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Ecological intensification for biocontrol of aphids requires severing myrmecophily

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Abstract

With the rollback of insecticides, novel tools for pest control are urgently needed. Aphids are particularly a major concern with few sustainable control alternatives. Ecological intensification has been promoted as a way of “inviting” back nature’s self-regulating abilities into agricultural production systems. Although such measures enhance the presence of natural enemies in agroecosystems, we demonstrate that in an ecologically intensified apple orchard, biocontrol of rosy apple aphid was minimal. We verified why the biodiverse settings did not result in enhanced ecosystem services, i.e., biological control of the rosy apple aphid. Close monitoring of food–web interactions in thousands of aphid colonies showed that tending ants dominated responses, while those of natural enemies were weak or absent. However, application of artificial aphid honeydew diverted ants from tending aphids and flipped the myrmecophily-dominated state into favoring numerical responses of a guild of natural enemies. Responses were swift and controlled both *Aphis pomi* and *Dysaphis plantaginea*, provided intervention was synced with aphid and predator phenology. Although myrmecophily in aphids is well-known on its own accord, it has been completely overlooked in ecological intensification. To unlock the aphid-biocontrol potential provided through ecological intensification, myrmecophily needs to be disrupted. Although particularly true for perennial systems, generally practices that reduce soil disturbance favor ants and may amplify aphid pests, thereby reducing biocontrol impacts in ecological intensification efforts. Harnessing ecosystem services requires careful analysis and good understanding of agroecosystem intricacies.

Keywords Ecological intensification · Myrmecophily · Aphids · Biological control · Flower strips

Sebastian Larsson Herrera and Zaid Badra have contributed equally to this work.

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Introduction

Since the dawn of agriculture, humanity has been in an arms race with insect pests, which seemed to be concluded in favor of our agricultural production systems with the advent of insecticides. These agrochemicals further permitted unbridled expansion of monoculture cropping systems, thereby increasing efficiency and production levels (Blaxter and Robertson 1995). Little did we understand ecology, or we would have foreseen the humongous negative impacts of agrochemical-based monoculture on ecosystem health. It is now generally accepted that the practices are largely responsible for dwindling biodiversity and the erosion of nature's own checks and balances (Benton et al. 2002, 2003; Hallmann et al. 2017; Cardoso et al. 2020). To reverse this trend, frequently referred to as the sixth mass extinction (Ceballos et al. 2015, 2020), insecticides are rolled back on a large scale, which, combined with sustainable management practices and ecological intensification, should reestablish and support biodiversity in our agroecosystems (Bommarco et al. 2013; Isbell et al. 2017; Kleijn et al. 2019; Tamburini et al. 2020). However, whether enhancing biodiversity in agroecosystems translates into increasing self-regulating properties of ecosystems, and to a desired level, is subject to debate (Balvanera et al. 2014; Albrecht et al. 2020).

Regulations that rollback agrochemical inputs, however laudatory, are frequently enforced in the absence of rigorously tested alternatives (Lamichhane et al. 2015), leaving farmers with limited to no options to protect their investments against unchecked pests, or, counterproductively, revert to broad spectrum insecticides that are still allowed. In apple, the rollback of neonicotinoids and the transition to organic farming in particular poses serious challenges and leaves few tools to control sap-sucking insects, such as aphids (Alins et al. 2017). A frequently proposed remedy is ecological intensification. This can include for instance a series of measures to increase the complexity of the landscape, offering shelter and alternative nutritional sources to arthropods, including natural enemies of pests. In apple production, ecological intensification often includes, among other measures, flower strips (Bommarco et al. 2013). Indeed, heterogeneous and complex landscapes appear to increase the abundance of natural enemies of aphids (Haenke et al. 2009; Rusch et al. 2016). However, an important factor that separates aphids from many other pests is myrmecophily: Aphids maintain a close association with ants, which provide protection in return for honeydew, an abundant source of nutrition (Stadler and Dixon 1998, 2005).

As myrmecophily poses a problem in our agroecosystems by reducing aphid vulnerability to natural enemies,

severing this relationship may reduce protection and increase exposure to biocontrol. Indeed, exclusion of the black garden ant, *Lasius niger* (L.), in apple trees by using sticky barriers on the bark of trees (Stewart-Jones et al. 2008; Minarro et al. 2010; Nagy et al. 2013), or diverting *L. niger* using aphid-infested plants or sugar baits may reduce aphid colonies and/or increasing natural enemy presence (Nagy et al. 2015; Pålsson et al. 2020). However, these studies showed effects on small-scale, e.g., the level of individual colonies, and do not provide a full scale, spatiotemporal picture of the effects on population dynamics of aphids, ants and the guild of natural enemies. Further, their impacts and limitations in biocontrol of aphids in ecologically intensified orchard settings have not been tested. This is increasingly important in the light of conflicting literature about ecological intensification and biocontrol of aphids (Albrecht et al. 2020).

