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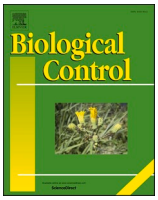
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Effects of strawberry resistance and genotypic diversity on aphids and their natural enemies

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HIGHLIGHTS

- Intrinsic resistance in wild strawberry plantations inhibited generalist aphid population.
- Plant genotypes that were resistant against a chewing beetle (Galerucella tenella), conveyed resistance to generalist aphid only.
- There were more specialists aphids on high diversity plots.
- Anthocorids and Lacewing adults were more on high diversity plots, whereas other specialist predators followed aphid prey.

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ABSTRACT

Ecological theory hypothesizes that plant trait diversity may be as important as the presence of specific functional traits (e.g., resistance) for the herbivore and predator communities within a population. We used experimental populations of wild woodland strawberry (*Fragaria vesca*) to test whether the degree of plant genotypic diversity and/or the existence of specific resistance traits play a role in the host plant's community structure specifically, the community of generalist and specialist aphids and their natural enemies. In 2019, we studied the aphid abundance and relative predator abundance in an experimental field site in Alnarp, Southern Sweden; the field consisted of plots planted with combinations of 20 different wild strawberry genotypes. These strawberry genotypes were previously identified as either susceptible to or resistant against the herbivorous beetle (*Galerucella tenella*). Two aphid species, *Chaetosiphon fragaefolii* (specialist) and the exotic *Aphis gossypii* (generalist) were found in the plots and of the two species *A. gossypii* was dominant. The abundance of the specialist aphid (*C. fragaefolii*) was highest in susceptible plots with high genotypic diversity, while the generalist (*A. gossypii*) was highest in plots with a mix of resistant and susceptible plants with high genotypic diversity. Anthocorid predators, developed significantly higher population densities in strawberry plots with high genotypic diversity. Overall, predator abundance showed a positive correlation with aphid abundance. These results show that the specific functional trait of resistance as well as plant diversity affected aphids. Knowledge about these effects can be important factors to consider when designing strawberry plantings less susceptible to aphids.

1. Introduction

Plants defend themselves against insect herbivores by employing various direct and indirect resistance traits. Plants respond differently to chewing insects then they do to hemipterans, and their different modes of feeding. Chewing insects can cause extensive damage to plant tissues whereas hemipterans which have piercing-sucking mouthparts, cause only small direct physical injuries to plant tissues but drain plant

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nutrients (War et al., 2013). Plant resistance against chewing insects is primarily regulated by the jasmonic acid (JA) pathway, while resistance against fluid feeding insects is typically regulated by both JA and the salicylic acid (SA) pathway (Thaler et al., 2012; Züst and Agrawal, 2016). To overcome these complex plant defenses, many herbivores have become specialized feeders on only one or a few host plants.

Even within a species, plants typically show genotypic variation in resistance and other traits which in turn, increases the food diversity and complexity for herbivores. In fact, the effects of intraspecific diversity on herbivore deterrence can be as strong as the effects of plant species diversity on herbivory (Cook-Patton et al., 2011). Such intraspecific plant diversity may explain why herbivore outbreaks rarely occur in wild plant populations, while cultivated monocultures composed of a single variety usually more vulnerable to pest outbreaks.

New concepts such as *cultivar mixing* (Ninkovic et al., 2011) and *resistance mixing* (Koski et al., 2021) describe strategies that take advantage of intraspecific plant diversity to combat herbivory in crop plantations. However, relatively few studies have assessed the relative importance of resistance and diversity within the same plant species (Hauri et al., 2021; Weber et al., 2020; Grettenberger and Tooker, 2015).

Although the importance of plant traits have mainly have been studied in relation to herbivores, several studies have shown that predators are also affected by plant traits, which in turn can have implications for predator–prey dynamics (Sigsgaard, 2010;Ågren, G. I., Stenberg, J. A., & Björkman, C., 2012). Plant species diversity can also impact the structure of predator communities (e.g., Wetzel et al.2018; Grettenberger and Tooker, 2017; Crutsinger et al., 2006; Hauri et al., 2021). In general, increasing plant genotypic diversity tends to increase predator densities, lower herbivore densities and reduce plant damage in both agricultural and natural ecosystems (Grettenberger and Tooker, 2017); however, inconsistent outcomes for increasing intraspecific diversity suggests that our knowledge about genotypic diversity and its mechanism of of influence on multi-trophic interactions remains limited (Moreira and Mooney, 2013).

