

Arthropod predator identity and evenness jointly shape the delivery of pest control services

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Abstract

BACKGROUND: Maximizing the effectiveness of natural pest control requires a detailed understanding of how service delivery is affected by natural enemy community diversity and composition. Many studies have investigated the effects of natural enemy abundance and species richness on pest control. Studies examining the effects of evenness and species identity are fewer and have produced inconsistent results. Here we test the effects of arthropod predator community evenness and species identity on natural pest control by exposing aphid (*Sitobion avenae*) colonies in experimental cages to arthropod predator communities that had the same abundance and species richness but differed in evenness and dominant species.

RESULTS: We found that the identity of the most dominant species in the arthropod predator community predominantly drove the pest control efficiency. However, additional to the effects of species identity, we also found a causal positive relationship between the evenness of arthropod predator communities and the suppression of pest growth.

CONCLUSION: Our results provide support for the hypothesis that ecosystem service provision is generally a function of the abundance and efficiency of the most dominant species of the service-providing groups. This could partly explain why management practices aiming at promoting abundance of natural enemies often have mixed effects on pest control. Our results also demonstrate that diversity components such as evenness have important additional effects. However, in real-world ecosystems these effects may be obscured because evenness is generally confounded with abundance or species richness in natural enemy predator communities.

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Keywords: cage experiment; *Coccinella septempunctata*; community composition; dominant species; natural enemy; *Sitobion avenae*

1 INTRODUCTION

Agriculture relies heavily on ecosystem services provided by multiple guilds of service-providing species.^{1–4} In recent decades, agricultural management intended to enhance productivity has resulted in significant loss of species that regulate key processes underlying agricultural production.^{5,6} Crop yield and quality often no longer respond to additional agricultural inputs because ecosystem service-providing species have become the limiting factor.^{7,8} A wealth of studies examining the biodiversity–ecosystem functioning relationship has shown that service provision increases with the species richness of service-providing communities.^{9–11} This implies that restoration management should target species richness.¹¹ At the same time, species communities in agricultural landscapes are generally dominated by a few generalist species^{12,13} and service provision is mainly determined by the abundance of a small subset of dominant species.¹⁴ This could indicate that service provision can be safeguarded by enhancing the abundance of a few easily manageable species.¹² However, these two observations are not mutually exclusive because service-providing species communities that have a more even

distribution of species could still outperform communities of the same richness that are heavily dominated by one or a few species. While species-richness effects on ecosystem service provision have been examined extensively (reviewed by van der Plas¹⁵), we know much less about the effects of dominance and evenness on service provision.^{16–18}

Pest control provided by natural enemies is one of the most important regulating services that can reduce the reliance of agricultural production on pesticides.¹⁹ Many studies show that higher abundance or species richness of natural enemies provide a higher pest suppression rate.^{9–11} This is because larger numbers of natural enemies consume more pest food resources and because more species-rich natural enemy communities deploy a

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wider range of predation strategies with different species complementing each other.^{18,20} However, the evidence base for the effects of the evenness of natural enemy communities on pest control is much smaller¹⁸ and the few studies to date that have addressed the topic have demonstrated positive,^{21–23} neutral^{22,24} and even negative¹¹ effects of higher natural enemy evenness on the delivery of natural pest control services.

The conflicting results could be explained by the effects of species identity. It has been suggested that the efficiency of a community to provide ecosystem services is determined by the proportion of the species that most efficiently provides the ecosystem services.¹⁶ If higher evenness is achieved by lowering the relative abundance of the most efficient species this will reduce service provision. However, if it is achieved through lowering the relative abundance of a less efficient species this may increase service provision.²⁵ An additional complicating factor in the case of pest control is that natural enemies not only prey on pest species but may also predate one another.²⁶ Such intraguild predation, or interference effects, may strongly affect the outcome of studies examining species richness effects on pest control because outcomes will depend on the exact combination of species regardless of richness or evenness.²⁷ Species identity has been found to have a larger impact on pest control than species richness,^{28,29} but evenness has been found to contribute to pest control independently from species identity effects.²¹ Which mechanisms explain the effects of evenness on pest control is not well understood.¹⁸ The mechanisms are probably similar to the ones underlying predator richness effects; positive complementarity effects that are counteracted by the negative effects of enemy interference.^{21,30} Given the potential importance of evenness to the provision of pest control services, it is important to develop a better understanding of its effects and underlying mechanisms.