To assess the potential of diverting ants, its impact on population dynamics of aphids, ants and natural enemies, as well as its contribution to biocontrol of aphids, we designed a large-scale experiment in an ecologically intensified organic orchard. During a 2-year period, we performed an orchard-scale spatiotemporal analysis of *Dysaphis plantaginea* (Passerini) and *Aphis pomi* (de Geer) colonies. Concurrently, we mapped the effect of artificial honeydew on the functional response (concentration of individuals) of *L. niger*, as well as the numerical response (increased number of eggs and/or survival) of three taxa of natural enemies larvae of which reside within the colonies, Coccinellidae, Syrphidae and *Chrysoperla* spp. (Miñarro et al. 2005; Dib et al. 2010; Porcel et al. 2018).

Material and methods

Pilot trials for evaluating artificial honeydew

In a separate apple orchard (Alnarp, Sweden, 55° 39' 36.6" N 13° 04' 41.3" E), we tested the preference of artificial honeydew, as a pilot experiment to the diversion experiments. In this orchard, five to seven active ant colonies were selected. The selected colonies were each provided with four treatments in a separate medicine cup lid ($\varnothing = 4$ cm), all placed equidistantly in a circle on a plastic plate (24.5 × 18.5 cm). Trials were repeated three times with different combinations of treatments. Alanine, L-aspartic acid, glutamate, histidine and isoleucine (all Merck KA, Darmstadt, Germany) mixed accordingly to the ratio found in the honeydew of *D. plantaginea* (Pålsson et al. 2020). The preference for two different levels of sucrose (4 and 20%, Nordic sugar A/S, Copenhagen, Denmark), with or without amino acids, and with or without the addition of a trisaccharide, melezitose (4%, Merck KA, Darmstadt, Germany) was scored by counting

the number of visiting ants on each treatment multiple times throughout the day.

Experimental orchards

We used an experimental apple orchard, established in 2005, located at Trädgårdslabbet, Swedish University of Agricultural Sciences, Alnarp, Sweden (55° 39' 37.3" N 13° 05' 08.4" E). The orchard had 10 rows, each with 38 trees spaced at approximately 1 m distance. The interrow consisted of a 3-m-wide grass strip with in its center a 1-m-wide flower strip, established in early Spring 2019 (Table S1). Every 10th tree was a pollinator tree. "Aroma", "Discovery" and "Elise" (apple cultivars) on EM9 rootstock were spread in blocks of 10 trees across the orchard.

The entire orchard was organically managed and surrounded by a hedgerow of alder (*Alnus* sp.) on one side and different, organically managed horticultural fields on the other three sides. To properly evaluate the impact of artificial honeydew, single ant territories should not contain both control (no intervention) and treatment trees (intervention consisting of artificial honeydew, see section "Ant mapping and diversion" below). We therefore performed ant aggression tests (Liu et al. 2000) to establish territories of ant nests and match treatments and controls accordingly. However, these tests appeared too time consuming, invasive (potentially affecting ant colonies) and frequently inconclusive. Therefore, in 2019, we divided the orchard into a block of treated and control trees, each consisting of five rows and with a similar ant and aphid distribution and with similar ant densities. In 2020, to make sure there was no spill-over effect across years, the experimental orchard was divided into four sections, two containing the treatment trees and two the control trees (each section thus having 85 trees in total). In addition, sections of trees within areas that had the highest aphid colonies and lowest natural enemy density in 2019 were selected as treatment, to avoid potential carry-over effects across years that could artificially favor an effect of diversion of ants on aphid population dynamics.

The scale ruled (full orchard of 400 trees) out localized effects (e.g., local contraction of natural enemies in ant-free space in the immediate vicinity), whereas the ecological intensification ruled out lack of numerical responses due to e.g., insufficient natural enemy population levels.

Ant mapping and diversion

To assess the spatial distribution of ants and its dynamics, we mapped ant activity in the orchard. In 2019, mapping was done throughout the season, and in 2020 at the beginning and end (May 10th and July 10th). Bait stations, consisting of petri dishes filled with a 20% sucrose solution were placed at alternate trees in each row in the morning (10.00–11.00),

and ants in and on the petri dish were counted between 13.45 and 15.00.

To divert ants, artificial honeydew composed of sugars and amino acids was experimentally derived from above pilot trials and consisted of sucrose and amino acids (Table S2). Feeding stations, vials of 25 mm diameter × 100 mm (Fisher Scientific Co LLC, UK), were filled and plugged with cotton balls to permit diffusion of the liquid and prolong the availability for the ants. The solution and the cotton plug were changed at least once per week. The vials were placed at the base of each treated tree from 16 June 2019 to 10 May 2020 onward.

Aphid, ant and natural enemy monitoring

The establishment and growth of *D. plantaginea* and *A. pomi* colonies were carefully monitored weekly from early May until early July in 2019 and 2020, from their establishment to their collapse of colonies. Artificial honeydew was placed after establishment of aphid colonies. The trees were continually checked for aphid colonies, marking each new colony with a unique identifier. Within each colony, we counted the number of aphids, ants and larvae of three natural enemies, Coccinellidae, Syrphidae and *Chrysoperla* spp. Larvae of these three taxa reside within the colonies and served as a proxy for the natural enemy guild. Other, often invasive and disruptive, methods of sampling natural enemies were avoided.

