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BIOLOGICAL CONTROL

Agricultural Intensification Affects Communities of Plants and Arthropods in Field Borders and Their Potential to Engender Biological Control

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Abstract

In agriculture, spontaneous field border vegetation offers numerous benefits, such as reducing soil erosion, enhancing carbon sequestration, conserving biodiversity, and supporting biological control. However, the extent of these benefits often depends on the contexts of location and time. As for biological control, field borders can promote natural enemy conservation if the plants therein can provide adequate resources (e.g. shelter, alternative food, microclimate). In the context of location, field borders can be adjacent to areas with varying degrees of agricultural intensification, including fields with annual crops, perennial crops, or forest areas. While many studies have investigated how field borders can influence arthropod communities in adjacent crops, the opposite direction of effect (i.e. how crop areas can influence adjacent field borders) remains an underexplored topic. Therefore, in this three-season study, we selected vegetated field borders next to annual crops, perennial crops, and forest areas, to study their communities of spontaneous plants and arthropods as well as their potential to engender biological control nearby. In general, our results indicate that both plant and arthropod community composition were influenced by the type of adjacent land use and season. Field border vegetation next to areas with higher level of agricultural intensification (i.e. annual or perennial crops) harbored more herbivores, flowers, and natural enemies, although some of these results were season dependent. Field borders adjacent to annual or perennial crop areas promoted stronger biological control of aphids, likely due to complementary food resources (herbivores and floral resources) provided for natural enemies by the plants within those borders. Taken altogether, our results reinforce the importance of preserving spontaneous field border vegetation, especially in areas under intensive agriculture management.

Keywords Field margin · Weeds · Conservation of natural enemies · Habitat management · Banker plants · Aphids

Introduction

Field borders (i.e. field margins) are often left uncultivated by farmers, thereby engendering places for spontaneous growth of vegetation and consequent sheltering of invertebrates and small vertebrates (Marshall and Moonen 2002; Aschwanden et al. 2007; Anderson et al. 2013; Mkenda et al. 2019a; Obanyi et al. 2023). Nevertheless, the formation of these vegetation segments at the borders is rarely intentional, and more often it is actually due to the challenges of maneuvering properly the agricultural machinery close to those borders (especially when close to fenced borders) (Marshall and Moonen 2002). While some farmers may worry about losing farming space for spontaneous vegetation at the borders (Morris et al. 2002), many others already acknowledge the potential benefits of these vegetated borders to mitigate

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soil erosion, increase carbon sequestration, conserve pollinators, and promote sustainable pest management (Balzan and Moonen 2014; D'Acunto et al. 2014; Mkenda et al. 2019a, b; Albrecht et al. 2020; Crowther et al. 2022; Aviron et al. 2023). Several studies have indicated that the border vegetation can promote biological control of pests by conserving natural enemies in field borders and causing their spillover into agricultural fields (Amaral et al. 2013; Bischoff et al. 2016; Rand et al. 2006). Specifically, the spontaneous border vegetation can provide natural enemies with resources such as shelter, alternative/complementary food, microclimate, hibernation/aestivation habitat, and protection from pesticide sprays (Landis et al. 2000; Tscharntke et al. 2007; Rusch et al. 2010; Gontijo 2019). The presence of spontaneous border vegetation might be particularly relevant in fields containing conventional annual crops where continuous cycles of planting and harvesting (i.e. high disturbance) create a constant necessity for natural enemy protection and recolonization (Wissinger 1995).

It is known that the intensification of land use can have detrimental effects on the diversity of plants and animals, which can significantly impair the functioning of ecosystems (Benton et al. 2003). Land use intensification typically aims to boost agricultural production by converting natural or semi-natural habitats into farmland. It is often accompanied by increased agrochemical use (e.g. pesticides, fertilizers), which can further disrupt key ecological functions such as pest control, nutrient cycling, and pollination (Tscharntke et al. 2005; Geiger et al. 2010; Rusch et al. 2016). In the context of pest control, numerous studies have shown that landscape degradation and simplification resulting from agricultural intensification can negatively impact ecosystem services like biological control (Thies et al. 2011; Rusch et al. 2016). For example, the destruction of field borders (e.g. hedgerows) contributes to loss of semi-natural habitat and to the further simplification of agricultural landscapes, which can engender a scarcity of food and shelter resources for natural enemies (Robinson and Sutherland 2002; McHugh et al. 2020).

Often, field borders with spontaneous vegetation may be adjacent to areas with varying degrees of management/disturbance, including areas with annual crops (very high disturbance), perennial crops (high/medium disturbance), and forest areas (low/very low disturbance). Here, disturbance refers to the frequency of agricultural practices carried out in the area, including activities such as plowing, pesticide and fertilizer application, harvesting, and the use of machinery. It is hypothesized that the intensity of land use (i.e. level of management/disturbance) may influence the composition and structure of plant and arthropod communities inhabiting nearby field borders. While many studies have investigated how field borders can influence the arthropod communities in adjacent crop areas (Balzan and Moonen 2014; Inclán et al. 2016; Luna et al. 2016; Obanyi et al. 2023; Salat-Moltó et al. 2023), the opposite direction of effect (i.e. how crop areas can influence field borders) remains an underexplored topic (Boinot et al. 2022). Nonetheless, it is noteworthy that these interactions are likely to be bidirectional, where field border vegetation and adjacent crop areas may influence each other. Regardless, understanding the driving forces that influence spontaneous border vegetation, and consequently the community of arthropod pests and natural enemies therein is paramount to devise effective management strategies to promote natural biological control of pests in the field. Therefore, in this three-season experiment (summer, winter, and spring), we investigated vegetated field borders adjacent to annual crops, perennial crops, and forest areas. In each border type, we examined the spontaneous plant and arthropod communities, along with the potential for biological control. All annual and perennial crops referred here were cultivated conventionally. The novelty of our study is the concurrent assessment of spontaneous plant and arthropod communities within borders. Our hypotheses were (i) there would be lower plant and arthropod richness in the borders adjacent to annual crop areas (i.e. higher disturbance), (ii) we would find differences in community composition of plants and arthropods in relation to border location (i.e. next to annual, perennial, or forest areas), and (iii) there would be a lower potential for biological control in borders closer to annual crop areas.

