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Host availability, repulsive companion planting, and predation interact and shape how a parthenogenetic aphid population responds to a stratified ecological challenge

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Running title: Multiple bio-stressors alter aphid fitness

Abstract—Phloem-feeding insects strive to offset the disadvantageous effects of stressors to sustain their offspring and survive. Adaptive responses to environmental stress are not well understood under complex influences of companion planting, natural enemies, and host gradient. In this study, under predation by lacewing *Chrysoperla carnea* Stephens (Neuroptera: Chrysopidae), we survey the responses of green peach aphid *Myzus persicae* Sulzer (Hemiptera: Aphididae), reared on different densities of cabbage *Brassica oleracea* L. (Brassicales: Brassicaceae) to its shallot companion *Allium cepa* (L.) var. *aggregatum* G. Don (Asparagales: Amaryllidaceae). Firstly, aphid aggregative abundance was strongly influenced by shallot perturbation, predator presence and changes in cabbage-host biomass, altering aphid phenotypic plasticity. Interestingly, the shallot and predation negative impacts can be of similar magnitudes. Secondly, changes in the cabbage-host availability and biomass, especially under predation, had a strong impact on aphid traits. Our study underscores the benefits of including shallots as crop-companions in augmenting pest control, but also suggests that the outcome of coupling companion planting with natural enemies is context-dependent and thus should be empirically applied. At the confluence of ecology and agronomy, this work provides insights on how manipulated functional biodiversity may function as an alternative strategy for pestilent herbivory management in model and green-house systems.

Keywords

Shallot, cabbage, green peach aphid, lacewing, bio-stress, companion planting

Introduction

Green peach aphid *Myzus persicae* (Sulzer), a major plant-virus vector, that reproduces rapidly and explosively, causing considerable damage to many crops around the globe (Blackman and Eastop 2000; van Emden and Harrington 2007). The fitness, behaviour and virulence of this phloem-feeding insect are strongly affected by the nutritional and chemical values of its wide range of vulnerable host plants (Bell and Cardé 1984; Andow 1991). Plant chemicals can inform aphids whether specific plants may be viable hosts that are suitable for settlement and colonisation (Pickett 1992; Visser 1986; Visser and Piron 1995), or a poor choice that should be avoided (Tosh *et al.* 2003; Powell *et al.* 2006; Amarawardana *et al.* 2007; Ikeura *et al.* 2012; Parker *et al.* 2013).

Companion planting is a useful multi-purpose horticultural practice where natural processes are utilised to repel pests or disrupt their settlement and reproduction on a target crop or both (Parolin *et al.* 2012; Parker *et al.* 2013). The companion plant, inter-planted with a target crop, can have a perturbing effect on the populations of phloem-feeding crop pests like aphids, via its deterring or repellent properties (Block 2010; Parker *et al.* 2013; Claros Cuadrado *et al.* 2019), thus altering pest fitness, behaviour, and host selection (Tang *et al.* 2012). As such, the application of companion planting accentuates the effects of functional plant-plant associations (Lopes *et al.* 2015) on the population dynamics of vegetable-associated insect communities and hence may impede the outbreak of pest infestation (Vandermeer 1989; Sullivan 1998; Kuepper and Dodson 2001; Mousavi and Eskandari 2011; Claros Cuadrado *et al.* 2019), whilst conveniently providing plants that are edible by human but inedible by pest in the vicinity of vulnerable crops.

Plants from the genus *Allium* are recognised for their insect-perturbing properties (Block 2010; Parker *et al.* 2013). Few studies have evaluated the effect of growing *Allium sp.* with various vulnerable cash crops on pest control (Block 2010; Parker *et al.* 2013; Pahla *et al.* 2014). For example, intercropping systems of different ratios and mixes of cash crops and *Allium sp.* have been documented to lead to reduced aphid fitness in the mixed blocks when compared to monocultures (Mutiga *et al.* 2010; Baidoo *et al.* 2012; Pahla *et al.* 2014). Onions of the species *Allium cepa* (L.) are rich with distinctive metabolites: organosulphur volatile compounds (Block *et al.* 1992; Amarawardana *et al.* 2007) as well as glucosides and flavonoids (Block 1985; Rodrigues *et al.* 2017; Singh and Kaur 2018; Fernández-Bedmar *et al.* 2019). Specifically, shallots *Allium cepa* (L.) var. *aggregatum* (G. Don) are replete with phenolics (Lanzotti 2006; Rodrigues *et al.* 2017) and organosulphur compounds (diallyl sulfide and diallyl disulfide) (Izawa *et al.* 2010) which are shown to have insecticidal activity (Lattanzio *et al.* 2006; Plata-Rueda *et al.* 2017). These biochemicals effectively give alliaceous plants their anti-pest properties. Also, *Allium*-specific chemicals can help reduce the onset of soil-borne diseases due to their biocidal effects (Ratnadass *et al.* 2012). Contrary to sustainable ‘anti-pest’ botanical insecticides (owing to plant secondary metabolites) (Isman 2006; Mnayer *et al.* 2014; Hikal *et al.* 2017; Kasmi *et al.* 2017), conventional synthetic insecticides are usually costly, non-environmentally friendly with negative impacts on health and the environment (Larramendy and Soloneski 2014), and to which generalist pests, such as *M. persicae*, may develop resistance over time (Devonshire *et al.* 1998; Digilio *et al.* 2008). The vast array of potential host plants vulnerable to this polyphagous aphid species might have been evolutionarily associated with a conferred degree of resistance of this generalist pest to the phytotoxicity of specific target plant substances over others (Digilio *et al.* 2008).

The application of companion planting harnesses the effects of their secondary metabolites in pest control and this has been gathering increased interest in integrated aphid management (Agelopoulos *et al.* 1999; Isman 2006; Digilio *et al.* 2008; Rodriguez-Saona and Stelinski 2009; Kasmi *et al.* 2017). The regulation of pest populations, via companion planting, may depend directly on the abundance of each plant species in the culture mix (host plant abundance, in particular) (Baidoo *et al.* 2012; Khan *et al.* 2012). This may also support plant growth and improve soil quality (Wu *et al.* 2016), enhancing the properties of the target crop (Mutiga *et al.* 2010; Parker *et al.* 2013) and increasing leaf mass in culture mixes in comparison to the situation in monocultures (Pahla *et al.* 2014). However, the effects of Alliums, for example shallots *Allium cepa* (L.) var. *aggregatum* (G. Don), on the abundance linked to aggregation as well as phenotypic plasticity (production of alates) in aphids are yet to be explored and weighed against the effects of predation by aphid's natural enemies.

Along with the effects of abundance and diversity of plants available within a locale, as a bottom-up effect, the presence of natural enemies adds another layer of stress to the challenging surroundings of aphids through a top-down effect (Costamagna and Landis 2006; Xie *et al.* 2012), with evidence for species diversity to simultaneously be a cause and a consequence of resource density in plant-aphid-predator systems (Cardinale *et al.* 2006). There are various efficient predatory 'agrobionts' that feed on aphids, such as lacewing *Chrysoperla carnea* (Stephen) (van Emden and Harrington 2007), that are particularly potent in greenhouse environments (McEwen *et al.* 2001; Sarwar 2014). It is noteworthy that the "enemies hypothesis" by Root (1973) predicted that predators can be more effective at controlling a herbivore population in diverse environments than single-crop cultivation; more evidence has been accrued on the vital role of landscape complexity in aphid control (Martin *et al.* 2015). Although, the application of natural enemies and the use of companion planting have been previously explored discretely, the use of both methods simultaneously, whilst taking into account variable availability or shortage of the target crop (host plants for the pest), has not received much attention heretofore. Moreover, examining alata production, as an indicator of phenotypic plasticity, in response to combined biotic stressors, such as when the primary crop is accompanied by toxic or perturbing plant companions has not been, thus far, adequately conducted. Investigating how aphids respond to complex stress in terms of reproductive success, aggregation, and phenotypic plasticity will help examine and develop a novel genre of 'green' integrated pest management comprising aphidophagous agrobionts and companion planting. Although some research investigated the effects of garlic *Allium sativum* (L.) and onion *Allium cepa* in polyculture, as cited above, studies on the application and effects of *shallots* are thus far lacking.