In this study, we use the woodland strawberry (*Fragaria vesca*) and its aphid and predator community as a model system, to investigate the relative effects of plant resistance and plant diversity on the insect community. Previous studies have shown that woodland strawberry exhibits genetic variation in its resistance to chewing herbivores (Weber et al., 2020). Both resistance and plant diversity *per se* help protect woodland strawberry from chewing herbivores (Koski et al., 2021). Although aphids are among the most destructive herbivores, causing serious production losses to both wild and cultivated strawberry (Valério et al., 2007), it remains unknown how herbivore resistance might affect aphids and their natural enemies –especially in combination with plant diversity. In general, plant resistance to aphids is presumed to be regulated by other pathways than those that regulate resistance to chewing herbivores (Thaler et al., 2012; Züst and Agrawal, 2016). Aphids often inflict more damage than chewing herbivores Because of their ability to vector plant viruses (Cédola and Grecob, 2010). Among the several species of aphids that attack strawberries (Rondon et al., 2005; Rabasse et al., 2001) two inparticular are important: *Chaetosiphon fragaefolii* (Cockrell), commonly known as strawberry Aphid and the generalist, melon aphid *Aphis gossypii* (Glover) (Solomon et al., 2001) – these are also the two species that were observed in the present study. Two important predictions can be made about the comparative responses of specialist and generalist herbivores to plant defences; first, specialist should be less influenced than ageneralist by a given plant (Whittaker and Feeny, 1971); second, upon feeding, specialists and generalists should show distinct induced defense responses (Whittaker and Feeny, 1971; Krieger et al., 1971). The idea that specialists can completely avoid plant defense traits is an inaccurate one, as there are cases where specialists are negatively affected by plant defense traits (e.g., Ali and Agrawal, 2012).

This study was conducted to test three hypotheses: (a) Intrinsic resistance in wild strawberry plantations inhibits both aphid species – in particular, the generalist; (b) Higher intraspecific plant diversity inhibits both aphid species – in particular, the specialist; (c) Plant genotypic diversity and/or the existence of specific resistance traits effects the community structure the communities of natural enemies.

2. Material and methods

2.1. Study species

The woodland strawberry, *F. vesca* (Rosacea) is distributed widely throughout the Northern Hemisphere and grows naturally in a variety of habitats including forests, mountains and farmlands (Hancock, 2008). *Fragaria vesca* a rosette-like habit stands upright at 5–30 cm tall and produces axillary buds that develop into a branch crown or a cluster of flowers (Darrow, 1966). In addition to sexual reproduction, *F. vesca* also reproduces clonally by producing a large high numbers of runners (Schulze et al., 2012). *Fragaria vesca* ($2n = 2x = 14$) is a relatively small plant with a small genome that makes it a versatile plant for experimental study (Darwish et al., 2015, Shulaev et al., 2011).

2.2. Selection of wild germplasm for experimental setup

For the purpose of this study, we selected 20 genotypes of woodland strawberry. Half of the genotypes were previously identified as very resistant and the other half as very susceptible to chewing insect herbivores (Weber et al., 2020). Chewing herbivores and hemipterans have different modes of feeding can activate both similar and different defence pathways. Both groups of insects activate JA (jasmonic acid) pathways, but the resistance against hemipterans may also be regulated by SA (salicylic acid) pathways (Thaler et al., 2012). Whether the genotypes used in this study are resistant to aphids is not known; therefore, this study can potentially elucidate if resistance to chewing herbivores in specific strawberry genotypes might also confer resistance to insects with piercing-sucking mouthparts. All 20 genotypes originate from a germplasm collection based on random sampling of wild strawberry from central Sweden (Muola et al., 2017).