Material and Methods

Field Experiment

The study was conducted from March to November 2019 in open fields located within a landscape containing mosaics of agricultural lands and patches of forest (these fields were specifically situated within a radius of 3 km of the geographic coordinates: – 19.874617, – 44.419997). This region is situated in the transition zone between the Cerrado and Atlantic Forest biomes, with red latosol as the dominant soil type. The experimental design consisted of three treatments, for which a selected field border would be next to either (i) forest area (dense natural forest), (ii) perennial crop (i.e. either coffee, guava, citrus, pear, or cassava), or (iii) annual crop (i.e. either soybean, maize, or wheat). These experimental treatments (i.e. border location) were chosen to depict a gradient of land use intensification, with the greatest agricultural intensification represented by fields containing annual crops (i.e. greatest disturbance) and least intensification in forest patches. In these agricultural fields, the management is carried out conventionally. At the time of data collection, all annual crops were either at the end of the vegetative stage or in the middle of the reproductive stage (i.e. no crop flowers were present during data collection). All selected borders faced their respective treatments on one side (i.e. annual crop, perennial, or forest patch), and an uncultivated area (fallow land) on the other side (Appendix S1: Fig. S1). This experiment was repeated in three different seasons (i.e. summer, winter, and spring) with three replicates per treatment in each season, thereby yielding a total of 27 replicates. None of the borders was repeated across seasons (i.e. in each season, a new border was selected according to the treatments). During the summer, winter, and spring, the minimum–maximum field temperature registered were 24–36 °C, 19–30 °C, and 22–35 °C, respectively.

In general, each selected border was characterized by a strip of spontaneous vegetation located at the periphery of one side of either an agricultural field (annual or perennial) or forest patch. In the particular case of forests which have very lengthy sides (i.e. edges), any clear discontinuity in border vegetation was used to help visually delineating the beginning/end of the experimental border, and thereby stablishing its length. None of the borders was mowed or treated with pesticides during this study. Likewise, the annual or perennial crops were not sprayed with pesticides, at least 10 days prior to data collection. The selected experimental borders had an approximate width of 5.40 ± 0.85 m, and a length of approximately 31.20 ± 3.30 m (Appendix S1: Table S1). Despite a relative variation in border width and length, we carried out the same number of samples (see below) across time and treatments, aiming to adequately capture any proportional differences in plant and arthropod abundance within the borders.

Specifically, we measured through samplings the richness of plant species and abundance of arthropods within borders. For plant species richness, all plants within each field border were identified *in situ*, or collected and taken to the laboratory for further identification. The abundance of plants was not measured. The plant identification in the laboratory was carried out by using reference exsiccata and books under the guidance of a plant specialist. Nonetheless, because of the high number of plant material collected and the appearance of very rare taxa, some of them were identified just as morphospecies. Because not all plant species were identified to the species level, in this current study, the terms plant species and plant taxa are interchangeable. As for arthropods, we sampled both herbivores and natural enemies by using the following methods: (i) pitfall traps: these traps consisted of a plastic cup (500 ml) filled with 200 mL of ethanol solution (70%). Three pitfall traps were installed at surface level and left in place for 48 h within each field border, aligned lengthwise. The traps were positioned equidistantly: one at the center and the other two placed 1 m inward from each end of the border. After field exposure, the traps were taken to the laboratory for identifying and counting the arthropods under stereomicroscope. This sampling was carried out once during each season. Pitfall traps were chosen to sample specially epigeal predators and herbivores, which are known to commonly scan the soil surface. (ii) yellow sticky traps: three sticky traps (10 × 30 cm) were individually mounted on bamboo stakes and positioned equidistantly along the length of each field border—one at the center and the other two placed 1 m inward from each end. The traps were suspended 0.8 m above the soil surface and remained in place for 48 h. This was done once during each season. This sampling method was used to estimate mainly the abundance of flying arthropods occurring in each field border. The arthropods collected on the sticky traps were also taken to the laboratory for count and further identification under stereomicroscope. Because of the high number of sampled arthropods to process (pitfall + stick traps), it was not possible to identify all of them to species level, especially considering the parasitoids. We thus use the terms 'taxa' for herbivores and predators, and 'morphospecies' for parasitoids in this current study. This level of identification is sufficient for our objectives, since we are more interested in community patterns than the response of individual species. Moreover, we assessed the occurrence of flowers in all borders once in each season. To do so, we selected three 30 × 30 cm areas distributed equidistantly lengthwise within each border and recorded the number of flowers on plants therein (all flowers on every plant), regardless of plant species. The flowers were not identified by any taxonomic classification.