In this work, we manipulate the biological stress regimes in a model agroecosystem composed of savoy cabbage *Brassica oleracea* (L.) var. sabauda, green peach aphid, and an aphidophagous predator (lacewing), with and without shallot as an aphid-perturbing companion of cabbage. Conducting two experiments, we investigate stress-driven ecological changes in the aggregative abundance and phenotypic plasticity (via the production of dispersive winged morphs), on a single clone of the generalist aphid *Myzus persicae*. In the first experiment, the applied stress comprised predation by lacewing, or perturbation by variable shallot density relative to cabbage (host plant), or the combination of these two stressors. The second experiment entailed stress by the predator (lacewing) on different host-plant densities. General comparisons of the outputs of both experiments are also drawn in terms of aphid response to complex biological stress. We raise and answer the following questions:

1. With and without a predator, does shallot companionship with cabbage, alter aphid abundance, aggregation and the production of dispersive morphs within the microcosm, as a result of escalating shallot perturbation and different availability of consequent cabbage biomass?
2. With and without a predator, in the shallot-free contexts, does decreasing cabbage density alter the abundance of aphids and the production of dispersive morphs, subject to different availability of consequent cabbage biomass?
3. How does the parthenogenetic aphid population respond to elevated complex biological stress caused by active predation, escalated shallot perturbation, changing host biomass, and declining host availability?

Materials and Methods

Study organisms, set-up, measured traits, and statistical analysis

One green clone of *M. persicae* from a sample provided by JKI (Julius Kühn-Institut, Berlin), was raised for four months on kale *Brassica oleracea* (L.) var. Acephala under controlled conditions (light cycle of 16h light and 8h night, and 22 – 24°C) in a greenhouse at the Freie Universität Berlin, Germany. We used savoy cabbage cultivar (Vertus 2), ordered from Sperli seed company, Germany, as the experimental host plant. We also employed shallots, purchased from a local store, Berlin, Germany, as companions of the cabbage primary model plant.

In order to create differential host availability and various ratios of cabbage (host plant) or cabbage to yellow shallot (companion with insect-perturbing properties), different numbers of cabbage seeds with shallots were sown in plastic pots (13 cm height and 15cm in diameter) filled with steam-sterilised soil. In *Experiment I*, the plants were grown diagonally at opposing corners 1 cm away from the pot ridge. This was done universally in each repeat. In *Experiment II*, where certain pots contained less than four host plants, they were arranged in the same way but with the position of the missing plant/s left vacant. A light plastic frame was attached to each pot to hold a cylindrical fine-mesh sleeve (70-cm height, 20-cm width), that enclosed each microcosm, upright. The microcosms were placed apart from each other on individual trays in the greenhouse to minimise plant aerial communication and they were watered every other day. After 17 days of cabbage germination, 24 early nymphs of *M. persicae* were released into the middle of each pot using a fine wet brush. Lacewing larvae were ordered from a biocontrol firm (Sautter & Stepper, Germany); a 2nd instar was randomly selected and added to each of the relevant microcosms approximately 1 hour after the introduction of aphids, to ensure the aphids had made their host-plant choice.

We conducted the study as two synchronised experiments. In total we applied 7 different environments, with and without predator presence, resulting in 14 treatments and a total number of 87 microcosms (48 for *Experiment I*, and 39 for *Experiment II*), as detailed below; see also (Table S1) for further specifications. Data collection took place 13 days after the introduction of aphids and lacewing larvae. We recorded total aphid numbers (*i.e.*, aggregative abundance, hereafter) according to the distribution of aphid densities within the microcosm (off-plants and on-plant: leaf upper- and downsides, and stems), aphid dispersion, as a proxy for phenotypic plasticity, by counting the number of alates (winged aphids), and the dry biomass of savoy cabbage (the host plant). At the end of the experiment, the cabbage plants were collected, washed, dried, and then oven-dried for 48h (50°C), before being weighed; subsequently, we calculated the pooled mean (grand mean) of the cabbage plants in the microcosm.

Experiment I: Effects of elevated shallot perturbation, predator presence, and changes in host-plant biomass

The predictors were: 1) Perturbation (the ratio of the number of shallots to the number of savoy cabbage plants present in the microcosm); a categorical contextual variable ranging from 0% Shallot (shallot-free optimal microcosm of 4 cabbage plants as the reference frame), 25% Shallot (1 Shallot:3 Cabbage), 50% Shallot (2 Shallot:2 Cabbage), to 75% Shallot (3 Shallot:1 Cabbage as the most perturbing as well as the least nourishing context). 2) Predator presence: A categorical variable (0, 1), 3) Plant dry biomass (PDB, hereafter): The calculated pooled mean of the dry biomass of the cabbage hosts in the microcosm; a continuous numerical variable representing plant well-being and the food available for aphids in the microcosm; PDB was used as a covariate to add further precision to the examination of the tested aphid traits across treatments. 4) All possible interactions between the predictors.

Experiment II: Effects of decreasing host-plant availability, predator presence, and changes in host-plant biomass

The predictors were: 1`) Host plant availability (HPA): A categorical contextual variable of four levels representing the number of cabbage plants available in the microcosm comprising 4-Cabbage hosts (the optimal context and reference frame), 3-Cabbage hosts, 2-Cabbage hosts, or 1-Cabbage host (the least hospitable and nourishing context). 2`) Predator presence (*vide supra*). 3`) PDB (*vide supra*). 4`) All possible interactions between the predictors.

For the statistical analysis, we used RStudio (RStudio Team 2016). The following traits were investigated per experiment, where the explanatory variables were (1-4) and (1`-4`) in *Experiment I* and *Experiment II*, respectively. The following aphid traits were measured and tested as response variables to the aforementioned predictors:

Aphid aggregative abundance and dispersion

Aphids were counted on a spatially fine-scale, as described above. This made a quaternary response variable that links aphid reproductive success logistically with aphid plant-colonising propensities in the microcosm. This established method provides valuable information on aphid utilisation of space and biotic environment (*i.e.*, their host plants where they reside, aggregate, feed, and reproduce). Hence, this response variable, termed aggregative aphid abundance, was tested using a vectorised generalised linear model (vGLM), per experiment, with a multinomial family, R package VGAM (Yee 2015, Yee 2017). The main effects of the output of this multinomial logistic regression model were displayed thereof using an Anova function (Analysis of Deviance, Type II test; predictors are tested irrespective of the order they are listed in the model), R package car (Fox and Weisberg 2011).

Also, a generalised linear model (GLM) was used, per experiment, with a quasi-Poisson family (due to over-dispersion and non-normal data distribution; typical of aphid count data), R package multcomp (Hothorn *et al.* 2008), to test the fractions of produced alates in relation to the total aphid numbers in the microcosm, serving as a proxy for polyphenism (distinct phenotypic plasticity). The main effects of the regression model were displayed using the Anova function.