2.3. *Experimental field* set-up

Located on the Alnarp campus of the Swedish University of Agricultural Sciences in southern Sweden (55° N, 13° E) the field site, established in 2017 covered a total area of 130 m × 40 m. The area was divided into 60 equally sized plots in a full factorial design with 10 replications of two levels of genetic diversity (high and low), and three levels of plant resistance (i.e. resistant genotypes only, susceptible genotypes only, and a 50/50 mix of resistant and susceptible genotypes). Each plot within the field was ca. 5 m × 5 m. in size and each included forty plants that were grown in soil bags. Thus, there were 2400 plants in total in the 60 plots. An overview of the experimental setup is provided in (Supplementary Fig. S1.).

We assessed the population of aphids and natural enemies on 12 plants per plot, six times from May to July (twice per month), with the same plants observed each time. The plant genotypes of each plot were initially randomly selected and were tagged, and observations were then repeated on the same tagged plants for the rest of the observation period. Plants were randomly selected within each plot, leaving the outer rows as a buffer. The plants initially selected were followed throughout the season. We also evaluated the impact of aphid density on yield at the whole plot level. Total yield per plot (fruit weight) was recorded for the months of May and June 2019. Ripe fruits were harvested on a weekly basis and fruits were weighed on the day of harvest (Koski et al., 2021).

2.4. *Visual scoring* of aphids and predators

The number of aphids and predators was visually assessed every second week from spring (May) until summer (June/July) in 2019

(week numbers: 20, 22, 24, 26, 28, 30). Aphid density on individual strawberry plant was visually assessed for 12 plants per plot, a total of 720 plants per assessment. Aphid count was determined by parting individual strawberry plant in two halves, each half was then evaluated for about two minutes, to record aphid number and morphotype (nymph, adult winged, adult alate) of aphids. During sampling, aphids were also collected for identification. The aphids were identified following Heie (1993).

After the visual assessment, an estimate of the abundance of active predators was made by gently knocking the plants over a white plastic tray (also known as 'knock-down sampling') to estimate the abundance of active predators. The number of generalist predator spiders (*Araneae)* and Anthocorids (Hemiptera: *Anthocoridae*) and specialist aphid predators, ladybird adults and larvae (Coleoptera: *Coccinellidae*), lacewing eggs and adults (Neuroptera: *Chrysopidae*) and hoverfly adults (Diptera: *Syrphidae*) was determined in the same manner as above, both during and after aphid count.

2.5. Statistical **analysis**

The counts of aphids and predators were analyzed in separate Poisson regressions with a log-link and with fixed effects of the categorical variables of *Week* (levels: 20, 22,…, 30), *Diversity* (levels: high, low), and *Resistance* (levels: resistant, mixed, susceptible), and random effects of *Block* (10 levels), *Plot* (60 levels), and *Genotype* (20 levels). To investigate potential synergistic or antagonistic effects the 2-way and 3-way interactions between the fixed effects were included in the statistical models. Visual assessment of model validity was done by inspecting the cumulative residual plots as proposed by Lin et al., (2002). Backward model reduction of the 3-way design was done based on the Akaike Information Criterion, and statistical significance of the selected effects was quantified by asymptotic likelihood ratio tests. Post hoc comparisons of the levels of the significant effects on a 5 percent significance level was done by using estimated marginal means (Searle et al., 1980).

To investigate whether predators control aphid,the statistical analysis of the number of aphids as described above was redone after including the number of predators as a continuous explanatory variable. To accommodate the log-link in the Poisson regression, the number of predators were also log-transformed, and a specific categorical effect was introduced for the observations with no predators. In this way, a power relation between the mean abundance of aphids and the number of predators was introduced, while avoiding the mathematical problem by taking the logarithm of zero. Similarly, to investigate whether aphid abundance caused higher herbivore damage and disrupted the yield (fruit weight) of woodland strawberry, a statistical analysis of the number of aphids was done like above for aphid and predator count, after including the fruit weight as a continuous explanatory variable and removing categorical variable *Week* from the fixed effects. In this way, a relation between abundance of aphids and fruit weight was initiated.

All analyses were performed in R version 3.6.1 using the packages *lme4*, *gof*, and *emmeans*.

