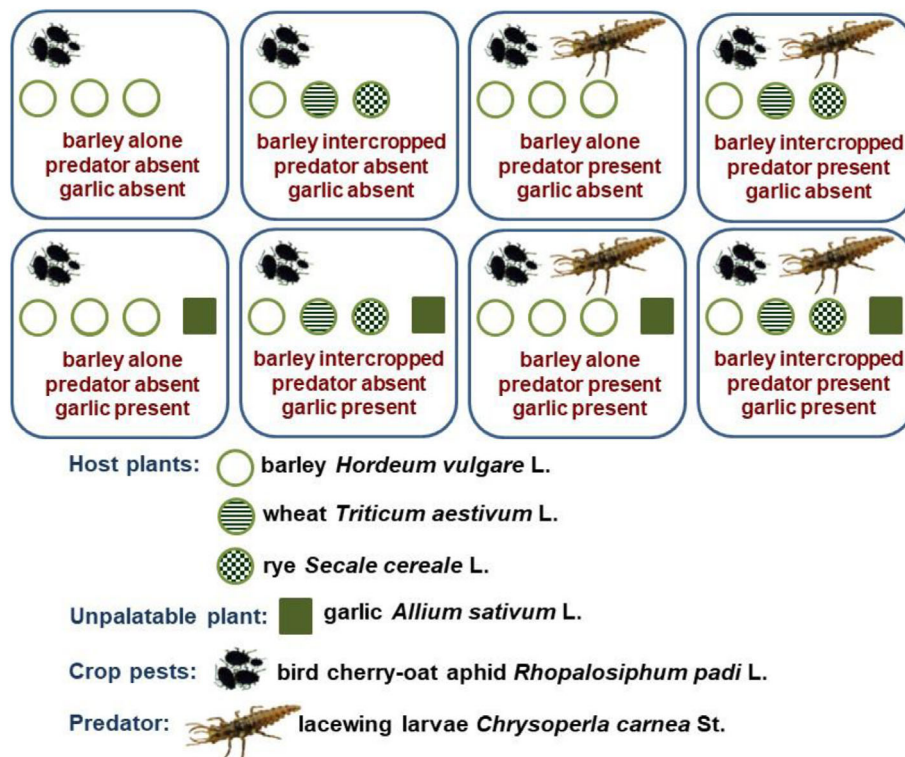


FIGURE 1 Experimental design showing all treatments. We used three plants of barley per microcosm in the monocultures and one plant of each of the barley, wheat and rye in the host-plant intercropping. Garlic (one plant/microcosm) in combination with the three host plants was used in the companion planting with garlic treatments. Only late aphid instars (10 aphids per each host plant resulting in 30 aphids/microcosm) were used in all treatments. One second instar of lacewing larvae (one individual/microcosm) was used in all predator treatments. Each of the eight treatments was replicated with five microcosms, thus resulting in 40 microcosms in total.

We used a standard soil substrate (peat substrate PEATFIELD® Universal PL-3, PeatField™, Ukraine) with the following properties: pH = 6.1, 89% organic substances, 134 mg/L total N, 131 mg/L P₂O₅, 135 mg/L K₂O. We used three individuals of host plants per each microcosm ($n = 120$ host plants in total). Thus, for barley monoculture treatments, three plants of barley were planted in the microcosm, while the host-plant intercropping treatments consisted of one plant of barley, wheat and rye each. The position of plants in each microcosm of the host-plant intercropping treatment was randomly allocated using dice. In the treatments of companion planting one garlic plant per microcosm was present in addition to the host plants (Figure 1). The dice was used to also randomly determine the position of garlic in each microcosm relative to the host plants. The position of the microcosms of different treatments on the lab table had a completely randomized design, where the position of each microcosm was randomly allocated using dice. The plants were watered as necessary by pouring water into pot trays. Throughout our experiment, we observed no signs of water stress in plants. To minimize any possible effects of local microclimatic conditions, such as light and temperature, we arbitrarily changed the positions of pots every other day after watering.