Results

Aphid aggregative abundance and dispersion

Experiment I: Effects escalated shallot perturbation, predator presence, and PDB

The majority of aphids resided below leaves especially under predation, in two contexts 50% Shallot (2 Shallot:2 Cabbage) and 75% Shallot (3 Shallot:1 Cabbage), where the aphid population experienced active predation by lacewing and elevated perturbation by the shallots. The propensity to abandon the host plant was the clearest in the 75% Shallot context (without predator) where PDB was the smallest (ranking 8th), (Fig. 1). Aggregation above leaves was fairly consistent across contexts, with and without predation, but there was less tendency to dwell on the exposed uppersides of the leaves, under predation, within the 75% Shallot and 50% Shallot contexts. Also, in the presence of the predator, across all contexts, the aphid population appeared to be more risk-averse as the stems were clearly less populated (more exposure to predation here compared to leaf undersides) and the propensity of aphids to leave the host plant was less apparent, (Fig. 1). Noticeably, the proportions of aphids on plant shoot parts in the 25% Shallot context (with predator) was a little larger than the combined whole populations of the 75% Shallot context without predator (4th PDB rank) and with a predator (8th PDB rank).

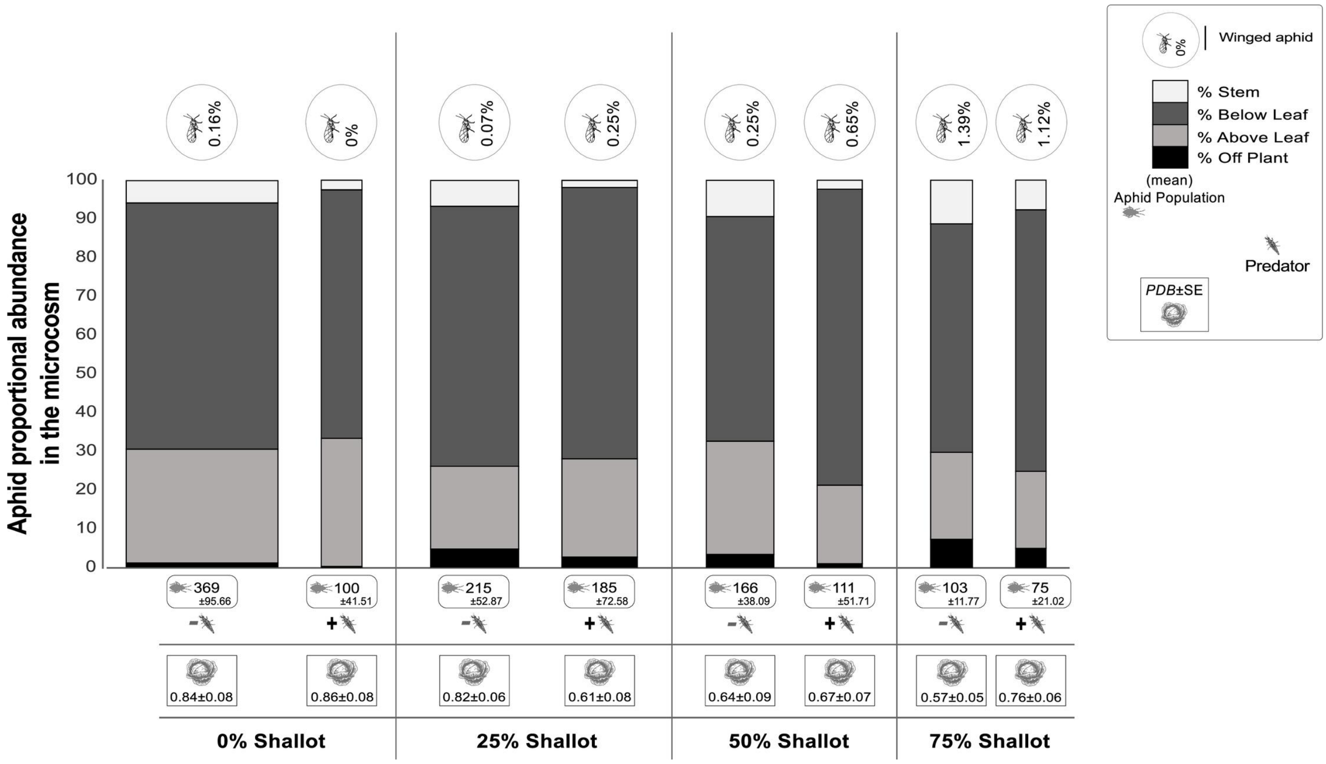

Fig. 1. Experiment I, aphid aggregative abundance. The bars are proportionate in width representing aphid numerical success as aggregative abundance (mean of total numbers in the microcosm per treatment at the end of the experiment ± SE); the different proportions of aphid aggregation/spatial distribution on- and off-plant are presented in grades of grey and all bar stacks are proportional. The left bars per treatment illustrates aphid aggregative abundance in absence of lacewing larva (*i.e.,* aphids alone without predation); whereas the right bar details aphid abundance in the presence of lacewing larva (*i.e.,* with predation). The respective encircled percentages at the end of the bars refer to the average proportions of winged aphids (dispersive morphs). The abbreviations for the different treatment lines (ecological contexts) are centred and displayed in bold. This included the contexts of *0 shallots to 4 cabbage hosts* (0% Shallot), *1 shallot to 3 cabbage hosts* (25% Shallot), *2 shallots to 2 cabbage hosts* (50% Shallot), and *3 shallots to 1 cabbage host* (75% Shallot). The overall average plant dry biomass (PDB±SE) per treatment is shown below the bars in rectangles. In total, we applied 4 different environments, with and without predator presence, resulting in 48 microcosms (8 treatments x 6 replicates).

Contrasting aphid abundance, *within context and subject to predation*, shows that for the context 75% Shallot, the abundance was ~27% smaller (with 33% larger PDB) than when the predator was absent; for the context 50% Shallot, the abundance was ~33% smaller (with 5% larger PDB); for the context 25% Shallot, the abundance was ~14% smaller (with 26% *smaller* PDB). Whereas, in the optimal shallot-free context, 0% Shallot, a stark change can be seen in aphid abundance, as the predator led to a population that was ~ 73% smaller (with 2% larger PDB) than the observations in predator absence. As such, the control of aphid population, under elevated shallot perturbation, was considerably better when the predator was present in the microcosm, especially in the 50% Shallot context, suggestive of synergistic interactions of the two stressors; Supplementary Material (Table S2). Also, by and large, there was more cabbage biomass in the presence of the predator than in its absence except in the context 25% Shallot, (Fig. 1), and Supplementary Material (Table S2) for further drawn contrasts. This suggests context-dependent additive suppressive effects of predation and escalated shallot perturbation on the aphid population.

Clearly, there was greater cabbage mass, when the predator was present, as the rates of increase in PDB and decrease in aphid abundance were more pronounced where more shallots were present in the microcosm, in the contrasts (75% Shallot *versus* 25% Shallot) and (50% Shallot *versus* 25% Shallot); see Supplementary Material (Table S2) for further contrasts with relation to the predator-exposed microcosms. Our findings, therefore, indicate that combining predation with shallot perturbation, as means of integrated pest management, is generally beneficial for the crop in question. See Supplementary Material (Table S2) and *Note 1*, for extra information and further contrasts.