The potential of borders to promote biological control was also investigated by using sentinel collard plants *Brassica oleracea* L. (cultivar Manteiga) manually infested with aphids. Therefore, weeks prior to the field experiments, we cultivated collards under greenhouse conditions in plastic pots of 3 L (2 plants per pot) containing regular potting soil. Potted-collards were kept inside organza cages and watered manually about 2–3 times a week until experiment. Additionally, collards were artificially infested with aphids *Brevicoryne brassicae* (L.) (Hemiptera: Aphididae) inside the cages by placing a detached small collard leaf containing aphids (from a stock colony) atop the clean plants. Infested collards with 4–6 completely expanded leaves were used as sentinel plants in the field, where each selected border had one sentinel plant on both sides (1 m away from both sides of each border vegetation). The potted collards were buried to the soil surface level to simulate a realistic situation. All aphids on sentinel plants were counted and adjusted to have approximately equal initial numbers on the day of the experiment setup (~ 250–300 aphids/pot). Thereafter, the infested plants were allowed to stay in the field for 48 h. Following the 48-h field exposure, the number of aphids was counted again to estimate any potential increase/reduction in aphids. Furthermore, after the 48-h exposure and the aphid counts, the sentinel plants were individually enclosed by organza bags, and brought to the greenhouse to later assess any potential parasitism that might have taken place in the field (i.e. to count the number of mummified aphids).

Lastly, we carried out a bibliographic search for published articles that informed which of the plant species identified at the borders would commonly host aphids, and what species those aphids belonged to. For this search, we used keywords that included the species names of the most common plants along with the term 'aphid*' (or 'pulgão' and 'pulgões' for search in Portuguese). The search was conducted using Google Scholar and Web of Science. We consider this additional information to be important as some spontaneous plants in the borders might host aphids, which often can serve as alternative prey/host for natural enemies. Nonetheless, we did not sample for aphids *in situ* (i.e. to count visually) on the spontaneous plants at the moment of this study.

Statistical Analysis

All analyses were carried out in R statistical software (Development Core Team 2021). To test for differences of the proportion of plant species overlapping among border treatments (i.e. three-border overlap, two-border overlap, zero overlap), we carried out a Pearson chi-squared test through a contingency table analysis. Three-border overlap refers to the number of species present across all three types of border treatments. Two-border overlap indicates the number of species found in any two types of border treatments, while zero overlap refers to plants that occurred exclusively in a single type of border treatment. In this analysis, we assumed that the fewer the overlaps of plant species occurring among border treatments, the greater the differences in the composition of plant communities occurring in those borders. We did not assess plant diversity because measuring abundance would have required considerable additional effort, which was beyond the scope of this study.

The effects of border location (near annual crop, perennial crop, and forest areas), season (summer, winter, spring), and their interaction upon the richness of plant species inhabiting the borders were assessed by carrying out a Generalized Linear Model (GLM) analysis. Likewise, the effects of border location, season, and their interaction were tested on the abundance of herbivores (all taxa combined), natural enemies (all taxa combined), aphids, thrips, or whiteflies by carrying out analyses of covariance (ANCOVA) using the GLM function, in which the richness of plant species was set as the covariate. Normality of residuals and homogeneity of variance were also checked before running ANCOVA. All analyses aforementioned used a Poisson distribution in the models considering the counts of plant species or arthropods to follow such distribution. We also checked the data for overdispersion and the mean–variance relationship to ensure that the Poisson distribution was appropriate. Thereafter, any significant effect of the border location*season interaction led to post hoc pairwise analyses using the emmeans package (Lenth 2023) to compare within date (season) treatment means in regard to the effect of border location. Because borders were different across seasons, we took a conservative approach by comparing treatments within each season only. The potential identity effect—where differences between replicates might influence observed patterns rather than the treatment effect—was not investigated. This was because no borders were repeated across seasons; in each season, a new border was selected based on the treatments. Lastly, we investigated the effect of border location on the abundance of flowers by carrying out a Kruskal–Wallis analysis followed by Bonferroni-adjusted pairwise mean-comparisons (we used Kruskal–Wallis because of the lack of data normality).

To investigate whether field location and/or season could affect arthropod community structuring (i.e. composition) in the borders, we carried out Non-metric Multi-dimensional Scaling (NMDS) analysis using the package vegan (Oksanen et al. 2022). The analysis was carried out individually for the communities of herbivores, predators, and parasitoids. NMDS is a common way to summarize information from multidimensional data into a 2D representation or ordination. In such ordination, the closer two points are, the more similar the corresponding samples are with respect to the variables that were used to plot the NMDS graph. Furthermore, the NMDS analysis generates a 'stress' value, which somewhat works as the 'goodness of fit' of the data ordination (Clarke 1993; Smith and Mather 2012). Specifically, any stress value smaller than 0.2 indicates a good representation of the data. Moreover, anytime the NMDS analysis engendered a stress value smaller than 0.2 we followed up with a ANOSIM test to investigate whether there was a statistical difference between the arthropod communities (i.e. composition) in regard to border location and season. The ANOSIM test examines the relative similarity of samples 'within' versus 'between' groups, which is based on the Bray–Curtis percent dissimilarity index. This analysis generates a R-statistic value, which varies from 1 (meaning all similar samples come from the same group) to − 1 (meaning all similar samples come from different groups). Thus, a significant value of the R-statistic indicates that the community composition differs among borders. We employed different methods to assess community composition for plants and arthropods, as we only had species richness data for plants, whereas for arthropods, we had both abundance and richness data.