Here, we examine the effects of arthropod predator evenness and identity on aphid predation efficiency by using a model system with the aphid species *Sitobion avenae* on wheat (*Triticum aestivum*). We selected four species of natural enemies that prey on *S. avenae* belonging to different guilds: two flying species (the lady beetle *Coccinella septempunctata* and the mirid bug *Macrolophus pygmaeus*) and two ground-dwelling species (the carabid beetle *Poecilus cupreus* and the spider *Trochosa ruricola*). We introduced aphids on wheat plants in large experimental cages which were then exposed to five treatments: one control treatment with no arthropod predators and four treatments with different combinations of the arthropod predators that all had the same abundance and species richness but different evenness. These cages created confined environments to guarantee that aphids were only exposed to the experimental arthropod predator communities or the control situation without predators. We specifically asked whether and to what extent (1) the evenness of the arthropod predator communities and (2) the abundance of individual species affect aphid population growth rate.

2 MATERIALS AND METHODS

2.1 System design and species selection

Wheat (*Triticum aestivum*) as an important food crop is often severely damaged by many pests, among which *Sitobion avenae* is the most dominant and harmful.³¹ It can cause substantial wheat yield loss with as few as four aphids per straw³² and its risky areas are predicted to constantly expand globally.³³ *S. avenae* has a wide range of natural enemies, including predators and

parasites. In this study, we selected four species of arthropod predators (two flying species, the lady beetle *Coccinella septempunctata* and the mirid bug *Macrolophus pygmaeus*, and two ground-dwelling species, the carabid beetle *Poecilus cupreus* and the spider *Trochosa ruricola*) as the natural enemies of *S. avenae*. These species are native and dominant species in the Netherlands, which made them easy to purchase online or collect. *C. septempunctata* has been regarded as one of the most efficient predators on aphids^{28,34} and has been shown to play a key role in suppressing *S. avenae* in wheat fields.³⁵ *M. pygmaeus* as a polyphagous predator can consume multiple pests, including aphids, whiteflies, mites and thrips.³⁶ Furthermore, *M. pygmaeus* is commonly found in agroecosystems and can persist under a wide temperature range even without prey.³⁷ *M. pygmaeus* is therefore frequently used as biocontrol agent in practical agricultural production.³⁶ Besides the two flying arthropod predators, ground-dwelling arthropod predators like carabid beetles and spiders can also predate on aphids, and the effectiveness of ground-dwelling natural enemies in suppressing aphids has even been reported to outperform flying ones in some cases.³⁸ *P. cupreus* and *T. ruricola* are the most dominant ground-dwelling arthropod predator species in the Netherlands.¹³ Both these species can predate on *S. avenae*,³⁹ with *T. ruricola* displaying a strong preference for *S. avenae*.³⁹

2.2 Experimental design

The experiment was carried out at the experimental farm of Wageningen University & Research from 15 June to 2 October in 2021 (51°59'47" N, 5°39'36" E, Wageningen, the Netherlands). The objective of the experiment was to examine how natural enemy assemblages with different evenness but the same species richness and abundance affect the efficiency of pest predation. To this end, we used the aphid pest species *S. avenae* on wheat (*T. aestivum*) exposed to four species of arthropod predatory natural enemies (*C. septempunctata*, *M. pygmaeus*, *P. cupreus* and *T. ruricola*) as our model system. To exclude as much as possible any external interference with the experimental arthropod communities, the experimental sites were first plowed and then fully covered with a black polypropylene woven fabric that prevents growth of weeds and the emergence of arthropods from the soil. We subsequently placed 20 walk-in experimental cages (2 × 2 × 1.75 m, length × width × height), made of insect nets with a zippered opening on one side (1 mm mesh size; Mononet 1000, Rovero Systems B.V., Raamsdonksveer, the Netherlands⁴⁰). Cages were laid out in two rows of 10 on a 34 × 10 m area, with a distance of 4 m between the two rows and a distance of 1 m between cages within each row (Fig. S1). After establishment of the cages, the bottom edges and corners of each cage were sealed with polyethylene film, which was additionally secured with sandbags. Each cage thus represented a confined space that kept all experimental arthropods in and kept all other arthropods and vertebrates out. A drip irrigation system was installed in all cages to be able to sufficiently water the experimental wheat plants without having to access the cages.