Further inferential analysis supports the descriptive statistics displayed above as aphid abundance in the microcosm was significantly influenced by shallot perturbation ($F_{(9,96)}=13.67$; $P<0.0001$), predator presence ($F_{(3,96)}=13.87$; $P<0.0001$), and PDB ($F_{(3,96)}=5.28$; $P=0.002$). Aphid abundance was also significantly influenced by the interaction between shallot perturbation and predator presence ($F_{(9,96)}=6.74$; $P<0.0001$), the interaction between shallot perturbation and PDB ($F_{(9,96)}=3.52$; $P=0.0008$), the interaction between predator presence and PDB ($F_{(3,96)}=3.8$; $P=0.013$), and by the three-way interaction between shallot perturbation, predator presence and PDB ($F_{(9,96)}=2.56$; $P=0.011$), (Fig. 1). Furthermore, we also examined the effects of shallot and predator presence and their interaction on host-plant dry biomass and found no significant effects; see Supplementary Material (Table S3) for details.

As for aphid dispersion, the production of winged morphs was only significantly influenced by the perturbation effect of the shallot ($F_{(3,32)}=6.42$; $P=0.0002$), (Fig. 1) and Supplementary Material (Table S4). *Myzus persicae* was induced to produce more winged offspring with increasing shallot density (elevated perturbation). We, however, attribute the noticeable proportion of the winged morphs in the shallot and predator-free microcosm to a crowding effect therein.

Within context and under elevated shallot perturbation, clearly, the proportions of alates were larger in the presence (than the absence of predator) except for the case of 75% Shallot (alata production was ~ 0.27 percent smaller under predation, concomitant with low aphid abundance and the 4th largest PDB). The differences in alata proportions were the largest in the context 25% Shallot (~3.57 times bigger alata production under predation), followed by the context 50% (2.6 times bigger alata production under predation).

Relatively, contrasting the shallot-perturbed contexts (without predation) reveals that the sharpest difference (~19.86 times bigger alata production) observed when contrasting the context 75% Shallot with the context 25% Shallot; there was only 5.56 times bigger alata production when comparing the context 75% Shallot with the context 50% Shallot. Concurrently, the decrease in PDB and aphid abundance was the strongest with respect to the contrast (75% Shallot *versus* 25% Shallot). On the flip side, under predation, the sharpest difference (4.48 times bigger alata production) is shown when comparing the 75% Shallot and the 25% Shallot contexts; there was only ~1.72 times bigger alata production when comparing the contexts 75% Shallot and 50% Shallot. It is interesting that across contexts, the increase in PDB and the decrease in aphid abundance was the strongest in the contrast (75% Shallot *versus* 25% Shallot) when the predator was present, Supplementary Material (Table S2). Nevertheless, alata production was identical in the context 25% Shallot (*with* predator) and 50% Shallot (*without* predator), with semi-identical PDB values and close aphid abundances.

Experiment II: Effects of decreasing host plant availability, predator presence, and PDB

Aphids tended to populate the areas below leaves more than they did for other shoot parts, but the proportions below leaves were smaller under predation than in the predator-free microcosms. Generally, the propensity to abandon the host plant was remarkably low under predation. By contrast, in predator absence, in the 3-Cabbage context (with PDB of the 5th rank) and the 2-Cabbage context (with PDB of the 3rd rank), overpopulation led to noticeable off-plant aphid proportions. But, in the 3-Cabbage context, when the predator was present, the abundance was nearly 13.53 times smaller, co-occurring with a PDB of the 4th rank. There, aphids abandoned the stem and colonised the leaf (more abundant on leaf uppersides than without predation); the proportions off plant, almost identical to the case without predation, but were possibly induced by fear of predation rather than crowding. Other notable examples were: Aphids proportions below leaf in the 2-Cabbage context (without the predator, having the 3rd largest PDB) was nearly the size of the entire aphid population of the 1-Cabbage context (with the predator, having the largest PDB). Moreover, the population on both sides of the leaf in the 3-Cabbage context (without predator, having the 5th PDB rank) was almost more than 2.2 times the size of the combined whole populations of the 4-Cabbage context, without predator (8th PDB rank) and with predator (6th PDB rank), (Fig. 2) and Supplementary Material (Table S5).

