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Experimental evidence of multiple ecosystem services and disservices provided by ecological intensification in Mediterranean agro-ecosystems

Hila Segre[1] | Michal Segoli[2] | Yohay Carmel[3] | Assaf Shwartz[1]

[1]Faculty of Architecture and Town Planning, Technion—Israel Institute of Technology, Haifa, Israel

[2]Mitrani Department of Desert Ecology, The Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion, Israel

[3]Faculty of Civil and Environmental Engineering, Technion—Israel Institute of Technology, Haifa, Israel

Correspondence
Hila Segre
Email: hilasegre@gmail.com

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Abstract

1. Intensifying agricultural production in sustainable ways is pivotal to increasing food production while reducing environmental impacts. Ecological intensification is based on managing organisms that provide services underlying crop production to simultaneously intensify agricultural production and increase biodiversity. However, few studies address the interactions and trade-offs between biodiversity, multiple ecosystem services and crop production.
2. We experimentally quantified the effect of uncultivated field margins, a prominent practice of ecological intensification, on agricultural production, biodiversity, as well as on multiple ecosystem services and disservices, in an intensive Mediterranean agro-ecosystem. We used a split-plot design and sampled butterflies, rodent and arthropod pests, arthropod natural enemies (both parasitoids and predators), weeds, damage to crop and crop yield in different distances into the field in 3 tomato and 11 wheat crops along the growing season.
3. Field margins increased natural enemy densities, reduced pest-damage to crop and consequently increased yield in tomato crops. Notably, we found that pest control by one predator species was dominant in the field centre, whereas parasitoid natural enemies were confined to the field edges. Pest control was more prominent in the late crop-stage compared to early season sampling and field margins increased weed control in tomato crops by reducing weed cover.
4. Field margins increased natural enemy densities in wheat at the beginning of the season, but effects on arthropod pests were inconsistent. Field margins slightly increased weed cover, but had no impact on rodent densities and total yield.
5. Butterfly abundance, but not richness, was positively affected by vegetated field margins.
6. *Synthesis and applications*. Promoting ecological intensification requires a holistic approach that considers the complex relationships among ecological and economic aspects of agro-ecosystems. We found that ecologically intensified field margins provided pest and weed control in the highly intensive tomato crop, yet they increased weed cover in wheat, which could potentially restrict yields at the field scale. Farmers' guidelines should therefore consider the interactive effects

of multiple services on a variety of crops. Moreover, biodiversity components that do not provide crop production services should be independently targeted (e.g. by sowing plants that provide food resources).

KEYWORDS
biodiversity conservation, biological pest control, crop damage, edge effect, field margins, sustainable farming, weed control, yield

1 | INTRODUCTION

Intensification of agriculture in past decades has resulted in changes to the agricultural landscape, leading to simplified landscapes with larger fields and the conversion of natural habitats to cropland (Robinson & Sutherland, 2002). These changes were accompanied by increased use of agrochemicals, intensive cultivation and heavy use of machinery that increased food production but resulted in a major loss of biodiversity (Tilman, Cassman, Matson, Naylor, & Polasky, 2002). This loss of biodiversity is directly linked to the loss of important supporting and regulating ecosystem services (e.g. pollination, pest control, soil structure and fertility) that can limit or even reduce future crop production (Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005). There is therefore an urgent need to identify solutions for more sustainable food production that can meet rising food demand with reduced impact on biodiversity and ecosystem services (Foley et al., 2005; Tilman et al., 2001).