We applied four evenness treatments and a control treatment in which no arthropod predators were present (Fig. S1). In all four evenness treatments, we introduced four species of arthropod predators, amounting to 16 individuals in total. The evenness treatments varied from highly uneven to completely even and consisted of the following: E1, one, two, three and 10 individuals of the four species; E2, one, three, five and seven individuals of the four species; E3, three individuals of two species each and five

individuals of the other two species each; and (E4) four individuals of each of the four species. We randomly assigned each of the five treatments (four evenness treatments and one control treatment) to four cages (Fig. S1). To be able to examine the effects of species identity independently from the evenness treatment, we carried out the experiment for four rounds. In each round the total number of individuals, species and evenness treatments was the same but a different species was the most abundant, the second most abundant, the third most abundant and the least abundant species in all the treatments of that round (Table S1). The total sample size of our study was therefore 80.

At the start of the first round, the polypropylene woven fabric was removed from the soil of each cage to provide the arthropod predators with near-natural soil conditions. Prior to the introduction of the experimental plants and arthropods, the soil was cultivated again to eliminate any arthropods remaining under the fabric. Subsequently, six pitfall traps (white plastic beakers: top diameter 98 mm, height 151 mm, filled about two-thirds with water) and four sticky traps (28 × 12 cm; Horiver®, Koppert B.V., Berkel en Rodenrijs, the Netherlands) were set within each cage. When no more arthropods were captured by these traps for 3 days in a row, we removed the traps and moved the first batch of wheat plants into the cages. Sixteen pots with five wheat plants each were placed in each cage (Fig. S2), with the top of the pots level with the soil surface so that ground-active arthropods could easily move between different wheat plants. Aphids were inoculated on the wheat plants of the central four pots (see below) when the growth stage of the plants was around the watery ripe stage (BBCH 70) as this provides the best conditions for aphid growth.⁴¹ After data collection was finished, we manually collected any observed arthropod predators and removed the aboveground biomass of the wheat plants. We then set six pitfall traps and four sticky traps within each cage to capture any remaining arthropod predators, the abundance of recollected arthropod predators was recorded, and recollected living arthropod predators were set free and not used for the next round. Two days before we moved in the wheat plants for the next round, we removed the traps and cultivated the soil in each cage to eliminate weed seedlings and any remaining arthropod predators. This procedure was repeated between the first and second rounds, the second and third rounds, and the third and fourth rounds. After the fourth round finished, six pitfall traps and four sticky traps were set for 6 days to recollect introduced arthropod predators. The duration of each experimental round was about 1 month (from wheat plants being moved in until soil was cultivated).

2.3 Preparation of the plants and arthropods

Four batches each of 320 pots (volume 10 L, top diameter 28 cm, base diameter 24 cm, height 22.5 cm) of organic wheat were sown in a greenhouse at the experimental farm of Wageningen University & Research. The first batch was sown on 8 March 2021 and each subsequent batch was sown about 1 month after the previous batch to keep the growth stage of the wheat consistent between the four experimental rounds. Soil composition was 91% peat, 7% loam and 2% vermiculite (mass ratio). Eight to 10 seeds were sown in each pot and after germination the weakest plants were removed to leave five healthy wheat plants per pot. After the removal of the superfluous wheat plants, all pots were covered with fine mesh to prevent arthropods from colonizing the pots. The potted wheat plants were checked frequently and any observed arthropod or weed that had managed to

colonize the pots was removed manually. The fine mesh was removed when the wheat plants were moved into cages.

The aphids, lady beetles and mirid bugs were bought from Katz Biotech AG (Baruth/Mark, Germany). The carabid beetles and spiders were collected by deploying a total of 42 live pitfall traps (the same as the pitfall traps in the cage but without trapping liquid) that were placed around Wageningen (Fig. S3). The pitfall traps were installed in field margins and checked every 2–3 days. The targeted arthropods were collected and all other arthropods were released. Before the targeted arthropods were introduced, collected carabid beetles and spiders were kept in plastic containers separately and stored in a dry and cool chamber (moisture 50–60%, temperature 20–25 °C). Cloth soaked with water was placed in each tube container to keep it moist. The cloth was replaced two to three times per week.