Data analysis

Pilot experiment

Data on ant preference for combination of amino acids and sugar were pooled across observations for each replicate and for each of the pilots (Pilot 1–3). Data were fitted using a generalized linear model with a Poisson distribution or a negative binomial distribution, from package "MASS" (Venables and Ripley 2002), if the model was overdispersed, verified using package "AER" (Kleiber and Zeileis 2008).

Density maps of monitored ants, ant attendance, natural enemies and aphid density were created after normalization for unequal distribution of trees attributable to factors such as dead and pollinator trees in the orchard. Normalization was done through interpolation to an equidistant matrix using the package "akima" (Akima and Gebhardt 2020). The interpolated data were then superimposed on a satellite image downloaded from Google's api using "ggmap" (Kahle and Wickham 2013).

The number of aphids, number of aphid colonies and number of natural enemies over time, days since the start of experiment (date) was used as the explanatory variable in a cubic polynomial model, fitted with a Poisson distribution.

The number of ants and natural enemies in each aphid colony was summed across dates and modeled using a generalized linear mixed model, fitted with a negative binomial model with each tree as random effect using package “lme4” (Bates et al. 2015). For modeling, the natural log of aphids versus tending ants and natural enemies, a cubic polynomial model fitted with a Poisson distribution was used. Aphid north–south or east–west distribution and ants monitored over dates were verified using linear models.

All post hoc pairwise comparisons were done using package “emmeans” (Lenth et al. 2018), except for linear models where ANOVA from package car was used (Fox and Weisberg 2019). For the principal component analysis (PCA), the package “tidymodels” (Kuhn and Wickham 2020) was used and the data were centered and scaled. The variance contributed by each primary component was calculated from the standard deviation and divided by the total variance. Envelopes for groups were calculated using the Khachiyan algorithm through the package “ggforce” (Pedersen 2020). All visualizations, data manipulation and organization of the data were done using R (v. 4.4.1) and “tidyverse” (Wickham et al. 2019).

Results

Attractiveness of different artificial honeydew compositions

We first optimized the composition of the artificial honeydew using sugars and amino acids. The addition of amino acids and/or melezitose to sucrose increased, although not always significantly, visitation of *L. niger* compared to sucrose alone in all pilots (Fig. S1A–C). Using a 20% solution of sucrose instead of any combination with 4% sucrose increased visitation of *L. niger* (Fig. S1B, $p < 0.001$). The addition of both amino acids and melezitose to the 20% sucrose solution increased preference significantly over sucrose alone ($p = 0.014$). The attractiveness of this combination did however not differ from 20% sucrose to which either amino acids ($p = 0.22$) or melezitose ($p = 0.063$) was added (Fig. S1C). Because of affordability, a solution of 20% sucrose with amino acids was chosen for use in the artificial honeydew.

Ant mapping

We mapped the ant distribution in the entire orchard, through monitored ant visitation of bait stations. In 2019 and 2020, 3209 and 3548, *L. niger* were counted at the bait stations, respectively, with no differences between years and treatments (Fig. S2). Ants were distributed throughout the orchard, although not equally. Some higher density

spots in the southern part of the orchard were recorded both years. Ant densities did not change significantly during the course of the experiments (2019: $p = 0.33$, 2020: $p = 0.93$), or between control and treatment (2019: $p = 0.49$, 2020: $p = 0.82$).

Disruption of myrmecophily reduces the number of aphids

The weekly monitoring showed that the population dynamics of the two aphid species differed markedly. Whereas *D. plantaginea* exponentially grew after establishment of the fundatrix in early May, *A. pomi* colonies established around 2 weeks later had a much lower intrinsic growth rate and smaller final colony sizes (Fig. 1). Prior to onset of intervention, *D. plantaginea* and *A. pomi* were distributed throughout the orchard without any particular spatial pattern, except for a weak south to north decline of *D. plantaginea* in 2019 (Fig. S3).

In 2019, at the onset of intervention, *D. plantaginea* was already established and around that time their growth rate declined (Fig. 1). Placing artificial honeydew at the base of treatment trees largely failed to reduce the number and size of *D. plantaginea* colonies or accelerate the collapse of the colonies (Fig. 1). Of the 994 *D. plantaginea* colonies in total, 46% were in control trees. In contrast, *A. pomi* colonies, which established later and were still small at the start of the intervention, declined in size and number immediately following placement of artificial honeydew (Fig. 1, top panels). In total 470 colonies were recorded, of which 79% were in control trees. The total number of *A. pomi* was even more strongly suppressed than the number of colonies (Fig. 1, lower panels), which shows that in addition to fewer colonies, the average colony size was also suppressed in the treatment.

The impact of disruption of myrmecophily on *A. pomi*, but not *D. plantaginea*, observed in 2019, indicated the critical importance of timing on shifting the ecosystem balance. Therefore, the onset of the intervention was preponed in 2020, before colonies of either aphid species were established. Accordingly, diverting ants with artificial honeydew dramatically reduced the number of *D. plantaginea* colonies and individuals. Trees that received artificial honeydew also had significantly fewer colonies and individuals of *A. pomi* (Fig. 1). In total 441 *D. plantaginea* colonies were followed, 68% of these were in the control trees and 118 *A. pomi* colonies of which 63% in control trees.