Clonal descendants from one mother of *R. padi* were raised on barley (*Hordeum vulgare* L., Yukatan variety, Ukraine) under stable laboratory conditions (16 h of light and 8 h of darkness, and a temperature of 22°C). The initial samples of *R. padi* (also raised and maintained on barley) were ordered from a commercial supplier in Germany (SAUTTER & STEPPER GmbH, Ammerbuch, Germany). Two hours after potting up the plants into the microcosms, 10 nymphs of aphids (fourth instars) were placed on each of the three host plants in the microcosms using a fine wet brush (overall, 30 aphid individuals per microcosm). The congeners were all genetically identical due to parthenogenesis under the conditions of the experiment. Direct placement of aphids on host plant and the bladed morphology of the leaf seedlings of the cereals encouraged the fast settlement of aphids on their hosts.

In predation treatments (Figure 1), we used second instar larvae of the lacewing *Chrysoperla carnea* St., which were ordered from a commercial supplier in Germany (SAUTTER & STEPPER GmbH, Ammerbuch, Germany). One lacewing larva was released into each corresponding microcosm (predator presence treatments) 30 min after the placement of aphids on the host plants was completed. For this, we placed lacewing larva on the soil amongst the host plants using a fine brush. No starvation of lacewing larva was allowed prior to the experiment. We regularly examined the microcosms to assess the predation activity of lacewing on aphids. At the end of the experiment, we searched the lacewing larvae in each experimental unit to accurately assess their presence and potential impact on aphid populations. All lacewings were found alive at the end of the experiment.

We collected data 14 days after the introduction of aphids into the microcosms. We counted the number of aphid individuals on each host plant (40 microcosms \times 3 host plant individuals, $n = 120$ host plants in total), which was used as the measure of aphid density in our analyses. Furthermore, we collected the shoots and roots of each

plant in the microcosms including host plants and garlic. The plant material was dried at 70°C for at least 48 h or until dry, and dry weights were obtained for each plant per microcosm individually.

2.2 | Data analysis

All analyses were carried out in R version 4.2.2 (R Core Team, 2022). We applied structural equation modelling using *piecewiseSEM* package in R (Lefcheck, 2016) to explore the simultaneous direct and indirect effects of host-plant intercropping, garlic presence and predator presence on aphid density on each host plant ($n = 120$, Figure 2). Specifically, with the help of the SEM, we address our first and second study questions (see also Section 1 Introduction above): (1) If intercropping among host plants directly influences aphid density or indirectly through the altered host-plant biomass? (2) If garlic reduces the biomass of the target crops, thus leading to a trade-off between aphid control and crop production? For this, the following individual mixed effect models were constructed (with microcosm identity as a random effect because the aphid counts at individual plants within a microcosm cannot be considered independent):

1. host plant biomass \sim host-plant intercropping + garlic biomass;
2. aphid density \sim host-plant intercropping + host-plant biomass + predator presence + garlic biomass.

To fit the first individual model testing the effects of host-plant intercropping and of garlic companion planting, we used a linear mixed effect model (LMM) using *lme4* and *lmerTest* packages in R (Bates et al., 2015; Kuznetsova et al., 2017). To fit the second individual model testing the effects of host-plant intercropping, host-plant biomass, garlic biomass and predator presence on aphid density, we used a quasi-Poisson generalized linear mixed effect model GLMM (using *MASS* (Venables & Ripley, 2002)) given the nature of our count data (i.e., Poisson-distributed aphid density) and the model overdispersion. While both quasi-Poisson and negative binomial models can be used for overdispersed count data, they have different assumptions about how the variance is related to the mean, thus leading to different weights of large and small counts in quasi-Poisson and negative binomial regression (Ver Hoef & Boveng, 2007). In our study, both models showed similar results for our data but the residuals for the estimated mean from the quasi-Poisson model were relatively lower than those from the negative binomial model (Figure S5). In addition, the sum of residuals of the estimated mean from the quasi-Poisson model were consistent across the gradient of the predicted mean, whereas the sum of residuals in the negative binomial model increased with the predicted mean (Figure S5B). This suggests that the negative binomial error structure was worth fitting to the larger values in our data. This also agrees with the previous research showing that negative binomial gives more weight to smaller counts, allowing them to have a greater effect on adjustments for negative binomial regression (Ver Hoef & Boveng, 2007). We chose the quasi-Poisson over the negative binomial given that the quasi-Poisson