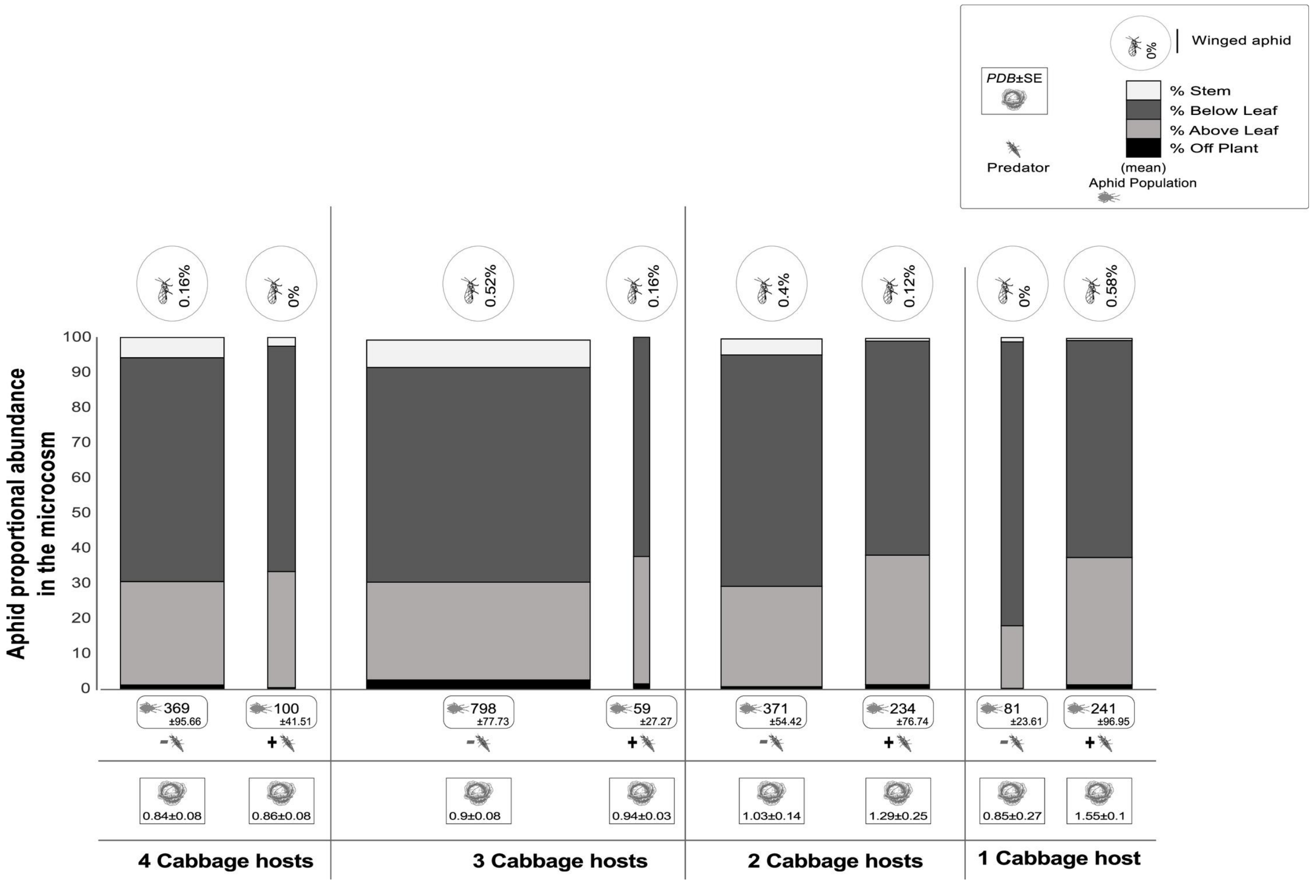

Fig. 2. Experiment II, aphid aggregative abundance. The bars are proportionate in width representing aphid numerical success as aggregative abundance (mean of total numbers in the microcosm per treatment at the end of the experiment ± SE); the different proportions of aphid aggregation/spatial distribution on- and off-plant are presented in grades of grey and all bar stacks are proportional. The left bars per treatment illustrates aphid aggregative abundance in absence of lacewing larva (*i.e.,* aphids alone without predation); whereas the right bar details aphid abundance in the presence of lacewing larva (*i.e.,* with predation). The respective encircled percentages at the end of the bars refer to the average proportions of winged aphids (dispersive morphs). The abbreviations for the different 8 treatment lines (ecological contexts) are centred and displayed in bold. This included the contexts of *4 cabbage hosts* (6 replicates with predator, 6 replicates without predator), *3 cabbage hosts* (5 replicates with predator, 4 replicates without predator), *2 cabbage hosts* (4 replicates with predator, 5 replicates without predator), and *1 cabbage host* (4 replicates with predator, 5 replicates without predator). The overall average plant dry biomass (PDB±SE) per treatment is shown below the bars in rectangles. In total, we applied 4 different environments, with and without predator presence, resulting in 39 microcosms.

Contrasting aphid abundance *within context and subject to predation* shows that in the 1-Cabbage context, the abundance was ~197% larger (with 82% larger PDB) than when the predator was absent; in the 2-Cabbage context, the abundance was ~37% smaller (with 25% larger PDB); in the 3-Cabbage context, the abundance was ~93% smaller (with 4% larger PDB). Whereas, in the optimal context (4 Cabbage), the predator led to a population that was ~73% smaller (with 2% larger PDB); the change in aphid abundance, with and without predator, was not far a difference from the observation in the 3-Cabbage context (but was contrary to the case in the 1-Cabbage context having more aphids with predator than without it). As such, the control of aphid abundance by the predator was the most effective in the 3-Cabbage context, followed by the 4-Cabbage then the 2-Cabbage contexts, as the predator performed poorly in the 1-Cabbage context.

It should be pointed out that the aphid population showed the most abundance and PDB difference, between the presence of the predator and its absence, in the 4-Cabbage and the 3-Cabbage contexts (negative impact on the aphid population), followed, by the 1-Cabbage context (unexpectedly, positive impact on the aphid population). However, in the microcosms having less than 4 cabbages, contrary to the pattern under predation, the aphid population was generally less abundant, when the predator was absent concurring with decreasing availability of the cabbage host. Furthermore, PDB was universally increasing by decreasing host availability, under predation, as aphids were always less abundant when there was more than 1 cabbage host in the microcosm. This suggests context-dependent suppressive effects of the employed stressors (decreased host availability and predation) on the aphid population, (Fig. 2); see also Supplementary Material (Table S5) and *Note 2* and (Table S5) for extra information and further contrasts when the predator was present in the microcosm.

Inferential analysis supports the descriptive statistics as aphid abundance in the microcosm was significantly influenced by the number of host plants available ($F_{(22,69)}$=5.06.67; P<0.0001), by predator presence ($F_{(11,69)}$=8.7; P<0.0001), and by plant dry biomass in the microcosm ($F_{(12,69)}$=6.05; P<0.0001). Aphid abundance was also significantly influenced by the interaction between host availability and predator presence (F($_{(10,69)}$=2.79; P=0.006), the interaction between plant dry biomass and host availability ($F_{(11,69)}$=4.83; P<0.0001), the interaction between plant dry biomass and predator presence ($F_{(4,69)}$=3.84; P=0.007), and by the three-way interaction between host availability, plant dry biomass, and predator presence ($F_{(9,69)}$=4.34; P=0.0002), (Fig. 2). We also examined the effects of shallot and predator presence and their interaction on host-plant dry biomass and only found the predator presence effect to be significant ($F_{(1,31)}$=4.2; P=0.049), Supplementary Material (Table S6).

As for aphid dispersion, the production of winged morphs was significantly influenced by host-plant dry biomass ($F_{(1,23)}$=10.87; P=0.003). However, the effect of the number of host plants available in the microcosm was marginally significant ($F_{(3,23)}$=2.95; p=0.054). The interaction between host plant dry biomass and predator presence was highly significant ($F_{(3,23)}$=9.13; P=0.006). So was the interaction between host availability and predator presence ($F_{(3,23)}$=9.52; P=0.0003), (Fig. 2) and Supplementary Material (Table 7).

The largest proportion of the morphs was found in the 1-Cabbage context (with predator); note that, in this case, the highest PDB was also observed. This was followed by the 3-Cabbage context (without predator) where the 5th largest PDB was detected. The smallest proportions of the morphs were recorded in the contexts of 4-Cabbage (with predator) and 1-Cabbage (without predator). The sharpest within-context differences, with and without the predator, was seen in the context 1-Cabbage (58 percent difference) and 3-Cabbage (36 percent difference). Interestingly, there was an identical production of winged offspring of 0.16% in the optimal 4-Cabbage context (without predator) and the 3-Cabbages context (with predator), despite the considerable difference in aphid abundance (far more larger population in the former) and PDB (larger in the latter), (Fig. 2). The noticeable proportion of the morphs in the shallot-free microcosm is attributable to a crowding effect in the absence of predation. See (Fig. 2) and Supplementary Material *Note 2*, for extra information and further contrasts.

Comparing the outputs of Experiments I and II

Useful comparisons can be drawn from the two parts of this work based on the stipulation that for each of the contexts with 1-3 cabbage hosts the challenge, from an aphid's position, comprised an added single stressor (shallot or predator) or combined stressors (shallot and predator) to the cabbage embedding context with declining host availability.

The population-diminishing effect of predation was stronger than the effect of shallot perturbation only when 3 cabbage hosts where available. Further, the total effect of the combined stressors was more population-diminishing than the effect of every single stressor when only 1or 2 cabbage hosts were available in the microcosm. By contrast, the effect of the combined stressors was only stronger than the shallot perturbation effect in the context having 3 cabbage hosts, (Table 1) and Supplementary Material (Fig. S1), (Fig. S2), and (Table S8). Aphid abundance values were intriguingly close under predation as well as under combined stress when 1 or 2 cabbage hosts were available (Table 1), (Fig. S1), and (Fig. S2). Overall, the lowest value of abundance was recorded under combined stress on the 1-Cabbage context where the second-highest propensity to produce alates was notable. Further, the largest production of alates was under combined stress in the 2-Cabbage and 3-Cabbage contexts but under the shallot effect only in the 2-Cabbage context. By contrast, the smallest alata production was under predation in the contexts of 1 or 2 cabbage hosts, but under shallot effect only in the context of 3 cabbage hosts. As such, there were fewer alates under predation than under shallot effect in two contexts only (2-Cabbage and 1-Cabbage), (Table 1) and Supplementary Material (Table S9), (Fig. S1) and (Fig. S2).

Context-wise, PDB was always the best under predation, when 1 cabbage host was present, even when compared to the respective controls (predator-shallot-free microcosms). PDB was universally better under the shallot effect; PDB was the smallest in shallot presence when 1 or 2 cabbage hosts were present; PDB was the smallest under the shallot and predation effects in the context of 3 cabbage hosts, (Table 1) and Supplementary Material *Note 3,* (Table S10), (Fig. S1), and (Fig. S2).