3. Results

3.1. ***Impact of*** *resistance* ***and diversity of plant genotypes on aphid populations***

The three different levels of resistance influenced total aphid population count. The highest number of aphids was observed in susceptible strawberry genotypes while the lowest number was found in resistant genotypes. The specialist aphid *C. fragaefolii* (Fig. 1.A.) was affected by different levels of resistance, the highest densities were found in susceptible genotypes and lowest densities in resistant and mixed plots. The pairwise comparisons of *C. fragaefolii* numbers between mixed and resistant genotypes showed no significant difference ($\chi^2_{df=1} = 0.326$, P = 0.567), while a comparison of numbers between mixed and susceptible genotypes was highly significant ($\chi^2_{df=1} = 93.03$, P < 0.001) with more aphids on susceptible plots. With respect to resistant and susceptible plant genotypes, the numbers of the specialist aphid were also highly significantly different ($\chi^2_{df=1} = 86.41$, P < 0.001) with more aphids on susceptible genotypes. Finally, the number of specialist aphids observed was highly significant between the weeks ($\chi^2_{df=5} = 43.08$, P < 0.001) and a clear increase in abundance of *C. fragaefolii* was observed in week 24. The generalist aphid, *A. gossypii* (Fig. 1.B.) responded to both plant resistance and diversity, with the highest densities found in mixed plots

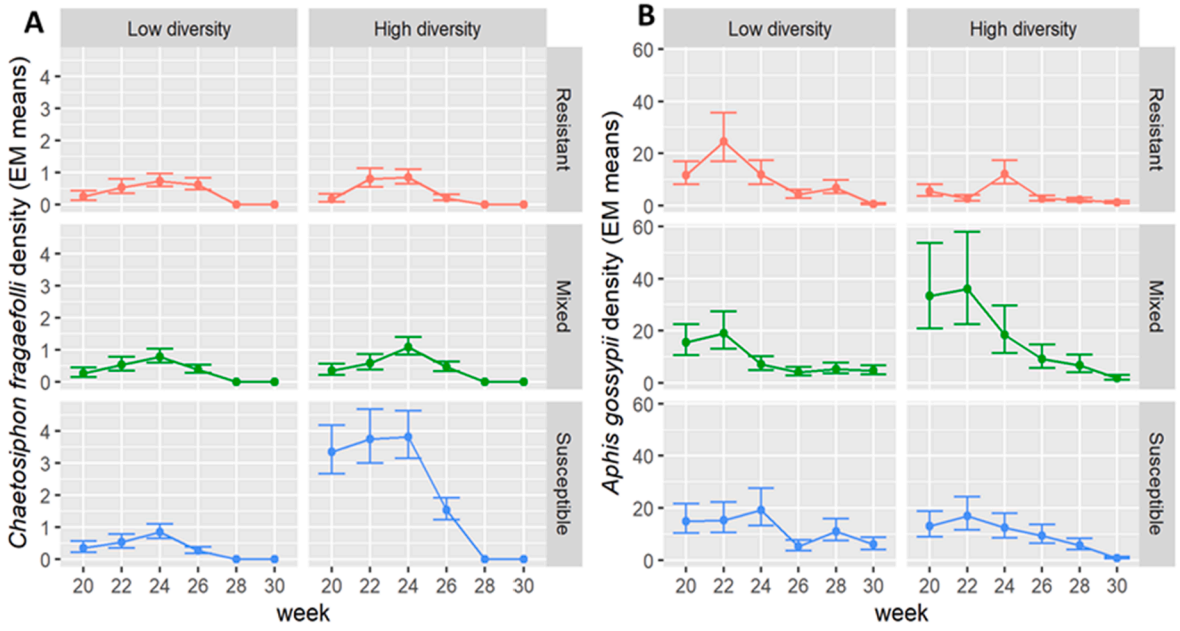


Fig. 1. The effect of woodland strawberry resistance (plots with resistant, susceptible, and mixed resistance plants) and diversity (plots with high or low diversity) on per plant density (estimated marginal means) of two aphid species A) *Chaetosiphon fragaefolii* and B) *Aphis gossypii* according to biweekly observations from early May until late July. Error bars indicate 95 % confidence intervals. Error bars have been removed for the observations = 0.