The functional response of ants tending aphids fades following diversion

Ant visitation was recorded in all aphid colonies throughout the orchard. Ant diversion through placement of

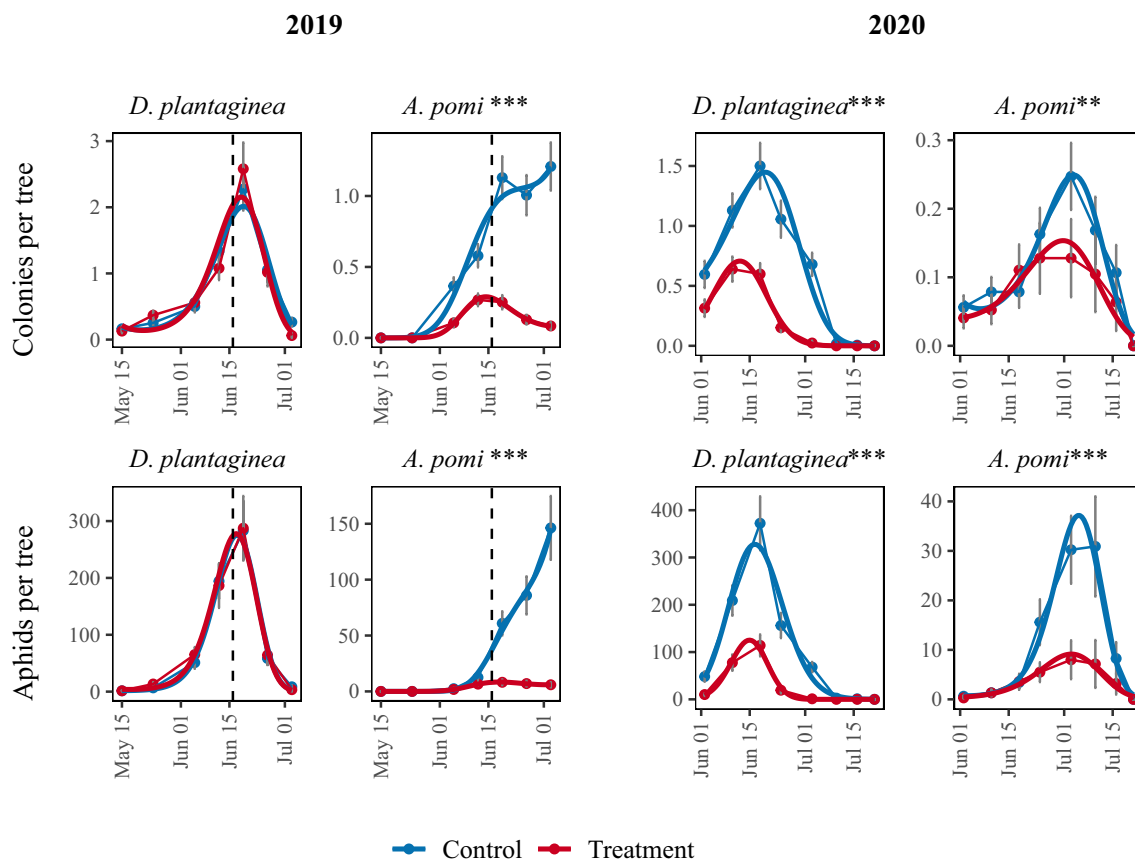


Fig. 1 Rosy apple aphid and green apple aphid population dynamic for 2019 and 2020. Note the different scale reflecting differences in the total number of colonies and aphids: in total 409,559 *D. plantaginea* and 81,162 *A. pomi* were recorded. Dashed line in 2019 plots represent timing of treatment. In 2020, the treatment was rolled out

before aphid monitoring started. A polynomial general linear model (smooth curve) is fitted to the original data (underlying colored lines) with the resulting p-value annotated after the species name (* < 0.05, ** < 0.01, *** < 0.001)

artificial honeydew significantly affected ant visitation rates per colony (Fig. 3, top panel). Even though treatment trees harbored significantly fewer aphid colonies, thereby potentially leaving a higher ant/aphid ratio, few ants tended these colonies, irrespective of aphid species.

In 2019, despite a late start of diversion of ants, colonies in treatment trees were significantly less tended than colonies in control trees (40% vs. 51% in treatment and control, respectively). In 2020, in treatment trees, the number of tending ants present in *D. plantaginea* colonies dropped significantly ($p < 0.001$), due to an earlier start of the intervention. This was also reflected in the percentage of colonies that were visited by at least one ant: only 22% of the colonies in the treatment trees, versus 60% in the control trees.

In *A. pomi*, a similar pattern was observed. The number of tending ants present in *A. pomi* colonies was significantly lower in treatment trees, compared to control trees ($p = 0.021$, $p = 0.009$ for 2019 and 2020, respectively). Similarly, the percentage of colonies with at least one visiting ant

also dropped from 70% in the control to 57% in the treatment in 2019, and 62% and 55%, respectively, in 2020.

Numerical responses of natural enemies of *D. plantaginea* increased.