All in all, a trade-off between curbed aphid abundance and decreased PDB (due to plant-plant space-sharing effect) to the overall advantage of the cabbage host is readable because lower aphid density equates with lesser infestation risk for the target crop.

Discussion

Using a model agro-ecosystem, we demonstrated a differential aphid response in terms of reproduction and phenotypic plasticity (alata production) against a challenging stratified ecological context. The latter was characterised either by changing host biomass, increasing perturbation by shallot or decreasing host plant availability, with and without predator presence. The parthenogenetic aphid population showed spatially distinct abundances in the microcosm with deferential dispersive propensities.

On shallot perturbation and predation as stressors of the aphid pest

In the first experiment, the stress in the embedding context was twofold: (1) host availability shortage accompanied by increasing shallot presence, and (2) predation. The first stressor is complex as it challenged aphids on two fronts: decreasing microhabitats, which are essential sites for aggregation, feeding and reproduction, with increasing hostile non-host density. This can alter the above-below-ground conditions to the benefit of the target crop (Mutiga *et al.* 2010; Xiao *et al.* 2013; Ehrmann and Ritz 2014); this also may negatively impact aphids due to the toxic nature of the companion plant's chemicals to aphids (Hori and Harada 1995; Block 2010; Mutiga *et al.* 2010; Baidoo *et al.* 2012; Parker *et al.* 2013), thus depriving aphids from adequate host availability absolutely necessary for their constant need of amino acids and shelter. Our results show that the more companion shallots were present in the microcosm, the fewer aphids there were across contexts, suggesting a clear negative effect of this stress in terms of challenging the otherwise exponential population growth of the aphid population. This receives support from the "resource concentration hypothesis", sensu Root (1973), on a context-dependent basis (Grez and Gonzales 1995), predicting that the abundance of phytophagous insects may decrease in areas where there is a lower concentration of preferred host plants. Aphids' biotic environment not only affects their reproductive success but also their aggregation (Turchin and Kareiva 1989) and dispersion (Weisser *et al.* 1999). The regulation of aphid populations, via companion planting, may also depend directly on the abundance of each plant species in the culture mix, host plant abundance in particular (Baidoo *et al.* 2012; Khan *et al.* 2012). The application of companion planting, therefore, extends the effects of functional plant diversity (Lopes *et al.* 2015) leading to tangible control of pest infestation and plant disease (Vandermeer 1989; Sullivan 1998; Kuepper and Dodson 2001; Mousavi and Eskandari 2011; Tang *et* *al.* 2012). This also may result in enhancement of host-plant properties (Mutiga *et al.* 2010) and increasing leaf mass in mix plantings in comparison to one-crop plantings (Pahla *et al.* 2014).

The second stressor, *i.e.*, predation, led, in this study, to diminished aphid population as the predator effect was obvious within each context and across the contexts, but with variable magnitudes, where shallot/s made companionship of the cabbage host/s. The largest population decline between being without predator and with predator was in the 50% Shallot context (2 cabbage hosts with 2 shallot companions) opposed to the least suppression in the 25% Shallot context (3 cabbage hosts with 1 shallot companion). In other words, the increased density of the shallot being hampering of aphid reproduction, without predation, continued to perturb aphid without interfering with the predator biocontrol efficiency in the 50% and 75% Shallot contexts. This suggests a degree of synergism between the effects of shallot and predation. However, since this was not the case when only one shallot accompanied three cabbage hosts, it can be inferred that for the manipulated functional diversity in the crop-companion-predator assembly to work with maximum success, it would be required to establish a certain adequate minimum of companionship densities in the micro-habitat.

Our findings suggest that higher shallot densities did escalate the status of aphid perturbation. That, in turn, interfered with the clarity of chemical cues emitted by the cabbage host owing to the discouraging nourishment and repulsive qualities of *Allium sp.* (Block 2010; Parker *et al.* 2013). To discern a potential environment as suitable for feeding and colonisation, *M. persicae* requires certain cues to process different sensory inputs out of the surroundings (Ben-Ari and Inbar 2014). This will always be challenged with various changes in the ecological context wherein the aphid population exists (Dixon 1998; van Emden and Harrington 2007; Ben-Ari and Inbar 2014; Martin *et al.* 2015; Vilcinskas 2016). The chemistry of the phloem of *Allium*/shallot and the olfactory cues they emit can be harmful to a vast array of aphids, including green peach aphid (Hori 1996); a cocktail of attracting/arresting cues (emitted by the cabbage host) and repulsive cues (produced by the shallot) might have created volatile chemical uncertainty (Ben-Ari and Inbar 2014) and inconsistency in host suitability (Scriber 1984). This cue mix underlain by plant-plant interaction between the crop and its companion is expected to affect organisms and their interactions in such manipulated species assemblages (van Emden 1995; Verkerk *et al.* 1998).

It should be underlined that in this part of the study aphid dispersion, within context, was more induced under the combined stress of shallot perturbation and predation than under the shallot perturbation alone, when there were less than three shallots in the microcosm. Winged morph production is considered to be a discrete plastic response (polyphenism) to challenging environments, which is regulated maternally to increase their progenies dispersion in order to survive on safer more palatable (or suitable) provisions elsewhere (Lombaert *et al.* 2006; van Emden and Harrington 2007). It is interesting, however, that in the most hostile context (three shallots to one cabbage host) there were more dispersive aphids due to induction by the shallot effect than predation effect. This can also be attributed to a combination of larger aphid population, poorer PDB, and more aphid spread-out aggregative abundance along with off-plant wandering (predator-threat lacking) attempting to escape the increased hostility of the elevated shallot density and perturbation in this context. At any rate, the proportions of alates, with and without the predator, within the said context are not far apart. One can speculate that perturbation by companion plants (shallot in our example) may negatively impact aphid population and ecology through the following consociated functional mechanisms that may severally or collectively alter aphid behaviour, reproduction and survival:

1- Physical mechanism: The companion planting creates a physical barrier obstructing pest mobility and thus the spread of pathogens they carry (Parolin *et al.* 2012; Ratnadass *et al.* 2012).

2- Chemical mechanisms through a) interference of companion-specific chemicals with the reception and perception of aphid pheromones (and perhaps predator kairomones, as well) emanating in the vicinity of the clone under sub-optimal/sub-lethal conditions (Tsao and Coats 1995; Digilio *et al.* 2008). b) mimicking aphid pheromones due to chemical similarity between specific companion plant's volatiles and alarm pheromones of dispersal, causing aphid populations to invest more in the alates which are energetically costly and moderately fecund yet dispersive (Kasmi *et al.* 2017). c) interference of the companion chemicals with the reception and perception of host plant cues and thus disrupting aphid feeding behaviour and plant settlement (Hori 1996; Ninkovic *et al.* 2013; Ben-Issa *et al.* 2017; Kasmi *et al.* 2017). d) interference of the companion's non-volatiles (*e.g.*, saponins) with the ingestion of the imbibed phloem (Koul 2008; Ben-Issa *et al.* 2017). e) aerial and below-ground communication between the plant neighbours (host [hospitable] and companion [hostile]) which alters the aphid-embedding context making it more uncertain and/or disturbing (Law and Regnier 1971; Ninkovic *et al.* 2013; Ben-Issa *et al.* 2017; Elhakeem *et al.* 2018; Kalske *et al.* 2019); this can be envisioned to occur in a trait-mediated fashion appertaining to the interaction between the metabolites and the microbiomes of both plants, as the companion plant might lead to quality changes in the shared microhabitat and in the accompanied crop (Wu *et al.* 2016; Ben-Issa *et al.* 2017; Khudr *et al.* 2018; Nordkvist *et al.* 2019).