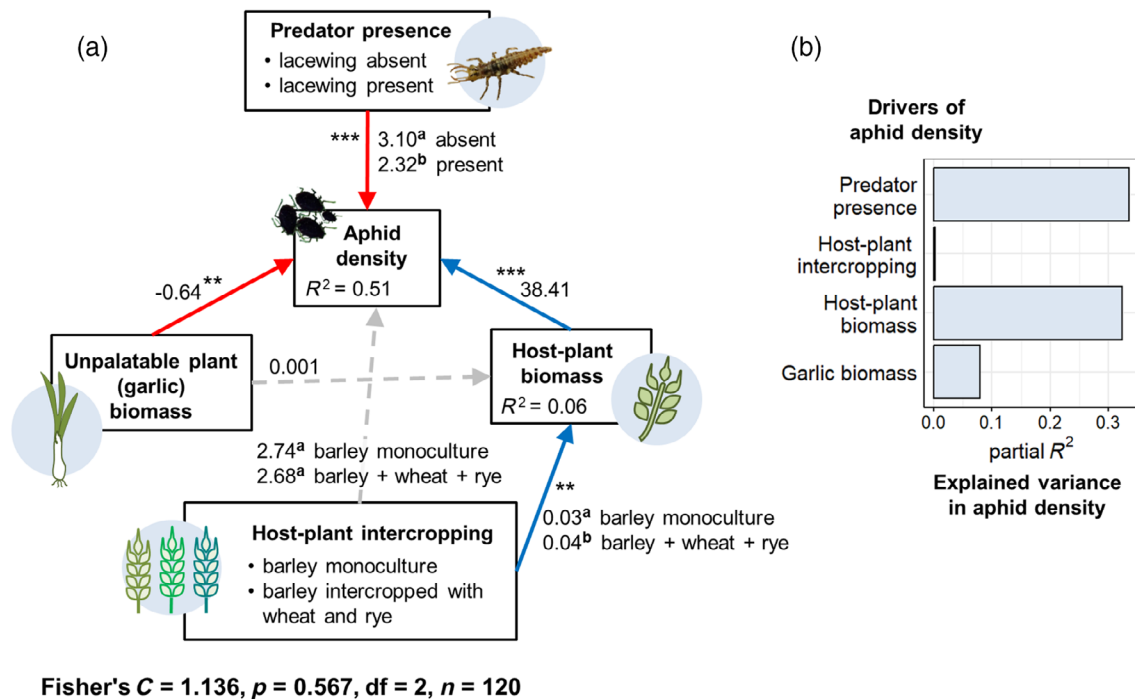


FIGURE 2 (a) Structural equation model (SEM) showing the simultaneous effects of predator presence, host-plant intercropping and host-plant biomass, and biomass of companion plant (garlic) on aphid density (number of aphid individuals per host plant). Fisher's $C = 1.14$, $p = .567$, $df = 2$, $n = 120$. Path coefficients are model estimates with the following levels of significance: * $p < .05$; ** $p \leq .01$; *** $p \leq .001$. Path coefficients for categorical predictors are the model-estimated marginal means for each level of categorical predictor with letters indicating significant pairwise differences among the model-estimated marginal means tested with post-hoc test. Solid paths are significant effects ($p < .05$) and grey dashed paths are nonsignificant effects ($p > .05$). Red and blue paths show negative and positive effects, respectively. R^2 are marginal (for fixed predictors) coefficients of determination showing the variance explained by the SEM for each response variable. See Table S2 for detailed SEM results. (b) The relative importance of each driver of aphid density, measured by partial R^2 (marginal coefficients).

model had lower residuals and fitted all values along the estimated mean relatively consistently.