We recorded the presence of larvae of Coccinellidae, Syrphidae and *Chrysoperla* that resided within each of the 1435 *D. plantaginea* and 588 *A. pomi* colonies, and scored the effect of diversion of ants using artificial honeydew. Whereas in both years, following the application of artificial honeydew, the presence of resident natural enemies in *D. plantaginea* colonies increased, the effect was much more pronounced in 2020, owing to the earlier start of the intervention (Fig. S4).

In 2019, application of artificial honeydew increased the presence of natural enemies in *D. plantaginea* colonies slightly, but significantly ($p = 0.011$, Fig S4), by a factor 1.6 (average 1.04 and 0.66 in treatment and control, respectively, $n = 994$). This was due to a significant

increase in the number of coccinellids ($p < 0.001$) after the roll-out of artificial honeydew. This negatively correlated with the number and size of aphid colonies only at the end of the monitoring period ($p = 0.005$, Fig. 1).

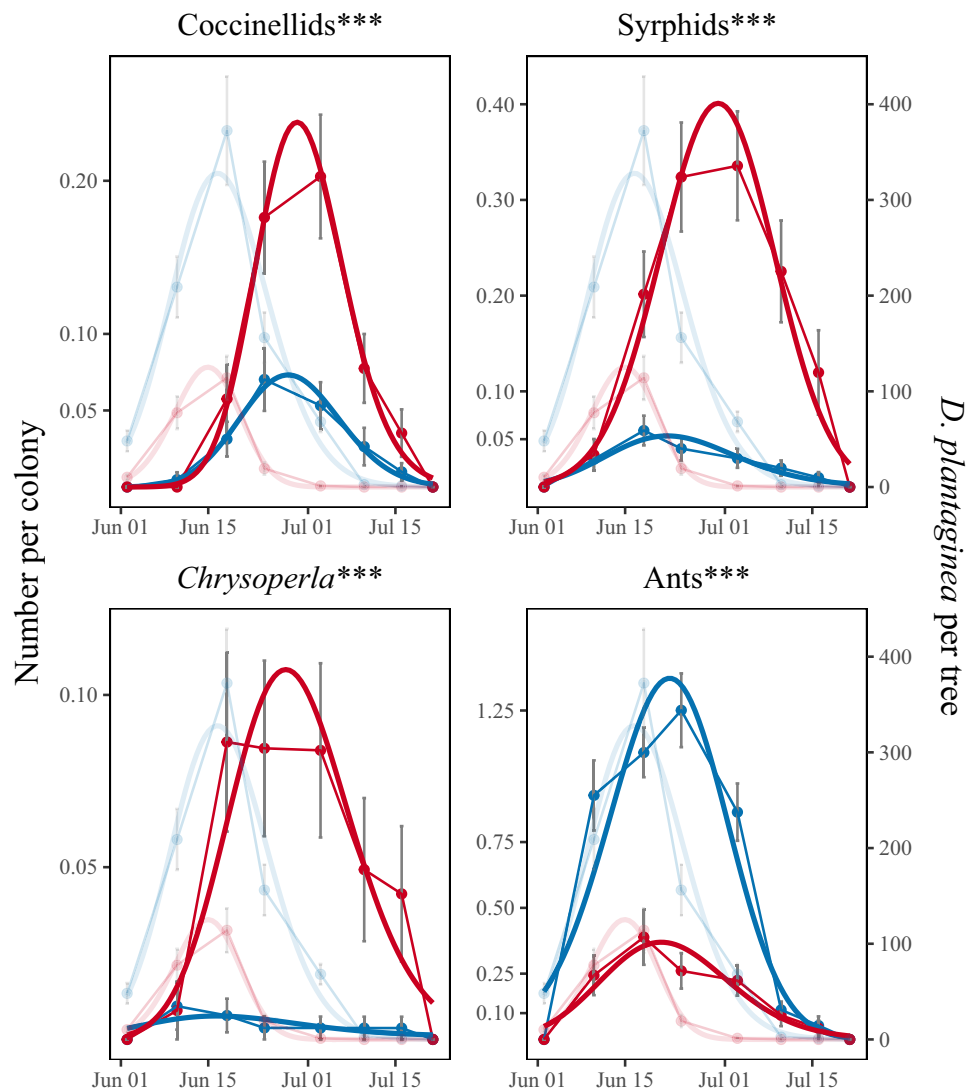
In 2020, artificial honeydew was placed before the establishment of aphid colonies. Accordingly, impacts of diversion of ants had a much earlier and more pronounced effect on the number of natural enemies residing in *D. plantaginea* colonies. On average 5.5 times, more natural enemies resided in *D. plantaginea* colonies in treatment than control trees (Fig. 2, on average 2.17 versus 0.39 for treatment and control, respectively).

Resident coccinellid, syrphid and *Chrysoperla* spp. larvae were few in *A. pomii* colonies, in both years. In 2019, the number of natural enemies per colony averaged only 0.20 and 0.17 per colony for the treatment and control, respectively, whereas in 2020, this was 0.09 and 0.11, respectively.