2.4 Data collection

In each cage and each round, we introduced approximately 600 adult apterous *S. avenae* on the wheat plants of the central four pots (i.e., about 150 aphids per pot). Aphids were inoculated on the top three leaves of the plants using a fine hair brush.⁴² We then closed the cage and allowed the aphids to establish. After 2 days we recorded all observed live aphids on the wheat plants (the first aphid count). In each of the evenness treatments, the arthropod predators were introduced immediately after the first aphid count by randomly placing them in the outer 12 pots in each cage to avoid initial intraguild predation. After the aphids had been recorded and the arthropod predators had been introduced in all cages, they were left undisturbed until the second aphid count on the sixth day. We only counted the aphids that were on plants as the dropped live aphids can quickly return to the plant canopy if they are not predated by ground-dwelling arthropod predators.⁴³ Thus abundance of the aphids on plants can also reflect predation by ground-dwelling arthropod predators. The aphid growth rate was calculated for each cage as the number of aphids in the second count divided by the number of aphids in the first count.⁴⁴ The data for four cages in the first round, two cages in the second round, four cages in the third round and one cage in the fourth round were excluded from the analyses as we found non-experimental natural enemies or recollected more experimental arthropod predators than had been introduced in these cages.

2.5 Statistical analysis

All analyses were conducted in R version 4.2.1.⁴⁵ In a first step, we used a linear regression model to analyze whether aphid growth rate differed between the different treatment levels and whether this differed between rounds (as species composition differed between different rounds, we therefore analyzed the identity of the most dominant species). This model included treatment, round and the interaction between treatment and round as explanatory variables. Since the interaction between treatment and round was statistically significant (see Section 3), we subsequently compared aphid growth rate between different treatments for each round separately, using linear models with treatment as an explanatory variable. Pairwise comparisons were made with Tukey honestly significant difference (HSD) tests using the `glht` function in the `multcomp` package.⁴⁶

The significant interaction between treatment and round (see Section 3) indicates that the effects of evenness differed across rounds and/or the identity of the most dominant species in each round. To better disentangle these effects, we further analyzed

the effects of the evenness treatments while taking into account the effects of the abundance of the individual arthropod predator species. Because the experiment was carried out over a period of more than 4 months, we corrected for the inevitable inherent differences in aphid growth rate between the rounds by using the relative growth rate as a response variable. Relative aphid growth rate was determined as the growth rate in each cage with an evenness treatment divided by the mean growth rate of the control treatment in that round. A relative growth rate of 1 would then indicate that the aphid growth rate of the evenness treatment was the same as the growth rate without arthropod predators, and relative growth rates below 1 would indicate suppression of aphid growth. We used linear mixed-effects models (package glmmTMB with Gaussian distribution⁴⁷) and an information theoretic approach to analyze the effects of the different evenness treatments and the abundance of different species of arthropod predators on the relative growth rate. We first constructed a global model that included the evenness treatment and the number of individuals of each of the four species as fixed effects and round as a random effect. We then constructed an all-subsets model set consisting of all possible combinations of the fixed variables. Given the sample size, we restricted the model set to all possible combinations with a maximum of three fixed-effect variables to limit model complexity and the total number of models in the model set.⁴⁸ Using package MuMIn,⁴⁹ we ranked the models in the model set (Table S2) based on their Akaike Information Criterion values corrected for small sample size (AICc) and calculated full-model averaged parameter estimates and parameter weights based on all models with $\Delta AICc < 6$.⁴⁸ Furthermore, because our results suggested a linear response pattern between relative aphid growth rate and the evenness treatment, we analyzed the shape of the relationship between arthropod predator evenness and aphid growth rate. To this end, we calculated Pielou's index (using the vegan package⁵⁰) for each treatment to express the different evenness treatments as a continuous variable, and re-ran the highest ranked model of the previous analysis with the continuous Pielou's index variable instead of the categorical evenness treatment variable. In this model, the arthropod predator abundance variable and Pielou's index variable were standardized (mean-centered and divided by one standard deviation) to aid comparison of effect sizes.