The two individual models were further pieced together using *piecewiseSEM* package to construct and test the causal structural equation model (Figure 2a). For the categorical explanatory variables in our models, the marginal means approach was applied (implemented in *piecewiseSEM*), which reports the significance of the effect of the categorical predictor, an average value of the response variable for the levels of this categorical predictor accounted for the other co-variables in the model (i.e., marginal mean), and also includes a post-hoc test to compare the differences in marginal means among the levels of this categorical predictor (Figure 2a and Table S2). Furthermore, to compare the relative importance of each explanatory variable in the model for predicting aphid density, we calculated the partial- R^2 values (Figure 2b) using *r2glmm* package in R (Jaeger, 2017). The Fisher's C statistic was used as an assessment for the goodness of fit of the SEM to the data and the existence of missing links was tested by the *d-Sep* test (Lefcheck, 2016). The path model did not explicitly consider interactions between control methods due to insufficient sample size, which could risk overfitting the model. But we tested interactions among the aphid control measures in separate GLMM models (Figure 3a–b and Tables S4 and S5) in order to answer our third study question (see Section 1

Introduction above): If the effects of predator on aphid density depend on host-plant intercropping and biomass and if garlic presence and biomass alter predator efficiency?

Furthermore, we tested if aphid density and host-plant biomass differed among the individual treatments used in our experiment (Figure 3c–e). For this, we used a quasi-Poisson GLMM with microcosm as a random effect and the host-plant biomass included as a covariate. Using this model, we also compared the differences in the marginal means for each level of the treatments applying the *emmeans* package in R (Lenth, 2023).

In addition, we tested if the three species of the study host plant (barley, wheat and rye) differed in their biomass (Figure S1A). For this, we used an LMM with microcosm as a random effect and compared the marginal means for each species using a post-hoc test in *emmeans*. Furthermore, we tested if the species identity of the host plant affects aphid density (Figure S1B) and aphid load (the number of aphids per host plant divided by the host-plant biomass, Figure S1C) by fitting a quasi-Poisson GLMM model with microcosm as a random effect and host-plant species as a predictor, while accounting for the effects of predator and garlic presence by including them as the covariates in the model. For these models, we compared the marginal means of aphid density (Figure S1B) and aphid load (Figure S1C) for each host-plant species using post-hoc test in *emmeans*.

3 | RESULTS

The population of *R. padi* in our study systems ranged from 0 to 59 aphids (mean \pm sd 17.6 ± 14.1) per host plant across all the treatments. Aphid density was not significantly different among the species of the host plants (i.e., barley, wheat and rye) (Figure S1B). There was an increase in host-plant biomass in the intercropping treatments, primarily driven by the growth of wheat plants (Figure S1A). Despite the relatively higher biomass in wheat compared to rye and barley, which thus provides more food resources and increased leaf surface area for aphids, we found no difference in aphid load (i.e., the number of aphids per unit of host-plant biomass), therefore indicating no differences in aphid preferences of specific host species (Figure S1C).

Fisher's C test indicated that the piecewise SEM model (Figure 2 and Table S2) was well supported by our data (Fisher's $C = 1.14$, $df = 2$, $p = .57$, $n = 120$) and explained 51% variance in aphid density (Figure 2a), with the majority of variance explained by predator presence and host-plant biomass (Figure 2b). The intercropping of host plants showed no direct effects while it increased aphid density indirectly via greater host-plant biomass available to aphids in the microcosms when barley was intercropped with wheat and rye compared to barley monoculture (Figure 2a). The increase in biomass with host-plant intercropping was due to larger productivity of wheat in comparison to other host-plant species, including barley—the focal host-species in our experiment (Figure S1A). Companion planting with garlic strongly decreased aphid density while having no significant influences on the biomass of host plants (Figures 2a and 3e), thus indicating no noticeable competition between companion and host plants.