Disrupting myrmecophily shifts functional responses from ants to natural enemies

In Fig. 3, the effect of application of artificial honeydew on shifts in the dynamics of aphids, ants and natural enemies was plotted against each other, which shows a shift from an ant-dominated to natural enemy-dominated state (Fig. 3 top left and bottom left, respectively). This was particularly evident in *D. plantaginea* colonies: *L. niger* displayed an exponential functional response to aphid colony size (Fig. 3, top left), which was almost completely absent in the presence of artificial honeydew. Conversely, without tending ants, the number of natural enemies was linearly correlated with the number of aphids, whereas this numerical response disappeared when ants were not diverted (Fig. 3 bottom left). A PCA analysis using this data underlines this by showing the control (blue) and treatment (red) of *D. plantaginea* having different directionality (Fig. 3, right panel).

Fig. 2 Response dynamic of three resident natural enemies and *L. niger* within colonies of *D. plantaginea* in 2020. Data are fitted using a polynomial generalized linear model. Faded lines: the number of *D. plantaginea* per tree (Fig. 2, scale using right axis). Stars after taxa names denotes significance level (* < 0.05 , ** < 0.01 , *** < 0.001)



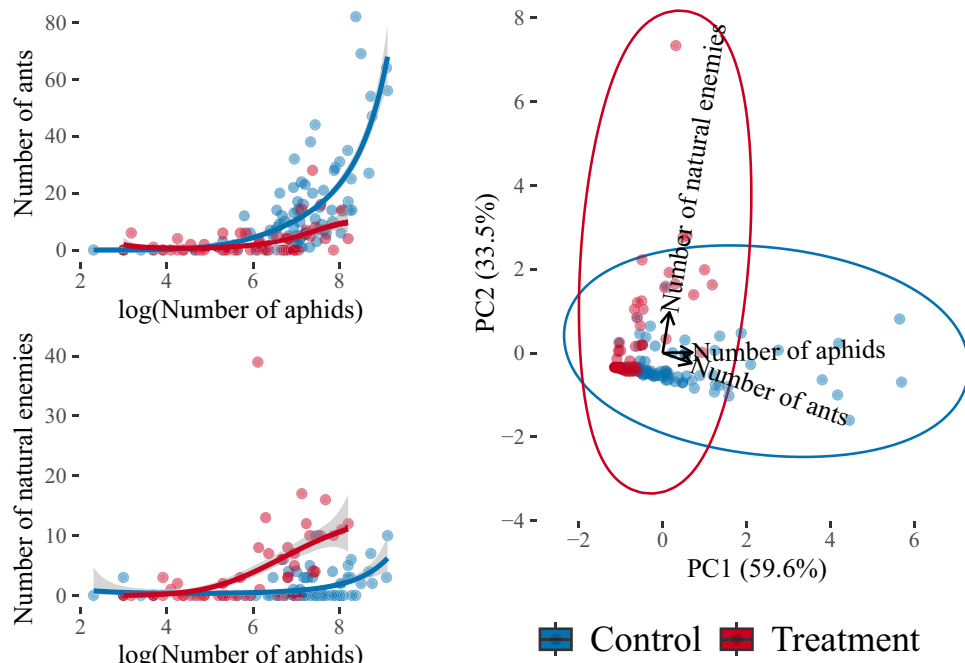


Fig. 3 Left panels: number of *L. niger* (top) and natural enemies (bottom) plotted against the logarithm of the number of *D. plantaginea* using polynomial models (lines). Control colonies displayed (blue lines) a strong functional response of ants to aphids and no numerical responses of natural enemies. Diversion of ants reverses this and rescues numerical responses of natural enemies (red lines). Right: a principle component analysis using untransformed data illustrates how the response shifted from ant dominance (blue) to natural enemy

dominance. The eigenvectors for “Number of ants” and “Number of aphids” are both pushing the data points of control along PC1. While the eigenvector of “Number of natural enemies” is pushing the data points for treatment in a perpendicular direction along PC2. The PCA illustrates the transition of the state of aphid ecosystem from one dominated by ants and aphids to a state benefiting natural enemies (right hand panel)

Besides an overall increase in natural enemies, Fig. 1 also shows strong differences between ants and natural enemies in terms of the time delay of population responses (see Fig. 1, light overlays). Ants show an immediate functional response to aphid numbers, whereas the time delay of the numerical response of natural enemies following disruption of myrmecophily was 7–15 days for a numerical response, being shortest for *Chrysoperla* spp. and longest for Coccinellidae. Finally, Fig. 1 shows that the effect of diversion of ants positively impacted the numerical response of *Chrysoperla* spp. and Syrphidae more strongly than Coccinellidae.

Discussion

Ecological intensification, bringing nature back into our agroecosystems, aims to restore ecological functions and biodiversity to harness ecosystem services in production (Tittonnell 2014). In terms of pest management, ecological intensification aims to diversify agroecosystems to “invite” natural enemies back, thereby enhancing the inherent pest-suppressing abilities (Bommarco et al. 2013). However, increased biodiversity may not equate functional ecosystem

responses to pests. In our perennial apple production system, myrmecophily obstructed biological control of aphids through hindering numerical responses of natural enemies, despite ecological intensification. Only when *L. niger* was diverted, could the increased abundance of natural enemies be levered into successful biological control.