To investigate the potential for biological control, we assumed that any reduction in aphid numbers assessed on sentinel plants at the end of the 48-h field exposure was due to predation, whereas any increase was most likely due to reproduction. The aphid population growth rate was used as a proxy for measuring the impact of biological control (predation + parasitism). To do so, the per capita growth rate of aphids was calculated for each border treatment from each date (season) according to the following formula (Chau et al. 2005).

$$r = \frac{\ln(N_{X+1}/N_X)}{t}$$

where N_X is the aphid population size at time x, N_{X+1} the aphid population size at time $x+1$, t is the difference in days between time $x+1$ and x, and ln is Napierian logarithm. The Nx was represented by the initial aphid counts on sentinel plants, whereas the N_{X+1} was represented by the final aphid counts (at the end of 48 h) minus the number of mummified aphids (counted later after the 48-h exposure) on the same sentinel plants. To assess the impact of biological control on aphid population growth, we subjected the per capita growth rate data to an ANCOVA analysis using the GLM function, where the plant species richness was inserted as the co-variable.

Results

There was a significant difference in the proportions of plant species overlap among the three categories: species overlapping across all three border types, species overlapping across two border types, and species not overlapping at all ($\chi^2 = 10.53$, $P = 0.0324$) during each season (Fig. 1). Nevertheless, the plant species overlap occurring among border treatments was very low in any season (i.e. most species did not overlap across border type), suggesting differences in the composition of plant communities in relation to border location (Fig. 1). Additionally, there was a significant effect of border location and border location*season interaction on the richness of spontaneous plant species occurring in the borders (Table 1). Specifically, higher plant species richness was found in the borders next to areas of forest and annual crops during winter and spring (Fig. 2a). A total of 186 plant species/specimens were found occurring in the field borders (Appendix S1: Table S2). In general, the most common plant specimens encountered were in the Families/Genera of Asteraceae, Fabaceae, Poaceae, Ipomea, Amaranthus, Desmodium, and Sida (Appendix S1: Table S2). Interestingly, most plants of Asteraceae or Fabaceae were found almost exclusively in borders next to forest areas, whereas plants of Poaceae were mostly found in borders next to perennial crop areas (Appendix S1: Table S2). The most common Genera of spontaneous plants known from the literature to harbor aphids were *Amaranthus*, *Baccharis*, *Bidens*, *Brachiaria*, *Chamaesyce*, *Commelina*, *Copaifera*, *Desmodium*, *Eleusine*, *Emilia*, *Lantana*, *Sida*, *Siparuna*, *Solanum*, *Vernonia*, *Veronica*, and *Zanthoxylum* (Appendix S1: Table S2). Although these plants can harbor a variety of aphid species, the most commonly identified aphid species to occur on those plants according to the literature is *Aphis gossypii* Glover, 1877 (Appendix S1. Table S2). Lastly, a higher abundance of flowers in general was found on plants occurring in borders next to annual or perennial crop areas (Fig. 3).

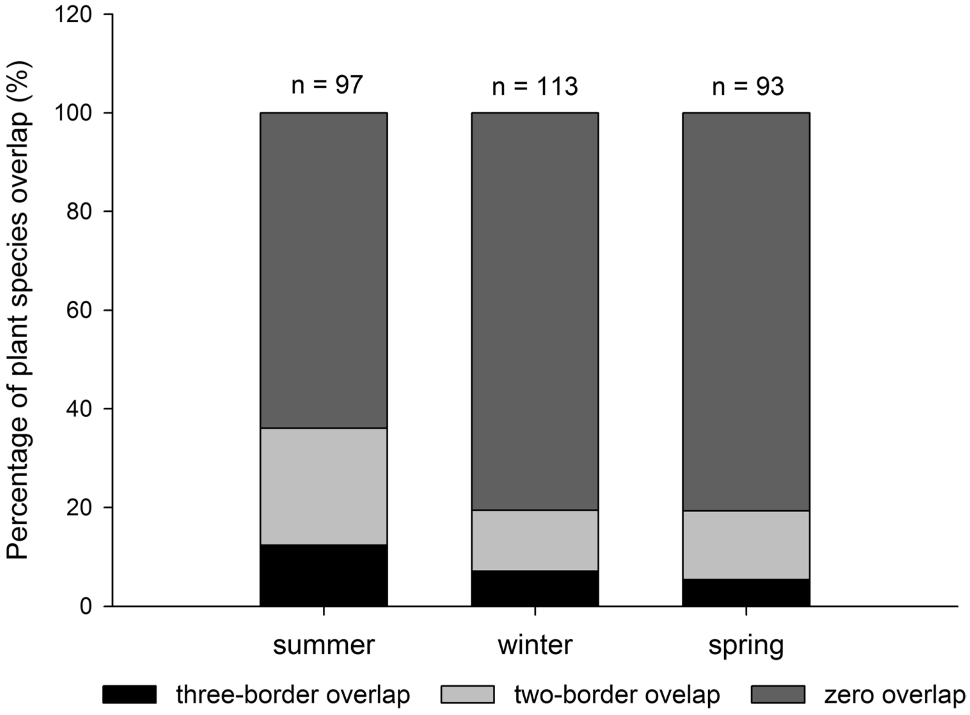

Fig. 1 The proportions of plant species/specimens overlap among border locations in each season. three-border overlap = same plant species/specimen occurring in the three border locations; two-border overlap = same plant species/specimen occurring in two border locations; zero-overlap = plant species/specimen that occurred only in one type of border location. *n* = number of plant species/specimens. Three-border overlap refers to the number of species present across all three types of border treatments. Two-border overlap indicates the number of species found in any two types of border treatments, while zero overlap refers to plants that occurred exclusively in a single type of border treatment