of high diversity (Fig. 1B). A pairwise comparison of *A. gossypii* counts between mixed and resistant genotypes was highly significant, with more aphids in mixed plots ($\chi^2_{df=1} = 43.08$, $P < 0.001$), while a comparison between mixed and susceptible genotypes was also highly significant, with more aphids in mixed plots ($\chi^2_{df=1} = 56.22$, $P < 0.001$). With respect to resistant and susceptible plant genotypes, the numbers of the generalist aphids was also highly significantly affected with more aphids found in the susceptible plots ($\chi^2_{df=1} = 48.62$, $P < 0.001$). Like specialist aphid, the number of generalist Aphids was also highly significant between the weeks ($\chi^2_{df=5} = 237.16$, $P < 0.001$) and a marked increase in the abundance of *A. gossypii* aphid was observed in week 22.

The specialist aphid (Fig. 1.A.) *C. fragaefolii*, was also affected by different levels of diversity, with higher densities found in high diversity plots and lower densities in low diversity plots. Pairwise comparisons of *C. fragaefolii* numbers between low and high diversity plots was highly significant, showing more aphids on high diversity plots found in the susceptible plots ($\chi^2_{df=1} = 59.33$, $P < 0.001$).

3.2. *Impact of resistance* and diversity of plant genotypes on predator populations

Of the six different groups of predators recorded the generalist predators, spiders (*Araneae*) (n = 987) and anthocorids (Hemiptera: *Anthocoridae*) (n = 1,243), were most abundant, while the specialist predators ladybird adults and larvae (Coleoptera: *Coccinellidae*) (n = 106), lacewing eggs and adults (Neuroptera: *Chrysopidae*) (n = 141, n = 109) and hoverfly adults (Diptera: *Syrphidae*) (n = 81) were least abundant. Spider densities were neither affected by different levels of resistance (Fig. 2.A), nor by plant diversity (Fig. 2.A). Spider densities increased with time, and the numbers of spiders were significantly affected by week number ($\chi^2_{df=5} = 83.12$, $P < 0.001$). The highest number of spiders was observed in the last week of the observations, i.e., week 30. Anthocorids were not affected by different levels of resistance (Fig. 2.B), but they were affected by different levels of diversity (Fig. 2.B), with higher densities found in high diversity plots. The pairwise comparison of anthocorids between high and low diversity plots was highly significant ($\chi^2_{df=1} = 558$, $P < 0.001$). The densities of ladybirds were neither affected by different levels of resistance (Fig. 2.C.), nor by the levels of diversity (Fig. 2.C.). The numbers of ladybirds were significantly different between the weeks ($\chi^2_{df=5} = 22.76$, $P < 0.001$) with more ladybirds observed in week 20. The densities of syrphids were also not affected by different levels of resistance (Fig. 2.D) or by levels of diversity (Fig. 2.D). Syrphid densities were significantly different between the weeks ($\chi^2_{df=5} = 26.76$, $P < 0.001$) with more syrphids observed in week 28. Likewise, different levels of resistance (Fig. 2.E) and diversity (Fig. 2.E) did not affect the densities of lacewing eggs. Lacewing adult densities were not affected by different levels of resistance (Fig. 2.F), but were affected by different levels of diversity with more adult lacewings found in the high diversity plots (Fig. 2.F). The pairwise comparison of lacewing adults between high and low diversity genotypes was highly significant ($\chi^2_{df=1} = 38.14$, $P < 0.001$). The densities of lacewing adults were significantly different between the weeks ($\chi^2_{df=5} = 11.92$, $P < 0.001$) with more lacewing adults observed in week 22.

The population responses of both specialist and generalist predators were positively correlated with the abundance of aphids per plant (Fig. 3). In the first weeks, lacewing egg density increased progressively, and decreased during week 28.

4. Discussion

The results of this study show that both plant resistance and diversity have significant effects on the studied aphid species *C.fragaefolli* and *A. gossypii*. The predator abundances also varied between treatments and mainly tracked the aphid prey. However, anthocorids responded positively to intraspecific plant diversity. Adult lacewings responded in a similar manner, with more individuals observed in more diverse plots. This positive response to higher intraspecific plant diversity is in agreement with previous findings on predator responses to plant species diversity (e.g., Wetzel et al., 2018; Grettenberger and Tooker, 2017; Crutsinger et al., 2006; Hauri et al.2021).The positive response of two of the predators to diversity can be the result of a more diverse habitat and/or prey resource, as plant diversity also has a positive effect on herbivore abundance. The lack of response in adult ladybirds and syrphids may be caused by the plot size, which was small relative to their high mobility (Corbett and Plant, 1993; Bommarco and Banks, 2003).The plot size may have also been too small for the spiders, as a one study suggests that even even 100 m may be too short (Sereda et al., 2012).