Myrmecophily blocks numerical responses in perennial cropping systems

Myrmecophily is well documented across many aphid species, and its importance in the fate of aphid colonies is well established (Herbert and Horn 2008; Detrain et al. 2010; Amiri-Jami et al. 2017; Stewart-Jones et al. 2008; Kaplan and Eubanks 2005; Glinwood et al. 2003; Wäckers et al. 2017; Devegili et al. 2020) Yet, when overall biological control of aphids in large-scale field studies was evaluated, the significance of myrmecophily in aphid control has been generally overlooked. Out of 20 studies on aphid management by ecological intensification using flower strips (Table S3), none assessed the significance of myrmecophily in the ultimate success rate. A closer look shows that successes and failures of aphid control through ecological intensification

are particularly strongly associated with annual/perennial cropping systems. In annual agroecosystems, flower strips increased the abundance of natural enemies of aphids and decreased aphid abundance (Pascual-Villalobos et al. 2006; Tschumi et al. 2016; Hatt et al. 2017; Ribeiro and Gontijo 2017; Toivonen et al. 2018; Pollier et al. 2019; Schoeny et al. 2019; Toennisson et al. 2019; Tiwari et al. 2020; Kujawa et al. 2020). In contrast, in studies in perennial cropping systems such as apple, blueberry, hops and strawberry, ecological intensification using flower strips significantly increased the abundance of natural enemies, but this had negligible effects on aphid populations (Walton and Isaacs 2011; Markó et al. 2013; Calderwood et al. 2017; Campbell et al. 2017; Hodgkiss et al. 2019; Rodríguez-Gasol et al. 2019; Cahenzli et al. 2019; McKerchar et al. 2020). It is interesting to note that under low/no-till sorghum and soybean, flower strips increased natural enemies populations, but, as in perennial cropping systems, did not enhance biological control of aphid populations (Cox et al. 2014; Mercer et al. 2020). Clearly, abundance and numerical responses of natural enemies of aphids are correlated under tilled annual cropping regimes, but not under perennial and no-till regimes, i.e., regimes with low soil disturbance that support ant colonies (Marti and Olson 2007; Baraibar et al. 2019). Besides important practical implications for ecological intensification for aphid control, it also highlights that ecological intensification should be accompanied by detailed studies on insect food–web interactions and how these are, or are not, impacted by an increased biodiversity.

Our study shows that in the perennial apple cropping systems, ecological intensification by itself did not support biological control of aphids. Number and impacts of natural enemies on both *D. plantaginea* and *A. pomi* were minimal, in spite of their abundance. Instead, myrmecophily upheld aphid colonies in an increasingly aphid-hostile ecosystem by obstructing numerical responses of natural enemies and completely blocking the enhanced biocontrol potential obtained through ecological intensification. Conversely, we show that diverting ants, which canceled out the functional responses of ants to aphids, unlocked the numerical potential of natural enemies. The fact that *D. plantaginea* colonies in treatment trees had on average more than five times the number of natural enemies per aphid colony in spite of only harboring a fraction of the number of aphids, underscores the importance of myrmecophily in aphid accessibility to predators.

Myrmecophily shapes predator guild dynamics

In response to disruption of myrmecophily, three important taxa of aphid predators, larvae of *Chrysoperla* spp., Coccinellidae and Syrphidae (Völkl et al. 2007), showed model-type numerical responses to aphid populations. It should be

noted that these three indicator species served as a proxy for other species of natural enemies in the orchard, but whose presence was more transiently associated with aphid colonies and are harder to detect without intrusive and disruptive methods, e.g., Forficulidae (earwigs), predatory heteroptera species, parasitoids and spiders (Völkl et al. 2007). In earlier, small-scale experimental studies in non-intensified ecosystems, trees were inoculated with aphid colonies and/or a few infested branches per tree were selected. Diverting ants using exclusion or alternative sugar sources increased pressure of natural enemies and resulted in reduced aphid colony number and size (Stewart-Jones et al. 2008; Nagy et al. 2013, 2015; Wäckers et al. 2017; Pålsson et al. 2020). We demonstrate that in spite of ecological intensification and high presence of natural enemies, numerical responses to naturally established aphid populations require severing myrmecophilic relationships, such that the ecological stable state shifts in favor of natural enemies instead of ants.

In our study, the numerical response of *Chrysoperla* spp., Coccinellidae and Syrphidae differed. *Chrysoperla* spp. were most affected by myrmecophily and were almost entirely absent in control trees, but closely tracking aphid colony dynamics after diversion of ants. Larvae of Coccinellidae beetles, on the other hand, showed numerical response in control settings, although weak. Finally, whereas in control plots, Coccinellidae were the most dominant predator in aphid colonies, this shifted to Syrphidae following disruption of myrmecophily. The niche opening through disrupting myrmecophily thus shifted aphid food–web dynamics and the relative importance of individual predators. Such changes following interventions need monitoring, and measures need adjusting to fit the phenology of pest and natural enemies to maximize ecosystem services. This is illustrated by our 2019 intervention, in which we missed the critical window for effectively controlling *D. plantaginea*. In our instance, strips with early flowering perennials which particularly support Syrphidae would appear effective in enhancing aphid control in apple (Haenke et al. 2009; Hogg et al. 2011).