Any injury in the tissue of the shallots, including haphazard aphid probing by stylets, will trigger the release of the defensive repelling volatiles (Sulvai *et al.* 2016); a process that adds an extra negative spin to the hostile environment of the pest through direct effect and indirectly through plant-plant communication (Karban *et al.* 2014; Kalske *et al.* 2019). We note, however, that the bioactive constituents of *Allium sp.* (Arand and Arand 1998; Nicastro *et al.* 2015) may have similar toxic and inhibitory effects of plant settlement, ontogeny, and reproduction in aphids (Hori and Harada 1995; Hori 1996), when compared to other components of plants from other families (such as Lamiaceae) (Hori 1999a; Digilio *et al.* 2008; Kasmi *et al.* 2017); however, *Allium*'s antifeedant effects may be comparatively weaker (Hori 1996; Hori 1999a; Digilio *et al.* 2008; Kasmi *et al.* 2017), but see (Simmonds *et al.* 1992).

The aphid pest versus host shortage under predation

In the second experiment, the embedding context entailed stress as per host availability shortage (with and without predator presence). The parthenogenetic aphid population showed different abundances contingent on the embedding context; the availability of only 1 cabbage severely impacted the population, although PDB therein was interestingly as much as the PDB of the optimal context of 4 cabbage hosts where aphids were considerably more abundant. On the contrary, the availability of 3 cabbage hosts greatly boosted the population, although PDB therein was notably less than the PDB of the context of 2 cabbage hosts where the aphid population was comparatively more than halved. As such, in this case, host density rather than PDB, was the decisive factor in curbing aphid abundance.

Predator presence strongly suppressed the aphid population in all contexts having 2 or more cabbage hosts. The predator impact on aphid population sizes varied in magnitude: 3 cabbage hosts > 4 cabbage hosts > 2 cabbage hosts. This outcome is generally in line with the reports on the efficacy of lacewing as a biocontrol agent of aphids in greenhouse settings (McEwen *et al.* 2001; van Emden and Harrington 2007; Sarwar 2014). However, the unexpectedly thriving aphid population where a single cabbage host was available, also associated with the highest PDB value, can be explained by induced changes in clonal *aggregation* in the microcosm. This evolved collective defensive trait of inclusive fitness (*e.g.*, Hartbauer 2010; Muratori *et al.* 2014) manifested, in this work, in densely populated spots on the leaf sides of the only host available that, in turn, fortified the clone chances against the lacewing singling out vulnerable individuals. However, holistically, the population suppression in the said context was nearly of the same magnitude as in the 2-Cabbage context, as opposed to the pattern seen in the contrast 4-Cabbage *versus* 3-Cabbage. This implies that the lacewing may be more efficient when multiple choices of hosts are available to aphids because more hosts equate with more spread through the resource and hence corresponds with more wandering aphids and less densely occupied plant spots making those easier targets for the predator. It may be mentioned here that according to the “enemies hypothesis”, Root (1973), predators can be more effective at controlling a herbivore population in diverse environments.

The induction of the dispersive morph may be caused by crowdedness (Müller *et al.* 2001; van Emden and Harrington 2007; Mehrparvar *et al.* 2013), the presence of natural enemies (Mondor *et al.* 2004), and also, especially for *M. persicae*, by changes in host quality as it has been reported that nutrition plays a considerable role in the induction of polyphenism (Müller *et al.* 2001; Martínez and Costamagna 2018). There were generally larger proportions of alates in more populated microcosms in our study. For instance, when only one cabbage plant was available aphids adjusted their reproduction rather than investing in dispersion. The smaller size of the aphid population therein did not make a sufficient trigger for the production of the more energetically costly winged morphs (Dixon 1998). Comparatively, when 3 host plants were available, in the absence of any other stressors, overcrowding occurred; most aphids aggregated on the most nutritive surfaces (*i.e.*, below leaves) but also occupied more of the stems, which we consider to be the main reason for the higher percentage of the dispersive morphs and the abandonment of host plant found therein. Whereas, the noticeable proportions of alates, in less populated microcosms when the predator was present, could be the result of induction by predator-borne cues (Kats and Dill 1998; Baranowski and Preisser 2018) in contact with or close to aphid aggregates as well as aphid alarm pheromones resulting from the perception of predator presence and consumption of kin clonal aphids (Mehrparvar *et al.* 2013; Hettyey *et al.* 2015; Hermann and Landis 2018), and/or perhaps indirectly through interaction with clone members that were in direct contact with predator cues (Haapakoski *et al.* 2018).

Complex biotic stress against the aphid pest

Our findings suggest that it may be rewarding to adopt a perspective that engineers the ecological challenge against the aphid population as being composed of different levels of bio-stress that spans a single stressor (shallot [non-host, toxic, and repellent], or lacewing [predator]) to the combination of these stressors. This is because such an angle provides a toolkit to aid in gaining further insights on the performance and dynamics of the model aphid-plant system in question, which can be otherwise more difficult to glean. For instance, across contexts, the diminishing of aphid population intensified from the contexts of 1 cabbage host to 3 cabbage hosts under shallot perturbation and also under the combined stress (predation and shallot perturbation), but not under predation on its own. By that token, from having 1 cabbage hosts to having 3, PDB decreased under predation; but increased under shallot effect and combined stress. Moreover, when stress was strong (75% Shallot), under combined stress, with increasing ecological challenge and generally decreasing PDB, the aphid population was generally investing more in energetically costly polyphenism (an escape tactic) rather than reproduction; the reason behind the considerable alata production in the stress-free 2-Cabbage context was simply overpopulation in the absence of the extrinsic stressors. However, that the only case where there were fewer alates under shallot perturbation than under predation was when 1 cabbage host only was available in the microcosm.

Our findings also reveal that, albeit having an apparent loss in cabbage PDB due to soil-sharing with the shallot, it may be more beneficial for the cabbage to be surrounded by shallots than cabbages because the heterospecific companion always led, in every predator-free context involving the shallot, to a reduced aphid abundance significantly less than the abundance accumulated in the 4-Cabbage context. However, the addition of the lacewing predator to the shallot companion resulted in different patterns with aphid abundance surpassing the abundance in the 4-Cabbage optimum in two contexts where 2 or more cabbage hosts were accompanied by the shallots. But still, combining the stressors was always better in diminishing the aphid population, within each context, than when the shallot stressor was employed alone.

Our findings support the suggestion that companion planting, as a utilisable botanical insecticide, helps negatively affect the target pest with minimal impacts on the pest's natural enemies (Hikal *et al.* 2017; Tembo *et al.* 2018) and even with a potential for enhancement of the pest control by natural enemies (Amoabeng *et al.* 2019). The latter might vary by context and stress conditions or combinations. The bioactive substances of Alliums have been demonstrated to be insecticidal and to inhibit plant settlement in aphids (Hori and Harada 1995; Hori 1996; Ikeura *et al.* 2012). But, Hori (1999b) proposed that polyphagous aphids, such as *M. persicae*, might depend more on visual than olfactory cues to find their host plants. As such, the described far-reaching effects of shallot volatiles may be less effective in preventing aphids from finding their host plants. In other words, influenced by host proximity (Ikeura 2014), generalist aphids may use non-hosts odours as cues to avoid and resort to detect their hosts more visually (Hori 1999b) and/or gustatory following phloem probing (Lattanzio *et al.* 2006). However, surely the alliaceous companion's bio-chemicals are effective in significantly perturbing the aphids via disruption, repellency or deterrence (Hori 1996; Amarawardana *et al.* 2007).