Table 1 Results of statistical analyses concerning the effects of the factors (i) border location (annual crop, perennial crop or forest area), (ii) season (summer, winter, spring), and covariable (iii) plant richness on several response variables

Response variables	Effect variables	Chisq	*P-value*
Plant species richness	Location	11.18	0.0037
	Season	4.35	0.1141
	Location*season	10.36	0.0348
Abundance of all herbivores	Location	2462.75	< 0.0001
	Season	568.56	< 0.0001
	Location*season	412.30	< 0.0001
	Plant richness†	123.22	< 0.0001
Abundance of all natural enemies	Location	152.08	< 0.0001
	Season	228.26	< 0.0001
	Location*season	280.18	< 0.0001
	Plant richness†	106.08	< 0.0001
Abundance of aphids	Location	208.45	< 0.0001
	Season	45.69	< 0.0001
	Location*season	0.70	0.7004
	Plant richness†	0.06	0.8096
Abundance of thrips	Location	555.26	< 0.0001
	Season	282.32	< 0.0001
	Location*season	337.62	< 0.0001
	Plant richness†	192.40	< 0.0001
Abundance of whiteflies	Location	353.75	< 0.0001
	Season	578.45	< 0.0001
	Location*season	348.98	< 0.0001
	Plant richness†	42.63	< 0.0001
Growth rate of aphids (*r*)	Location	5.81	0.0540
	Season	3.83	0.1469
	Location*season	3.67	0.4515
	Plant richness†	0.24	0.6215
Number of flowers	Location	8.17	0.0167

†Co-variable for the GLM/ANCOVA analysis

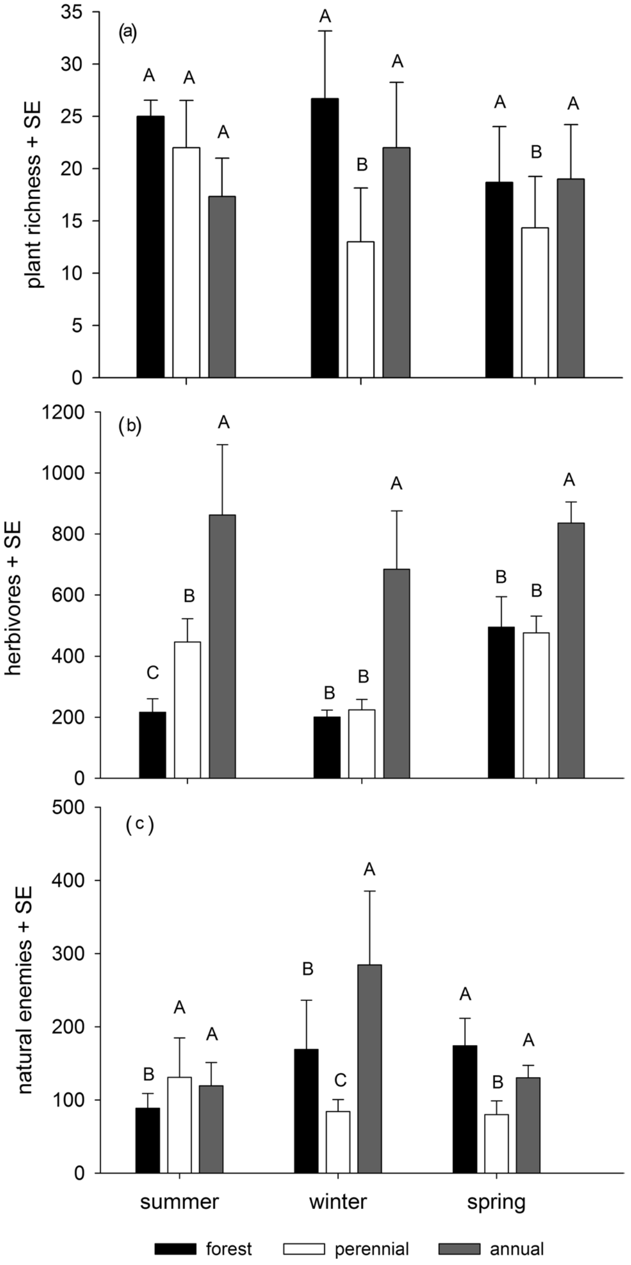

Fig. 2 Plant richness (a), total herbivore abundance (b), and total natural enemy abundance (c) in relation to border location (annual crop, perennial crop, forest) and to season (summer, winter, spring). Bar values followed by distinct letters within each season differ statistically at *P*-value < 0.05 (emmeans pairwise comparisons)