Despite the effects of plant resistance and diversity on the insect communities, there were no significant differences in strawberry yield between the treatments. It should be noted however, that aphid infestation levels were not very high, and compensatory growth together with predation and other mortality factors acting upon the two aphid species may have led to the lack of detectable levels of negative effect on yields. Below we discuss the effects of plant resistance and diversity in greater detail.

4.1. *Plant resistance* against chewing herbivores also protects against sucking herbivores

The classification of the experimental plant genotypes as either resistant or susceptible is based on their ability to escape damage by chewing strawberry leaf beetles (Weber et al., 2020). Plant resistance against chewing insects is typically regulated by the JA pathways, while resistance against phloem-feeding insects is typically is regulated by both the JA and SA pathway (Thaler et al., 2012; Züst and Agrawal, 2016). Thus, resistance against chewing insects (e.g., strawberry leaf beetles) does not automatically confer protection against phloem-feeders like aphids, though the fact that both elicit JA indicate a good probability that resistance towards chewing insects can also work against aphids. Indeed, lower densities of the generalist aphid *A. gossypii* were found in plots of resistant plants. This is good news from a plant protection perspective – it shows that simultaneous optimization of plant resistance to the strawberry aphid and chewing herbivores probably is likely possible.

4.2. *Effects of genotypic diversity on aphids*

In general, plant diversity is expected to promote generalist herbivores (e.g., most mammal browsers) while the opposite is expected for specialists herbivores (e.g., many insects) – sensu the Detoxification Limitation Hypothesis (Freeland and Janzen, 1974; Root, 1973). Concordantly, cultivar mixing has been proposed as a measure to combat insect herbivores. Previous studies on plant genotypic diversity in relation to aphids has been done using barley and bird cherry- oat aphids (*Rhopalosiphum padi*), *R. padi* is a major pest on cereals that overwinters on *Prunus* spp. The host plant acceptance of these aphids is strongly affected by cultivar mixing, but the outcome vary depending on the identity of the intermixed cultivars (Ninkovic et al.2011; Dahlin, I., Rubene, D., Glinwood, R., & Ninkovic, V., 2018). Our results found that the abundance of the specialist aphid *C. frageafolii* was higher in high diversity plots than in low diversity plots and this in direct contrast to expectations based on previous studies.We argue here that increased plant diversity may provide a greater resource for the specialist aphid (Keddy, 1984). According to a 2011 study by Underwood, aphids living among strawberry plants of variable genotypes moved more often than did aphids among strawberry plants of a single genotypic array which, in strawberry production, would constitute a single clone. Movement would thus lead to a less aggregated distribution with smaller colonies in diverse plots.