3 RESULTS

Our analysis of aphid growth rate per round showed that growth rate was significantly affected by treatment ($F_{4,49} = 222.5$, $P < 0.001$), round ($F_{3,49} = 7.572$, $P < 0.001$) and their interaction ($F_{12,49} = 22.34$, $P < 0.001$). Overall, mean aphid growth rate was 67% lower in the treatments with arthropod predators than in the control treatment without arthropod predators. The presence of arthropod predators significantly reduced aphid growth rate in all four rounds, but the magnitude of the effect differed between round and evenness treatment (Fig. 1). We did not find significant differences in aphid growth rate between the four evenness treatments in the first round in which the mirid bug was the most dominant species. However, in the third and fourth rounds, with two ground-dwelling guilds (spider and carabid beetle, respectively) as the most dominant species, aphid growth rate was generally lowest in the most even treatment (E4) and differed significantly from aphid growth rates in the most uneven treatment (E1). In contrast, in the second round, with lady beetle as the most dominant species, aphid growth rate was lowest in the most uneven treatment (E1), although the difference was only significant compared to treatment E3 (Fig. 1).

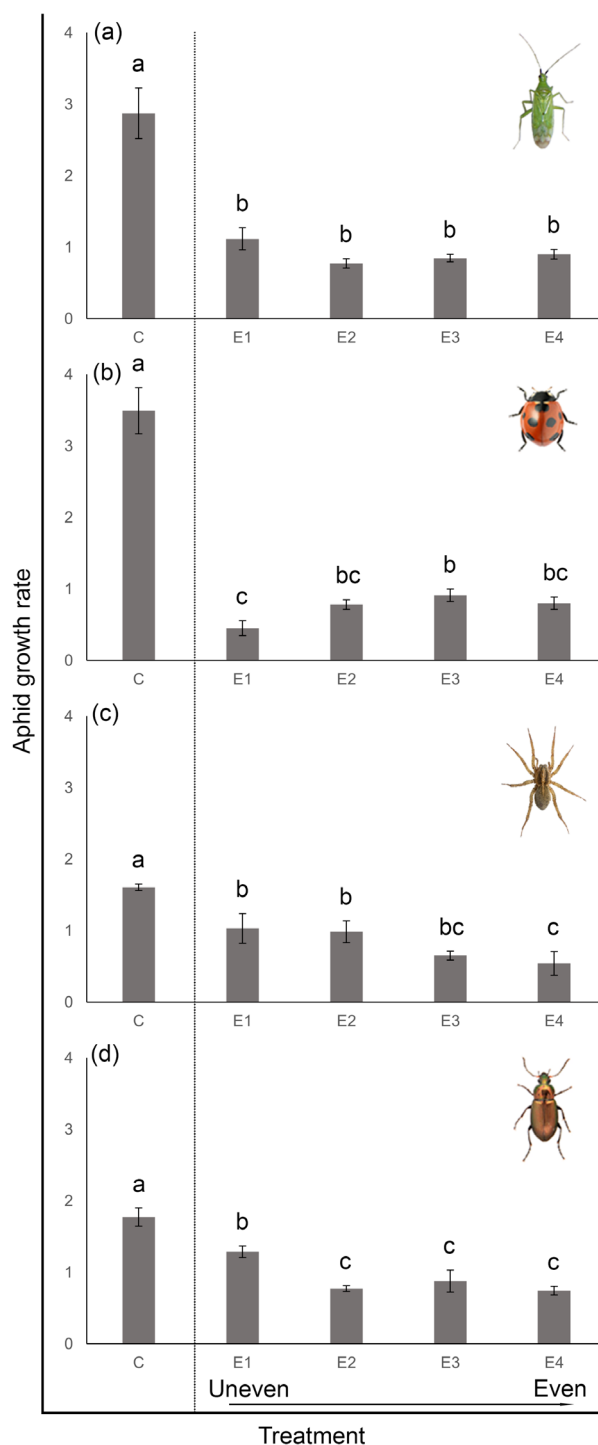


Figure 1. Effects of different treatments (C, control treatment with no natural enemies; E1–E4, evenness treatments with natural enemies) on mean \pm standard error of aphid growth rate in separate rounds: (a) first round, with *Macrolophus pygmaeus* as the most dominant species, (b) second round, with *Coccinella septempunctata* as the most dominant species, (c) third round, with *Trochosa ruficollis* as the most dominant species, and (d) fourth round, with *Poecilus cupreus* as the most dominant species (detailed community composition presented in Table S1). Different letters indicate significant differences among treatments (adjusted $P < 0.05$).