Natural enemies may have diverse strategies to overcome the selection pressures by ants. *Chrysoperla* spp. appears to have evolved a strong ant avoidance and was almost entirely absent in the presence of myrmecophily. Indeed, *Chrysoperla* spp. are rarely mentioned as aphid predators in perennial, but frequently in annual cropping systems (Messina et al. 1997; Clark and Messina 1998; Kaplan and Eubanks 2002; Hesler 2014). Similarly, inundative release of *Chrysoperla* spp. failed to control aphids in perennial systems, such as apple, strawberry and citrus (Hagley 1989; Grasswitz and Burts 1995; Michaud 2001; Easterbrook et al. 2006) but were successful in aphid suppression in annual/greenhouse systems (Zaki et al. 1999; Alghamdi et al. 2018; Eid et al. 2018). In contrast with larvae of *Chrysoperla* spp.,

larvae of Coccinellidae, including *Coccinella septempunctata* (L.) commonly found in our orchard, have evolved varying degrees of acceptance of ant presence, with some populations adopting and myrmecophilic behavior thereby avoiding predation (Sloggett and Majerus 2000; Takizawa and Yasuda 2006). This possibly underlies the numerical response of Coccinellidae observed in control settings. Further research on these interactions would help better understand the diversity of dynamics we observe in the field.

Aphid species themselves may further shape the relative importance of natural enemies. Although in this study both species of aphids declined, *A. pomi* harbored substantially lower numbers of the three key natural enemies, which may indicate that other natural enemies or mechanisms, not monitored here, contributed to their decline. Owing to differences in intrinsic growth rate particularly at lower temperatures (Graf et al. 1985), *A. pomi* formed much smaller colonies and expanded substantially slower compared to the *D. plantaginea*. This species may not sufficiently support the three natural enemies, larvae of which often reside within the colony (Hemptinne et al. 1992). *Aphis pomi* may thus be comparatively more targeted by other, freely ranging generalist predators, which were not quantified in this study. More detailed studies are needed on this point.

Ecological intensification requires a good understanding of ecosystems to harness ecosystem services

Our study provides a background of why ecological intensification increases biological control of aphids in annual crops, but not in perennial and low/no-till annual systems. Increased biodiversity alone did not translate into enhanced biological control of aphids, but required an additional intervention, the disruption of myrmecophily, to unlock the biocontrol potential and allow for a diverse guild of natural enemies to harness biocontrol of aphids.

The rollback of insecticides, particularly neonicotinoids, leaves farmers with few tools and increases pressure on finding sustainable innovation for aphids pest control in our production systems. Aphid-related issues may be further amplified by agricultural practices that are trending and favor ant establishment, such as no-till and perennation (Paustian et al. 2000). It is often suggested to reduce reliance on insecticides through diversification of our agricultural landscapes, with flower strips as the principal component. This should support biological control, besides providing a diverse range of other ecosystem services. However, if these recommended practices fail to deliver the services sought after, for instance due to insufficiently understood food–web intricacies, growers may get discouraged and abandon practices (Kleijn et al. 2019; Penvern et al. 2019). It is therefore advisable that policy and advisory instruments rolled out to support ecological

intensification are accompanied by research that details ecosystem interactions, assess the relative importance of various natural enemies in ecosystem services and provide insights into how to channel enhanced potentials into ecosystem services and develop interventions where necessary.

Future studies should look at complementary methods that could synergize aphid control through breaking myrmecophilic relationships, while carefully evaluating potential side effects, within and across seasons. For instance, methods that impact establishing aphids colonies early in the season (Hemptinne et al. 1992) and cultural practices that reduce establishment and impacts of ant nests (Markó et al. 2013). Further, measures that selectively support early attraction and establishment, survival and reproduction of natural enemies (Haenke et al. 2009; Tamburini et al. 2020) need to receive attention to reduce the observed time lag between predator responses to prey availability.

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Author contribution SLH, ZB, MFH, MT and TD designed the study, ZB, MFH, ACS and IK collected data, SLH analyzed the data, SLH, ZB and TD led the writing of the first draft of the manuscript, MT and TD supervised, MT and TD acquired funding, all authors have contributed and agreed to the final version.

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Data availability Data and all scripts used to compile the data are indexed at zenodo at <https://doi.org/https://doi.org/10.5281/zenodo.4437500>, both this and its associated github repository will be made publicly available at the time of publication. Until then the data are not publically available, but reviewers/editors can find the repository at: <https://zenodo.org/records/4518904?token=eyJhbGciOiJIUzUxMiJ9.eyJpZCI6IjZDA4NTQwLTUyYyZgtNGM4Zi04NTY4LTAxYjc4YzI1OGEyNSIsImRhdGEiOnt9LCJyYW5kb20iOiJkMTg4MGNmZThkNzg3ZTYyNjMwYTc1ZTU4MTA4ODNlZiJ9.e0ggz2WPYQhplkVJOpk-QiuC6fSptf-0eTt5DoEMhfW1sCY4yoDMHUIIu7SSjGxSfNRxUJE8Pn2NsY2N0ZUzPg>

Declarations

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