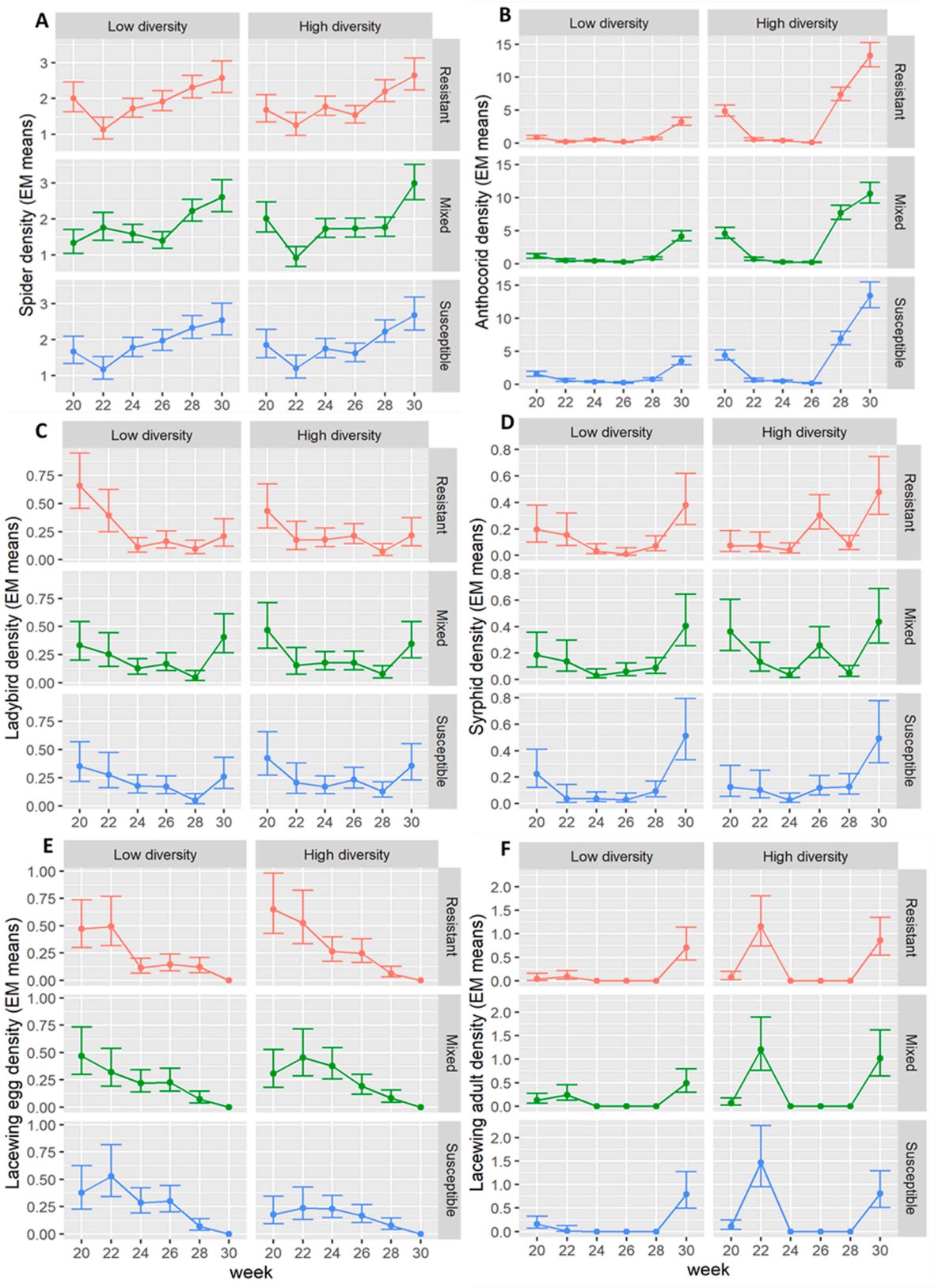


Fig. 2. The effect of woodland strawberry resistance (plots with resistant, susceptible, and mixed resistance plants) and diversity (plots with high or low diversity) on per plant density (estimated marginal means) of two aphid species A) Spiders B) Anthocorids C) Ladybirds D) Syrphids E) Lacewing eggs and F) Lacewing adults according to biweekly observations from early May till late July. Error bars indicate 95 % confidence intervals. Error bars have been removed for the observations = 0.