The combined analysis of the effects of evenness and the effects of the abundance of different species showed that relative aphid growth rate was mainly affected by the abundance of lady beetles

Table 1. Model selection and model averaging results for effects of abundance of four natural enemies and different evenness treatment on relative growth rate of aphids

Model no.	Explanatory variables							<i>k</i>	AICc	Δ AICc	ω_m
	Carabid beetle	Lady beetle	Mirid bug	Spider	E2	E3	E4				
1		−0.056	−0.018		−0.091	−0.109	−0.151	8	−113.1	0	0.632
2	0.013	−0.047			−0.090	−0.109	−0.152	8	−110.4	2.76	0.159
3		−0.052			−0.093	−0.114	−0.156	7	−110.3	2.78	0.157
4		−0.049		0.006	−0.093	−0.114	−0.156	8	−108.1	4.98	0.052
β	0.002	−0.054	−0.012	0.000	−0.091	−0.110	−0.152				
Lower 95% CI	−0.009	−0.070	−0.032	−0.004	−0.147	−0.169	−0.209				
Upper 95% CI	0.013	−0.037	0.009	0.005	−0.035	−0.051	−0.096				
ω_p	0.16	1	0.63	0.05	1	1	1				

Note: Candidate models (Δ AICc < 6) are ranked in order of increasing differences in corrected Akaike Information Criterion. Model averaged parameter estimates (β), 95% confidence intervals (CI) and relative importance (ω_p) are given for each explanatory variable. Model averaged parameter estimates with confidence intervals not overlapping zero are indicated in bold. The number of parameters (*k*) and Akaike model weight (ω_m , which indicates the probability that a model is the best approximating model in the candidate set) are shown for each model.

and the evenness treatments. These two variables featured in all models in the best subset, while the abundance of the other three species each featured in only a single model (Table 1). Relative aphid growth rate was negatively related to the abundance of lady beetles (Table 1 and Fig. 2(b)) and differed among evenness treatments (Table 1 and Fig. 2(a)), with the most even treatment (E4) resulting in the largest reduction in relative aphid growth rate and the most uneven treatment (E1) resulting in the smallest reduction. Replacing the categorical evenness treatment levels with the standardized continuous Pielou's index showed that the relative aphid growth rate declined linearly with increasing evenness of arthropod predator communities (Fig. 3). However, the effect of evenness was less pronounced than that of the abundance of lady beetles (standardized parameter estimates of −0.055 and −0.114, respectively).

4 DISCUSSION

Compared to community species richness and abundance, the contribution of evenness to ecosystem functioning is relatively poorly studied.^{16–18} Here we controlled for the total species richness and abundance of natural enemy communities and showed

that the effect of evenness of experimental natural enemy communities on natural pest control depends on the identity of the most dominant species in the community. However, after accounting for the abundance of the different predator species, we found positive evenness effects on pest suppression that are additional to the effects of species identity. Our results also suggest a linear relationship between natural enemy evenness and pest growth reductions.

In line with previous studies that produced inconsistent results,^{11,21–24,51} we also found that the effects of evenness on natural pest control were mixed (Fig. 1). One of the few studies that found a clear positive effect of evenness on pest control was done by Crowder *et al.*,²¹ who used a strictly experimental approach that accounted for the effects of natural enemy abundance, species richness and identity. Likewise, in our experimental study we found positive effects of evenness on pest control when accounting for the abundance of the most effective predator species. In contrast, many field studies showed that the effects of natural enemy evenness on pest control were neutral or even negative.^{11,24,51} One possible explanation for the discrepancy between the results of cage experiments and field studies could be the inevitable incomplete sampling in field studies.^{52,53}