The general abundance of herbivores and natural enemies was significantly influenced by all effect variables (border location, season, border location*season interaction) and co-variable (plant richness) (Table 1). Likewise, all key herbivorous pests (thrips and whiteflies) were also affected by all effect variables and co-variable (mentioned above), with the exception of aphids which were influenced significantly only by border location and season (Table 1). The abundance of either all herbivores together, or aphids alone, was significantly higher in field borders next to annual crop areas (Fig. 2b, Appendix S1: Fig.S2i), whereas the abundance of thrips or whiteflies was more season dependent (Appendix S1: Fig. S2ii and S2iii). Nonetheless, during the summer, the abundance of thrips and whiteflies was also higher in borders next to annual crop areas (Fig. S2ii and S2iii). Additionally, the abundance of aphids alone was also higher in field borders next to perennial crop areas when compared to those next to forest areas (Appendix S1: Fig. S2i). Because aphids were squished and tangled up on the sticky traps, it was not possible to safely identify them to Genus/Species level. Some other relatively common general herbivores encountered in the borders were leafhoppers, leaf beetles, dipterans, orthopterans, and stink bugs (Appendix S1: Table S3).

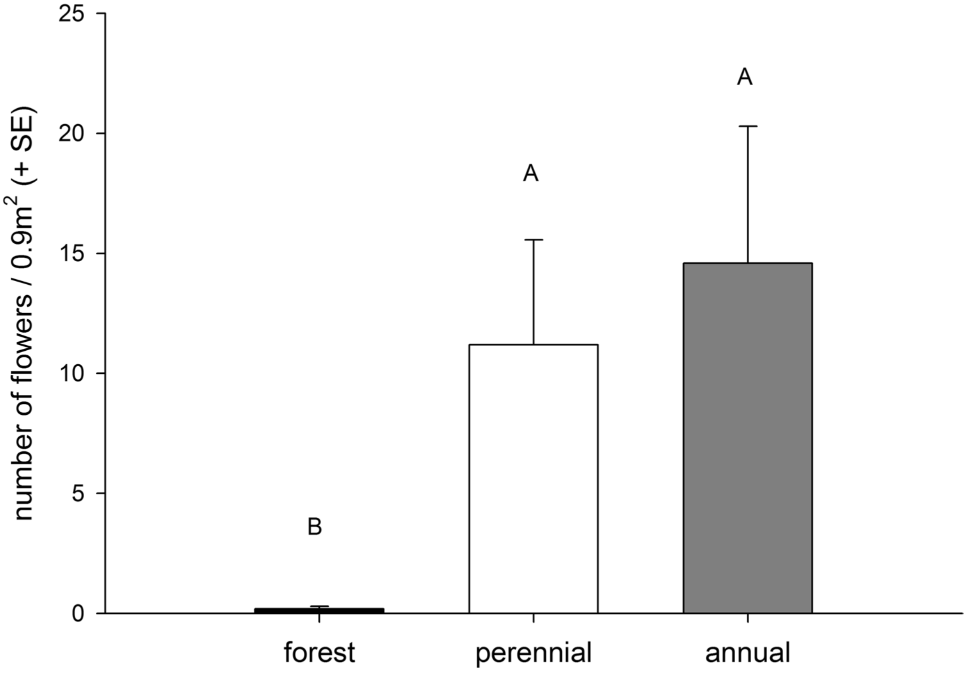

Fig. 3 Number of flowers per 0.9 m.^{2} (mean + standard error) on plants in field borders next to annual and perennial crop areas or forest. Bar values followed by distinct letters differ statistically at *P*-value < 0.05 (Bonferroni-adjusted pairwise comparisons after the Kruskal–Wallis analysis)

The most abundant predators found were long-legged flies, spiders, rove beetles, and wasps (Appendix S1: Table S4). In general, the abundance of predator taxa and parasitoid morphospecies occurring in the borders next to either forest or perennial crop areas was more season dependent, whereas their abundance in the borders next to annual crop areas tended to be high in all seasons (Fig. 2c, Appendix S1: Table S4).

The Non-metric Multi-dimensional Scaling (NMDS) analyses revealed significant differences in community composition/structuring for the functional groups of herbivores, predators, and parasitoids in relation to border location and/or season (Appendix S1: Figs. S3, S4, S5). All NMDS analyses (i.e. for herbivores, predators, and parasitoids) produced stress values smaller than 0.2, suggesting a good fit of the data ordination for testing the community structuring. Additionally, the ANOSIM test indicated that both variables border location and season influenced the differences in parasitoid or herbivore communities, whereas for predators only the variable season contributed to differences in community composition (Table 2). However, caution is warranted in interpreting these results. Although the difference is statistically significant, the strength of the effect is limited, and it is not possible to confidently assert a substantial biological difference.

As for the potential of biological control, the ANCOVA analysis showed that only the border location variable affected significantly the aphid per capita growth rate on sentinel plants (Table 1). Specifically, the growth rate of aphids was more negatively affected in the borders next to perennial or annual crop areas (Fig. 4).