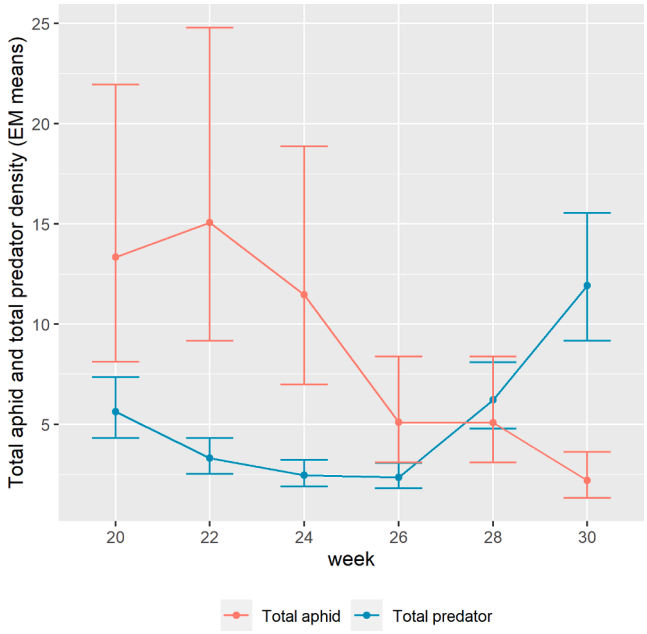


Fig.3. Prey –predator dynamics from early May until late July. Estimated marginal means of total aphids and total predators across diversity and resistance levels. Estimated marginal means are shown. Error bars denote 95 % confidence interval.

4.3. *Prey-predator* ***dynamics***

Top-down control inflicted by predator is typically as important as bottom-up control conferred by plant resistance in regulating herbivore populations (Krey, 2017; Hunter and Price, 1992; Vidal et al., 2018). Thus, the responses of predators to plant resistance and diversity can be of fundamental importance for the regulation of aphid populations. However, the results of this study showed that while anthocorids and adult lacewings responded to plant diversity, other predator groups responded solely to aphid density. We believe a likely reason for a lack of response may be that the plot scale was too small (Corbett and Plant, 1993; Bommarco and Banks, 2003). Aphid specialists such as ladybirds, syrphid flies, and lacewings prey mostly on aphids (Snyder and Ives, 2003) and the densities of ladybirds and syrphids increase as the the total number of aphid increases. Anthocorids and lacewing adults were directly affected by the plant diversity. Ladybirds and lacewings lay their eggs to the presence of aphids (Sarwar, 2016; Zhu et al., 2005); this may explain the lack of response to diversity in the ladybird larvae which themselves have relatively low mobility and in the lacewing eggs. Lacewings overwinter as adults; therefore their impact on the prey is delayed until reproduction and embryogenesis are complete (Canard, 2005). Eggs are laid near aphid colonies, and as larvae hatch, and oviposition of the first generation of lacewings ends, and the density of eggs naturally decreases.

A floral diet of pollen and nectar from strawberries could have supported Some of the predators, including anthocorids and coccinellids (He et al., 2020; Holm et al., 2021). In such cases, the predators could be exposed to secondary plant compounds, which might be present in the pollen and nectar (Jacobsen and Raguso, 2018). Pollen and nectar quality can differ among genotypes, as shown for garden strawberry varieties (Ahrenfeldt et al., 2019). Finally, resistance traits may affect predator oviposition, as in the case of anthocorids, when eggs are inserted into the plant tissue. However, since the scored predators showed no significant response to the distinct levels of resistance in strawberry, such possible negative effects can be expected to be of minor importance; this suggests that the use of resistant strawberry cultivars would not have adverse effects on biocontrol.

5. Conclusions

We found that plant genotypes which are resistant against a chewing beetle *G. tenella*, also convey high levels of resistance to at least one of the aphids, the generalist species, *A.gossypii*. Such double-edged resistance traits are potentially of key importance for plant fitness in situations where plants are exposed to multiple herbivores. Most predators only responded to aphid densities. However, anthocorids and lacewings responded positively both to plant diversity and aphid numbers. These findings are first and foremost of fundamental importance as they contribute to our general understanding of the consequential roles of plant resistance and diversity have in shaping higher trophic levels. Second, they contribute to the development of a knowledge base that can be used to update new IPM concepts of *cultivar mixtures* and *resistance mixtures*, thereby providing the basis for that future plantations designs that lower pesticide dependence and increase sustainable crop production.

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Author Contribution

Nimra Musaqaf (NM) and Lene Sigsgaard (LS) conceived the idea of the study and placed it in the strawberry field designed by Johan A. Stenberg (JAS) at SLU, Alnarp. NM conducted the field scoring of aphids and predators. The data analysis was done by NM and BM. (BS). Data was interpreted by NM, LS, and BS. Manuscript was written by NM and it was substantially revised with valuable inputs of LS, JAS and BS. All co-authors have read and approved the final version of the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocontrol.2022.104919.

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