On the whole, the shallot companion may entail a degree of negative neighbourhood effect on the accompanied crop but at the same time it offers a pay-off as the companion can act as a facilitator (de Haan and Vasseur 2014) and a conferred line of defence against the crop pest. This is in harmony with the results provided by Underwood (2009), who suggested that the average habitat quality (*i.e.*, plant dry biomass) and habitat variance (*i.e.,* different number of host plants) could have a notable impact on insect population dynamics. Further, shallots are quite similar to common onions but they are smaller in size and their volatiles are less pungent (Nicastro *et al.* 2015). Also, unlike onions which would require more space and resources to grow as companions of other vegetables, shallots bring about the alliaceous anti-pest effects yet with a less competitive nature for space with the target vegetable crop. In this vein, our work also draws on the knowledge and common practice that the perturbing effects of the companion plant are the most efficient when it is in close proximity to the accompanied target crop (Visser 1986). Additionally, shallots usually reach maturity faster than common onion and also they are hardy (Saraswathi and Sathiyamurthy 2017) making them good companions of winter cultivars of cabbage. Moreover, shallots are rich in saponins and flavonoids (Fattorusso *et al.* 2002); the yellow shallot (used in this study) is documented to produce considerable quantities of the flavonoid quercetin (Fattorusso *et al.* 2002; Swamy and Gowda 2006). Thus, controlling aphid populations via shallot companion planting can provide an ecologically sustainable insecticide-alternative in *Brassica* plantings, corroborating the mediated ecosystem services of companion planting (Mutiga *et al.* 2010; Parker *et al.* 2013; Debra and Misheck 2014; Pahla *et al.* 2014; Saldanha *et al.* 2019) and conferring on the target crop enhanced direct and indirect defence against the enemies of the crop (Shrivastava *et al.* 2010). As such, shallots should be integral to the much-needed trend of affordable green pesticides (Mossa 2016) that provide applicable low-priced pest management solutions (*e.g.*, Kuepper and Dodson 2001; Amarawardana *et al.* 2007). Furthermore, in the offspring of the population groups impacted by combined stress in our study, winged aphids were more common with variable proportions. It appears that the shallot perturbation, rather than crowdedness, was the driving force behind aphid dispersiveness and the latter was at large further induced by predator presence. The differential aphid dispersiveness could also be a result of the reduced food availability and increased contextual hostility by increasing shallot to cabbage ratios, which further contributed to the induction of extreme phenotypic plasticity (dispersive morphs) as a survival tactic (Stadler *et al.* 1994).

Conclusions

We have demonstrated that decreasing the number of hosts (vital for aphid feeding, reproduction and protection from intruders or enemies) and changes in overall host biomass had a considerable impact on aphid population across the host-plant gradient, especially under predation by the lacewing. Moreover, shallot presence was sufficient in producing a strong negative impact on aphid aggregative abundance, largely due to perturbation resulting from naturally deterring or repelling as well as toxic properties of shallots, which in turn led to alteration of aphid population dynamics and propensities for dispersal. Interestingly, the shallot effect can be of a similar magnitude to the predation effect.

Our study highlights the importance of shallots as beneficial companions to crop plants in impeding aphid population growth, and that combining the shallot effect with the inclusion of a natural enemy of the pest can lead to more desirable results for aphid control. This suggests that shallots can contribute to the enhancement of agro-ecosystem services in cropland as a sustainable pesticide-alternative with the added economic benefit of being also an edible commercial crop. However, the impact of the combined ecological stress may be contingent on predator-prey interaction, micro-habitat structure, and changes in pest population dynamics. As such, manipulated functional diversity in crop-companion-pest-predator systems appears useful and context-dependent at the same time, thus requiring further investigation across different spatial structures with different interactants. A careful application of said functionality is of particular importance for pest regulation, whilst growing produce with the least need for harmful chemicals in urban farming and multi-purpose greenhouse settings.

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Conflict of interest: The authors declare that they have no conflict of interest.

Data availability

The dataset generated during and/or analysed during the current study are available in the Figshare data repository [https://figshare.com/s/7c9137c3967ba936e01f].

Contribution statement

MSK envisioned the experimental design co-developed the analysis with LF and co-optimised and finalised the stats with OYB. MSK shaped and finalised the manuscript with LF and SAP. MSK expanded the manuscript.

LF contributed to the design and executed the experiment, did the data entry and provided insights on the optimisation of the analysis. LF provided the first draft of the manuscript and co-shaped and co-finalised the manuscript with MSK.

OYB co-optimised the statistics of this work with MSK. OYB also provided insights on the enhancement of the design and contributed to the enrichment of the final version of the manuscript.

SAP edited the penultimate draft and contributed to the shortening and the enhancement of the manuscript. SAP also proofread the final version of the manuscript.

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Tables

Number of Cabbage Hosts	minus (Predator+Shallot)	plus Predator	plus Shallot (minus Predator)	plus (Predator+Shallot)
4	**369.17** *(0.84 PDB)* *0.16% alates*	**100.33** *(0.86 PDB)* *0% alates*	NA	NA
3	***798.2*** *(0.9 PDB)* *0.52% alates*	**59.25** *(0.94 PDB)* *0.16% alates*	**215.33** *(0.82 PDB)* *0.07% alates*	**184.67** *(0.76 PDB)* *0.25% alates*
2	**371.25** *(1.03 PDB)* *0.4% alates*	**233.6** *(1.29 PDB)* *0.12% alates*	**165.67** *(0.64 PDB)* *0.25% alates*	**111** *(0.67 PDB)* *0.65% alates*
1	**81.25** *(0.85 PDB)* *0% alates*	**241** *(1.55 PDB)* *0.58% alates*	**103** *(0.57 PDB)* *1.39% alates*	**75.33** *(0.61 PDB)* *1.12% alates*

Table 1. Aphid abundance with polyphenism, and PDB under combined stress of aphids. According to aphid's perspective, the ecological challenge against the aphid population was of different levels of stress including single stressors (shallot [non-host, toxic, and repellent], or lacewing [predator]) or the combination of these stressors. There were 4 Cabbage hosts [optimal, the most hospitable] = shallot perturbation (0% Shallot [0 Shallot : 4 Cabbage], 3 Cabbage hosts shallot-free, 25% Shallot [1 Shallot : 3 Cabbage, the least perturbing], 2 Cabbage hosts shallot-free, 50% Shallot [2 Shallot : 2 Cabbage], 1 Cabbage host [least hospitable]), 75% Shallot [3 Shallot : 1 Cabbage, the most hostile and perturbing]), predator presence (0 or 1), minus (Predator+Shallot) = the cabbage context was free from predator and shallots, plus Predator = the cabbage context had lacewing (aphid predator), plus Shallot (minus Predator) = the cabbage context had shallot companionship but the lacewing was absent, plus (Predator+Shallot) = the cabbage context had shallot companionship and the lacewing was present, cabbage host plant dry biomass (PDB), alates = dispersive winged aphid morphs as a proxy for polyphenism. The values in bold refer to the arithmetic mean of the aphid population in the corresponding microcosm. There were always four plants in the microcosm.