Table 2 Results of ANOSIM test from investigating the effects of border location (annual crop, perennial crop, or forest area) and season (summer, winter, spring) on the community composition of arthropods (predators, herbivores, or parasitoids)

Response variables	Effect	R*	*P-value*
Predator community composition	Location	0.0082	0.3751
	Season	0.3000	< 0.001
Herbivore community composition	Location	0.2400	0.0027
	Season	0.2912	< 0.001
Parasitoid community composition	Location	0.3200	< 0.001
	Season	0.1100	0.0343

*R-statistic value varies from 1 (meaning all similar samples come from the same group) to – 1 (meaning all similar samples come from different groups). A significant value of the R-statistic indicates that the community composition is affected by the corresponding factor (i.e. location or season)

Discussion

Mitigating agricultural intensification has become a vital effort to preserve important ecosystem services as well as to promote food security and healthy environments. In this context, great efforts are underway around the globe to reduce the negative impact of pesticides, which has been one of the main problems of agricultural intensification. At the frontline of this endeavor, we have habitat management as a valuable approach to incentivize the natural biological control of pests. In this sense, spontaneous vegetation in field borders has shown the potential to contribute with

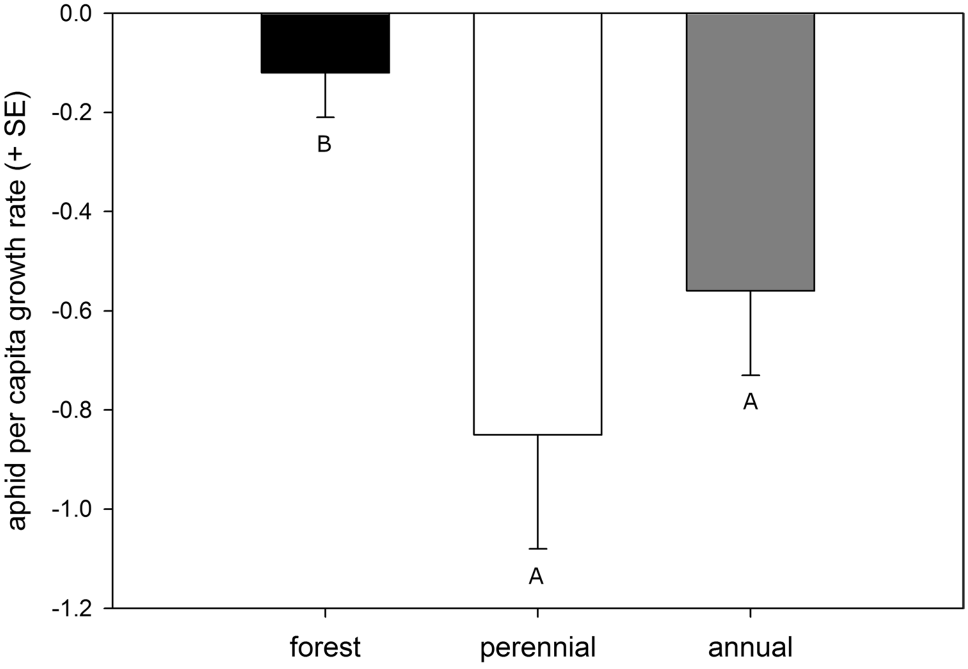

Fig. 4 Effect of border location (annual crop, perennial crop, forest) on aphid per capita growth rate (*r*) on sentinel plants (mean + standard error). Negative values signify reduction in aphid numbers over time. Bar values followed by distinct letters differ statistically at *P*-value < 0.05

natural enemy conservation at very low cost (or, at no cost at all) for farmers. However, very little is known about how field borders interact with land use intensification, and how this would play out in the perspective of supporting biological control in the field. In light of that, in the current study, we investigated at local scale how the context of land use intensification could influence the communities of plants and arthropods occurring spontaneously in field borders, and whether this could consequently affect the potential of those borders to promote natural biological control.

There was a very low overlap of plant specimens occurring in the different border locations, suggesting an influence of the land use type on the composition of plant communities. Regardless, the plant species richness was significantly higher in borders exposed to areas with contrasting levels of agricultural intensification (highest and lowest), i.e. more plant species in the borders next to either annual crop or forest areas. In fact, previous studies have indicated that local factors such as farming type and location can significantly influence the richness and composition of plant species occurring in agricultural fields (Tarmi 2011; Blaix and Moonen 2020; José-María et al. 2011; Poinas et al. 2023). Part of these results may be explained by the fact that variation in farming type and location could work as an environmental filter to select distinct functional traits, thereby leading to different plant communities (José-María et al. 2011). Our hypothesis of expecting lower plant species richness in borders next to annual crops was not supported by the data; but instead a higher richness was detected. Regardless, the data suggest that while exposed to opposite levels of agricultural intensification (highest and lowest), the annual crop and forest areas may each favor distinct plant traits that will result in high plant richness in both border types (with different species composition).