The presence of an aphid predator strongly reduced aphid density (Figure 2a). The interactive effect of the predator with host-plant biomass on aphid density was significant (Figure 3). The combination of predators and garlic led to a greater reduction in aphid density compared to the effect of either alone (Figure 3e). However, we found no evidence of interactive effects between predator and garlic (either presence or biomass) on aphid densities (Figure 3b and Tables S4 and S5).

4 | DISCUSSION

We used controlled experimental systems to disentangle the following simultaneous and potentially synergetic or antagonistic effects on cereal aphids: predation, aphid host-plant intercropping with other host plants and companion planting with a repelling non-host plant. We found strong simultaneous bottom-up control (by host-plant biomass and presence of companion non-host plant) and top-down control (via predation by lacewing larvae) over the aphid population in our experimental communities. Having garlic as a companion plant did not affect the biomass of target crops (Figures 2 and 3e and Figure S3) or reduce the efficiency of predators (Table S4, Table S5, Figure 3b), indicating no antagonistic effects of garlic on cereal crops or on predators. In fact, the simultaneous application of predator and garlic resulted in a stronger effect on aphid density compared to when each of these measures was applied solely (Figure 3d, Figure S3).

The intercropped cereal species and their planting with garlic, as used in our experiment, represent a model system for testing the efficiency of control factors of the cereal aphid population rather than realistic measures to increase cereal yields. The artificial nature of our controlled experiment requires field studies to further test the bottom-up and top-down effects observed in our study and their interactions in controlling cereal aphids for further implementation in integrative pest management and ecologically intensive agriculture (Buzhdygan & Petermann, 2023).

4.1 | Relative importance of aphid control measures

The presence of lacewing larvae demonstrated the strongest negative effect on aphid density compared to the other pest control treatments (Figure 2b). These results are consistent with earlier findings suggesting that natural enemies play a key role in the regulation of aphid populations (Guerrieri & Digilio, 2008; Van Veen et al., 2008). Following predation, the second most effective method of controlling aphid densities was companion planting with garlic (Figure 2b). Previous studies also recorded that garlic reduced population densities of aphids on target crops (Lai et al., 2011; Potts & Gunadi, 1991; Sarker et al., 2007; Zhou et al., 2013; Zhou et al., 2016) due to the aphid-repellent effects of garlic volatiles (Lai et al., 2011; Potts & Gunadi, 1991; Zhou et al., 2016). Host plant exposure to the volatiles of garlic or other *Allium* spp. has been shown to mask the odours of nearby host plants (Ben-Issa et al., 2017; Lai et al., 2011; Plata-Rueda et al., 2017). Furthermore, it can change host plant volatile emissions (Dahlin et al., 2015), ultimately leading to reduced host attractiveness for aphids (Potts & Gunadi, 1991) and disrupted host locating abilities (Ben-Issa et al., 2017). In addition, the volatiles of *Allium* spp. can have deterrent effects on aphid behaviour on their host plants (Lai et al., 2011). They have been demonstrated to alter or inhibit aphid reproductive success and feeding activities (Ben-Issa et al., 2017; Khudr et al., 2020). Furthermore, intercropping of companion plants, for example, with alliaceous plants, such as garlic, may also alter host plant morphology (Santillano-Cázares et al., 2019), nutritional quality (Xiao et al., 2013) and microclimate (Boudreau, 2013; Santillano-Cázares et al., 2019), and thus indirectly affect aphid population dynamics to a larger extent to the benefit of the host plant.