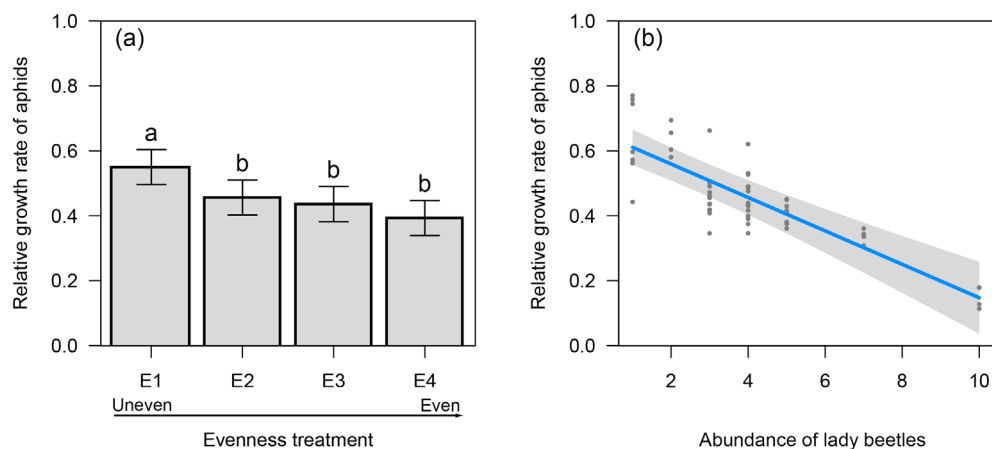


Figure 2. Effects of different evenness treatments (a) and abundance of lady beetles (b) on relative aphid growth rate. For (a) model-estimated means are shown with error bars indicating standard error, and for (b) the fitted line indicates the estimate effects and the shaded area indicates the 95% confidence interval.

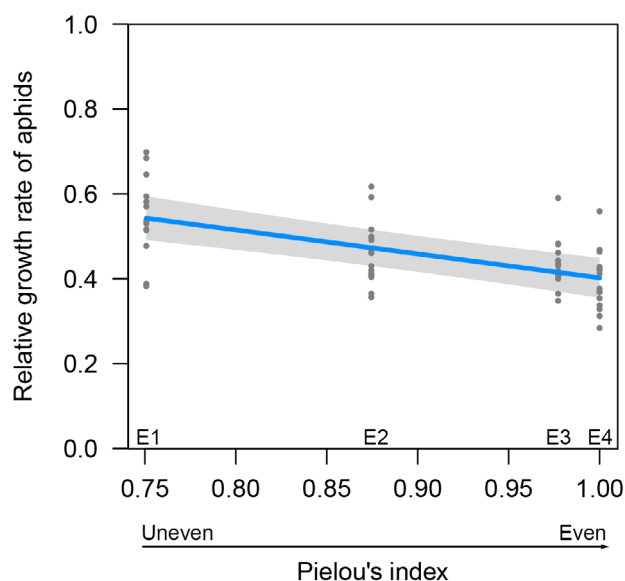


Figure 3. Linear relationship between Pielou's index of each evenness treatment (instead of the categorical evenness treatment variable, E1, E2, E3 and E4, in Fig. 2(a)) and relative aphid growth rate. The fitted line indicates the estimate effects and the shaded area indicates the 95% confidence interval.

This means that the true evenness may not be properly assessed in field studies, possibly causing bias in the relationship between natural enemy evenness and pest suppression efficiency. Furthermore, in real ecosystems it is often difficult to disentangle the separate effects of natural enemy evenness from other community metrics such as species richness and abundance. For example, environmental conditions that support higher natural enemy evenness can simultaneously promote their abundance, which results in a correlation between natural enemy evenness and abundance^{54,55} that makes it impossible to disentangle their separate effects. The inconsistent results between experimental and field studies, and the stronger effects of species identity than evenness in the present study, indeed suggest that the effects of evenness in real ecosystems are often obscured by the effects of abundance, species richness and/or species identity and only become apparent when these factors are accounted for. Furthermore, the natural enemy communities in experimental studies are often composed of functionally and taxonomically distinct species. In our study, the four species of arthropod predators were from four different families and differed greatly in, for example, morphology, behavior and diel activity.^{56–59} In real ecosystems, natural enemy communities are generally composed of many species that are more closely taxonomically related and/or functionally redundant, which may result in larger ecological niche overlap and more intense interspecific competition.^{60,61} Although the natural enemy communities in our experiment comprised functionally and taxonomically contrasting species, the evenness of the communities resembled values found in real-world agroecosystems. In a field study of natural enemy communities in winter wheat fields across four European countries, approximately 80% of the fields had pooled spider and carabid beetle communities with Pielou's index that were within the range of this study.¹³

Species identity, expressed as the abundance of the different individual species, had a more pronounced effect on aphid suppression than evenness. The abundance of the two flying natural enemies was negatively related to relative aphid growth rate (Table 1), particularly for *Coccinella septempunctata* (Fig. 2(b)) and to a lesser extent for