More herbivores (especially aphids) were encountered in borders next to annual or perennial crop areas. This result suggests that spontaneous vegetation bordering agricultural fields will be more prone to harbor more herbivorous insects, most of which in our study apparently are not considered key pests for the crops we considered (soybean, maize, or wheat). The abundance of natural enemies on the other hand was more season dependent when occurring in borders next to forest and perennial areas, whereas in borders next to annual crop areas their abundance was higher in any season. The more intensive management carried out for crops in agricultural fields and the lower plant diversity (i.e. crop monoculture) therein may jointly function as a ‘push-force’ driving arthropods to more plant-diverse adjacent areas such as field borders (Macfadyen and Muller 2013; Macfadyen et al. 2015). This may be particularly true in the case of generalist arthropods (e.g. herbivores) that are not directly related to the crop in the agricultural field, which therefore will seek alternative habitats (i.e. with more resources). Moreover, in the case of natural enemies, the higher abundance of herbivores in borders next to perennial or annual crop areas may work as a ‘pull-force’ because they can often serve as alternative prey/host, which in turn can engender an attraction and subsistence of natural enemies (Settle et al. 1996; Wyss 1996; Hardwood et al. 2007; Gontijo et al. 2018; Rowen et al. 2019). Many previous studies have shown that field borders in fact have greater arthropod abundance and taxon richness than adjacent crop fields (Denys and Tscharntke 2002; Asteraki et al. 2004; Woodcock et al. 2009; Cole et al. 2007; Moreby 2007; Ramsay et al. 2007).

The composition of communities of herbivores and natural enemies in our study was likely to be also indirectly affected by border location and season. This may be so because those variables had a significant effect on the composition of plant communities in the borders, which in turn is expected to consequently influence/drive the composition of higher trophic levels. It is likely that different plant communities in the borders could work to filter/favor distinct arthropod functional traits, which will lead to different community compositions. In fact, various studies and reviews point out to plant functional traits as a selective force that lead to distinct arthropod compositions in a given habitat (Ebeling et al. 2018; Gardarin et al. 2018; Perović et al. 2018; Schuldt et al. 2019; Dominik et al. 2022; Silva et al. 2022). Nevertheless, in our specific case, further studies are necessary to assess how effective spontaneous border vegetation can be in filtering/selecting distinct arthropod functional traits and how this would play out in the context of agricultural intensification.

The border vegetation next to annual or perennial crop areas showed a higher potential to engender biological control of aphids on sentinel plants, as these borders seemed to affect more negatively the per capita growth of aphids in our study. Nonetheless, the results cannot confirm long distance spillover effects as the sentinel plants were very close to the borders. This result may have been driven by a combination of favorable natural enemy composition and abundance in those borders. In the case of natural enemy abundance, this metric was particularly high in the border vegetation next to annual crop areas, regardless of season. It has been shown that field borders actually attract natural enemies out of the crop fields when the latter is too poor (Boinot et al. 2020). Additionally, the plants in those border locations (annual and perennial) appeared to have more flowers and to harbor more herbivores (specially aphids), both of which can promote biological control through natural enemy conservation. Specifically, flowers and alternative prey are known to attract and complement natural enemies' diet, potentially leading to improved biological control of specific pests (Hardwood et al. 2007; Straub et al. 2008; Gontijo et al. 2013; Snyder 2019; Zuma et al. 2023). Furthermore, flowers in field borders may attract both pest and non-pest thrips (Walton and Isaacs 2011; Canovas et al. 2023). While caution is warranted when attracting pest species, non-pest thrips could contribute to the conservation of predators by serving as alternative prey. In this sense, by providing alternative prey (e.g. aphids, thrips), field borders may also function as banker plants that could support natural enemy populations and enhance biological control (Frank 2010; Chen et al. 2022; Wang et al. 2022). Our hypothesis of expecting lower biological control close to annual crop borders was not supported by the data; instead a lower potential was detected in borders next to forest areas. In fact, the contribution of forest areas to biological control of pests in nearby fields has yielded mixed results in the past, including positive, negative, and neutral effects (Winqvist et al. 2011; Tscharntke et al. 2016). In the case of negative or neutral effects, these might happen because certain types of forests (e.g. rain forest) will not filter/select plant or arthropod functional traits that would be conducive to biological control in agricultural fields. Nevertheless, further empirical studies are necessary to investigate this assertion.

While our study yielded valuable insights into the general relationships between border location and plant–arthropod interactions, it does not yet allow us to pinpoint the underlying mechanisms driving some of the observed patterns. Identifying all plants and arthropods to the species level and quantifying their abundance could provide a deeper understanding of community composition, dominance structures, and the specific roles played by key functional groups. Therefore, to advance a more mechanistic understanding of how field borders influence both crop and non-crop plants and associated arthropods, future studies should incorporate comprehensive taxonomic identification and quantification of all species present in the system. Moreover, future similar studies should also investigate the direction and distance of arthropod spillover taking into account the interplay between border vegetation and the neighboring crop habitat.

Taken altogether, this multi-season study informs that the potential for field border vegetation to promote biological control will depend on the context of agricultural intensification. Specifically, the land use type had a significant influence on the communities of plants and arthropods inhabiting field borders, therefore turning out to be an important factor to be considered in habitat manipulation. Nonetheless, more studies ought to be carried out in order to investigate the mechanisms that drive this multi-faceted relationship concerning land use type, border vegetation, and biological control. It appears that land use type influences biological control by selecting/favoring border plants that will conserve/promote natural enemies through the provision of adequate resources. Furthermore, our study highlights the ecological value of spontaneous border vegetation and supports the idea that its presence should be encouraged in agroecosystems, particularly in landscapes dominated by annual crops.

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Author Contribution LG conceived and designed the experiments. AS, RC, and CM worked on setting up experiments and collecting data. JS worked on plant identification. LG acquired funding and resources. LG carried out statistical analyses. All authors contributed to writing and revising the manuscript.

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Data Availability Data will be made available on request.

Declarations

Ethical Approval Not applicable.

Conflict of Interest The authors declare no competing interests.

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