In our study, aphid density was not directly influenced by host-plant intercropping (Figure 2). Previous studies suggest that even highly polyphagous aphid species, such as *R. padi*, may perform better on specific species of host plants (Dixon, 2012; Weber, 1985), and therefore might do best in monocultures due to higher densities of a preferable host, following the *resource concentration hypothesis* (Root, 1973). However, we found no differences in host preference by aphids (Figure S1). This suggests that *R. padi* when given a choice among barley, rye, and wheat, can feed relatively equally on the different available species of host plants. This may be attributed to the close phenological relationship among our study host species. Previous research indicated that intercropping with less closely related

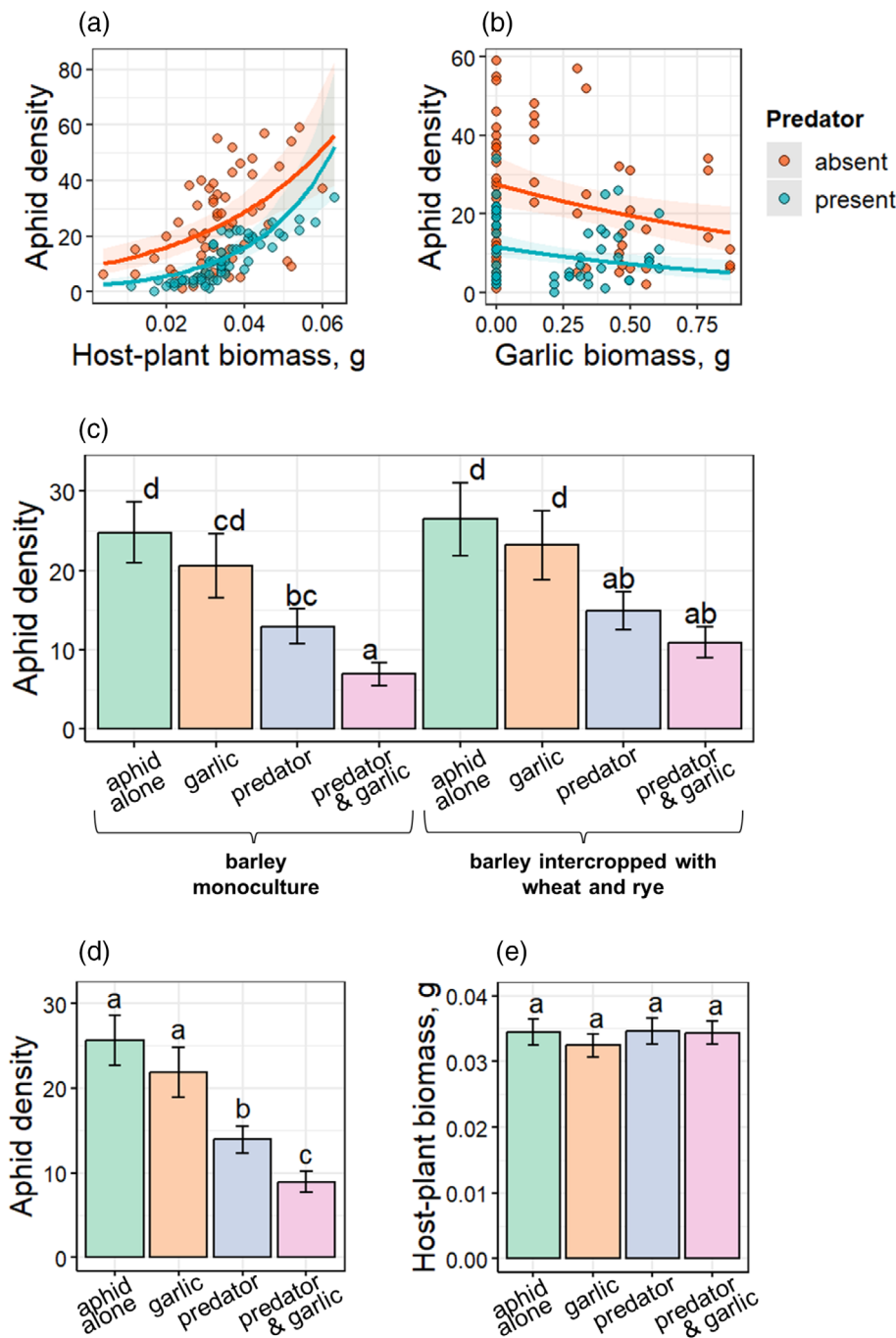


FIGURE 3 (a) Interactive effect of host-plant biomass and predator presence on aphid density ($\chi^2 = 8.04$, $p = .005$, Table S4). (b) Interactive effect of garlic biomass and predator presence on aphid density ($\chi^2 = 0.35$, $p = .55$, Table S5). (c) Effect of the experiment treatments on aphid density: Host-plant intercropping (barley monoculture vs barley intercropped with wheat and rye), companion planting with a repellent non-host plant (absence vs presence of garlic) and predator presence (absence vs presence of lacewing larvae). Effects of predator and garlic presence when applied each separately and simultaneously on aphid density (d) and on host-plant biomass (e). Bars represent the mean \pm SE. Letters indicate significant pairwise marginal means differences among treatments tested with post-hoc test (Table S3). Overall, 40 microcosms for 8 different treatment combinations were used, resulting in 5 microcosms per treatment. Colouring is used to facilitate the comparison between the same treatments in barley monoculture and barley intercropped with other host plants.

crops has been successful in controlling aphid populations (Mansion-Vaquí et al., 2019). The effects of host intercropping on aphid density in our experiment were driven mainly by the indirect path due to higher host-plant biomass (Figure 2). Borer et al. (2012) suggested that the frequently observed relationships between plant diversity and their consumers occur primarily via changes in plant