Macrolophus pygmaeus (Fig. S4(a)). In the experimental round where *C. septempunctata* was the most dominant arthropod predator, the highest suppression of aphid growth rate was observed in the most uneven treatment that comprised the largest number of individuals of lady beetles (Fig. 1(b)). The abundance of two ground-dwelling natural enemies, *Poecilus cupreus* and *Trochosa ruficola*, was not notably related to the aphid growth rate (Table 1 and Fig. S4(b),(c)) and when these species dominated the arthropod predator communities, aphid growth rate suppression was generally higher in the most even treatment (Fig. 1(c),(d)). This is generally in line with previous studies that found flying natural enemies to be more effective than ground-dwelling ones in suppressing aphid pests.^{62–64} *C. septempunctata* has been flagged before as a particularly effective, specialist predator of aphids.^{28,38} Each *C. septempunctata* individual can kill more than 50% of the *Acyrtosiphon pisum* individuals they encounter and dislodge the majority of the rest of the aphids from crop plants.⁶⁵ A similar predation efficiency was observed in the present study, with only 45% of the inoculated *S. avenae* remaining on the wheat plants in the most uneven treatment where *C. septempunctata* was the most dominant arthropod predator (Fig. 1(b)). One reason for the different suppression efficiency between flying and ground-dwelling natural enemies could be the location of aphids on wheat plants. *S. avenae* generally infests wheat ears and prefers to stay in the upper parts of plants. Even though *P. cupreus* and *T. ruficola* were reported to be able to climb on plants to prey on aphids,^{39,66} we did not observe this behavior in our experiment. The aphids are therefore generally more accessible to flying natural enemies than to ground-dwelling ones.⁶³ However, aphids may drop down from plants to avoid or escape from flying natural enemies^{65,67} and ground-dwelling natural enemies can complement flying ones by preying on the dropped aphids and preventing aphids spreading to other plants.⁶⁸

Another reason for the predominant role of lady beetles in suppressing aphids could be because lady beetles may have been less affected by intraguild interference. Even though our experiment did not enable us to directly identify intraguild interactions, such interactions can be inferred from the recollection rates of the natural enemies at the end of each survey round. The recollection rate was highest for lady beetles, with an average recollection rate of 99%, followed by carabid beetles (85%), mirid bugs (56%) and spiders (44%). Lady beetles are specialist aphid predators but sometimes also prey on mirid bugs as an alternative food source when aphid densities are insufficient.^{69,70} In contrast, mirid bugs can only prey on small arthropods and thus are at a disadvantage in the presence of lady beetles. The two ground-dwelling predators are generalist predators that also consume large arthropods. In agro-ecosystems, carabid beetles are known to predate on spiders, while there is little evidence that spiders predate on carabid beetles.^{71–73} We cannot assert that nonrecollected mirid bugs and spiders were predated in our study, but the low recollection rate of mirid bugs and spiders could imply they were negatively affected by intraguild interactions, which may have decreased their aphid suppression effectiveness.

5 CONCLUSION

Maximizing pest regulation services by natural enemies requires a thorough understanding of how natural enemy diversity and community composition affect pest suppression. While many previous studies found positive effects of natural enemy abundance, species richness and functional diversity on natural pest control,^{10,11,74} our study found that evenness and the identity of the dominant species play vital roles in suppressing aphid pests. In

our experimental system, the most efficient predator, *Coccinella septempunctata*, mainly determined the effectiveness of aphid control by the natural enemy communities. This provides support for the hypothesis that ecosystem service provision is generally the product of the abundance and efficiency of the dominant species,^{14,16} resulting in maximum natural pest control when the most efficient species dominates the community. When a less-efficient aphid predator dominated our natural enemy communities, pest control services were significantly lowered, which provides an additional explanation for why managing for more natural enemies through the provision of seminatural habitat does not always result in enhanced pest control.^{75–77} If management increases the dominance of a less-efficient predator or enhances intra-guild predation of species that are highly efficient natural enemies, pest control may even be reduced. However, on top of the effect of species identity, our study found more subtle positive effects of community evenness on aphid suppression. Because of the linear nature of the relationship, increasing evenness will result in straightforward increases in pest control, with possible associated benefits to community resilience and stability.^{17,78} Evenness is therefore an important component contributing to the functioning of natural enemy communities and the services they provide. However, evenness effects on pest control may be difficult to demonstrate in real-world ecosystems because here evenness is generally correlated with species richness and abundance.

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CONFLICT OF INTEREST

We declare we have no competing interests.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article and can also be accessed via <https://data.4tu.nl/datasets/4cecc6f9-f604-436b-94af-f49f9dfc515e4>.

SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

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