production rather than via plant diversity directly controlling consumers. Indeed, previous studies have found increased herbivore abundance with their host biomass as an increasing function of plant species richness (Borer et al., 2012; Hertzog et al., 2016; Petermann, Müller, Roscher, et al., 2010; Petermann, Müller, Weigelt, et al., 2010). Although our results align with these studies and indicate that host-plant

intercropping augmented aphid population through increased crop biomass (Figure 2), we cannot entirely dismiss the possibility that this observed phenomenon may be an artefact of our experimental design and not necessarily a direct biological consequence of intercropping itself.

4.2 | Simultaneous and interactive effects of aphid control measures

The efficiency of natural enemies of crop pests can be influenced by the variations in plant diversity or biomass (the *enemies hypothesis*,

Root, 1973). In our study, the interactive effect of barley intercropping and predator on aphid density was not significant (Table S4). Instead, we found positive interactive effects of host-plant biomass and predator presence (Figure 3a and Table S4), indicating that the rate of increase in aphid population with an increasing plant biomass was relatively higher in microcosms with predators compared to those without them. These results can be explained by potentially delayed predator action with respect to the more rapid growth of the aphid population in systems with higher host-plant biomass (Guerrieri & Digilio, 2008). The additional plant structures with greater host-plant biomass might also affect the searching efficiency of predator via modified prey accessibility (Clark & Messina, 1998; Gols et al., 2005; Risch et al., 1982) or due to predator sensitivity to particular vegetation texture (Sheehan, 1986) leading, as well, to higher herbivore abundance. For example, Risch et al. (1982) reported reduced foraging rates of lady beetle with an increasing density, but not richness, of plant community. Petermann, Müller, Weigelt, et al. (2010) showed that biomass of aphid host-plants increased abundances of aphid parasitoids but decreased parasitism rates of aphids. Overall, these results emphasize the importance of bottom-up effects of host-plant biomass that may modify the interactions among crop pests and their natural enemies.

Integrated pest management calls for more empirical evidence to complement natural enemies of agricultural pests with companion planting, aiming to enhance pest suppression while minimizing unintended negative impacts of these companion plants on predation efficiency (Barzman et al., 2015; Buzhdygan & Petermann, 2023; Gontijo et al., 2018). For instance, garlic volatile could disturb predator searching efficiency by masking the chemical cues originated from their prey (Vet & Dicke, 1992) or by altering the herbivore-induced host-plant volatile emissions (Dahlin et al., 2015; Mumm & Dicke, 2010), which attract aphid natural enemies. Some studies have reported that garlic can exert toxicity on aphid natural enemies (Singh et al., 2019). However, there is also evidence suggesting that companion planting with garlic or the application of garlic extract to target crops can enhance the efficiency of aphid natural enemies (Lai et al., 2011; Lai et al., 2017; Zhou et al., 2013, 2016). Our results showed non-significant interactive effects of predator with both garlic presence (Figure S3 and Table S4) and garlic biomass (Figure 3b and Table S5) on aphid density. This suggests that there were no differences in predator efficiency associated with either the presence of garlic or the gradient of garlic biomass. It is important to note that during our experiment, we frequently observed lacewings crawling on garlic stems (Figure S2), which also may indicate that there was no predator-repelling effect of garlic. Garlic stems could serve as an additional microhabitat for the lacewing. However, previous studies also suggest that additional habitat complexity (i.e., garlic presence in our work) may disturb enemy foraging (Gols et al., 2005; Helenius, 1991). Future studies would benefit from including experimental data on predator fitness that would allow further investigations of the *enemies hypothesis* along aphid host and non-host plant gradients.

Furthermore, more data are required to identify the most suitable companion planting species for target crops in order to ensure

effective pest suppression while minimizing the negative impacts that the companion plant may have, such as reduced crop production (Bommarco et al., 2013). The consequences for crop productivity when intercropping crops with garlic depend on the degree of competition or cooperation among them (Boudreau, 2013; Santillano-Cázares et al., 2019). In our study, planting with garlic showed no significant effects on host-plant biomass (Figures 2 and 3e and Tables S4 and S5), thus supporting the growing body of evidence for *Allium* spp. being an effective pest-control measure, especially when applied simultaneously with other integrative pest management agents (Khudr et al., 2020; Lai et al., 2011; Sarker et al., 2007; Singh et al., 2019; Zhou et al., 2013). Indeed, we found that the combined application of predator and garlic resulted in a greater reduction in aphid density compared to when each of these control measures was applied individually (Figure 3c,d).

Given the experimental setup of our artificial model system, it is important to note that some of the tested pest control treatments would need serious adjustments to be of commercial relevance. For example, intercropping barley with wheat and rye, along with their planting with garlic, would probably pose challenges to harvest for human consumption and might only serve as animal fodder. Therefore, the practical implementation of these natural pest control treatments under field conditions as well as their application on commercially relevant scales is yet to be examined. Nevertheless, within the limitations of our model system, our results suggest that the simultaneous application of aphid predator and companion planting with garlic may be an effective practice for controlling cereal aphid populations in grain crops on a small scale without compromising the production of the target crops. This approach holds promise for reducing the reliance on conventional pesticides, which are currently the primary method for controlling cereal pests.

AUTHOR CONTRIBUTIONS

OYB and MSK designed the conceptual framework for the study experiment. OYB designed the concept for the study analysis. TVF, OVB and OYB performed the experiment and collected data. OYB and JWZ analysed the data. OYB and JWZ wrote the original draft, and MSK, TVF and OVB substantially contributed to review and editing.

ACKNOWLEDGEMENTS

The authors thank Jana S. Petermann for comments on this work, which improved the manuscript. Acknowledgements to Tetiana M. Fylypchuk for the technical assistance and to Svitlana S. Rudenko (Department of Ecology and Biomonitoring, Chernivtsi National University, Ukraine) for providing the management support and facilities during the experiment. We thank the anonymous reviewers for their comments, which have greatly improved the paper. Open Access Funding provided by Freie Universität Berlin.

CONFLICT OF INTEREST STATEMENT

All authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data used to support the conclusions of this study and the source code to produce the results are available at <https://doi.org/10.5281/zenodo.12770321>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Zeller, J. W., Khudr, M. S., Fylypchuk, T. V., Bahlei, O. V., & Buzhdygan, O. Y. (2024). Simultaneous top-down and bottom-up control of cereal aphids by predation, companion planting and host-plant diversity. *Annals of Applied Biology*, 185(2), 274–283. <https://doi.org/10.1111/aab.12933>