A potential solution is ecological intensification, which promotes biodiversity-mediated ecosystem services that support agricultural production by restoring biodiversity (Bommarco, Kleijn, & Potts, 2013). It is based on the idea of replacing some or all anthropogenic inputs with natural capital by integrating ecosystem services into crop production (e.g. replacing fertilizers with rich soil biota to enhance soil fertility and pesticides with biological pest control), hence increasing both biodiversity and crop production. Reducing the dependency on anthropogenic inputs is essential for future crop production in the face of increased pest and weed resistance to agrochemicals (Bass, Denholm, Williamson, & Nauen, 2015; Westwood et al., 2018). One of the promising tools for ecological intensification is maintaining non-crop habitats in agricultural landscapes. Many studies have shown the importance of non-crop habitats such as fallow, field margins or forests to biodiversity in agricultural landscapes (Batáry, Dicks, Kleijn, & Sutherland, 2015; Marshall & Moonen, 2002). Non-crop habitats can provide essential resources, such as shelter and food, to both vertebrate and invertebrate species (Firbank et al., 2003; Holland et al., 2016). Some of these species provide valuable services, such as pollination and pest control, that can potentially increase the yield (Dainese et al., 2019; Kennedy et al., 2013). For instance, populations of natural enemies tend to increase in heterogeneous landscapes with high proportions of surrounding non-crop habitats (Chaplin-Kramer, O'Rourke, Blitzer, & Kremen, 2011; Rusch et al., 2016).

Despite these recorded benefits, there is little evidence that non-crop habitats are effective in providing pest control that results in increased crop production (Chaplin-Kramer et al., 2011). Even when non-crop habitats increase densities of natural enemies in nearby crops, this is not necessarily translated into decreased pest populations (Karp et al., 2018), and even decreased pest populations do not guarantee increased yields (Letourneau et al., 2011). One reason is that non-crop habitats may benefit natural enemies, but they can also increase unwanted pest populations (Sivakoff, Rosenheim, Dutilleul, & Carrière, 2013). For instance, non-crop habitats in the landscape increase weed richness and seed bank (Fried, Norton, & Reboud, 2008; Roschewitz, Gabriel, Tscharntke, & Thies, 2005) and provide resources and refuge from predators for rodents that can later colonize the field (Fischer et al., 2018; Rodríguez-Pastor, Luque-Larena, Lambin, & Mougeot, 2016). The result can be major crop losses due to various pests (Bommarco et al., 2013; Pretty, 2008; Wilcox, Perry, Boatman, & Chaney, 2000).

The net effect of ecological intensification on crop production depends on multiple services and disservices that may impede its potential (Gagic et al., 2017; Garibaldi et al., 2018). To date, only few studies have quantified the cumulative effect of ecological intensification on biodiversity, multiple ecosystem services and disservices and crop production (Garibaldi et al., 2017; Haddaway et al., 2018). Such understanding of the way various taxa interact to provide services or to damage crops, as well as the underlying mechanisms that drive these processes, is key to developing ecological intensification practices (Kremen & Miles, 2012). An additional major gap is the lack of experimental evidence, as the majority of existing studies remain correlative (Holland et al., 2017). Therefore, we need to move from studies focused on specific services to explore many services and disservices holistically (Dainese, Montecchiari, Sitzia, Sigura, & Marini, 2017; Pretty, 2008). Demonstrating that ecological intensification allows viable production and increased yields is important to promoting this approach among farmers who currently perceive non-crop habitats as a source of damage rather than benefit (Cordeau, Reboud, & Chauvel, 2011; Mante & Gerowitt, 2009).

Here, we quantify multiple ecosystem services and disservices of non-crop habitats and their cumulative effects on crop yield. We experimentally compared naturally regenerated field margins to cleared field margins and cultivated field borders to assess the potential benefits and damages attributed to the vegetation in field margins. We assessed multiple threats from weeds, invertebrate and vertebrate pests, and ecosystem services of weed and pest control, as well as crop production. We used butterflies as an indicator species for biodiversity since previous surveys have shown that this taxon is most sensitive to agricultural land use (Segre et al., 2019). Our aims were to (a) test whether field margins can simultaneously support both higher biodiversity and yield, (b) determine which ecosystem services and disservices significantly influence yield and (c) identify to what extent field margins affect biodiversity and ecosystem services inside the field.

2 | MATERIALS AND METHODS

2.1 | Study site and experimental design

The study was conducted on the eastern side of Jezreel valley, northern Israel. A set of 11 extensive cereal (wheat) fields and 3 intensive vegetable (tomato) fields was established before the 2016–2017 growing season (Appendix S1). Tomatoes were planted in March and harvested in July, and wheat was sown in November and harvested between April and June. Early wheat harvest is customary in fields that receive no irrigation and do not reach the ripening stage. All fields were conventionally treated with herbicides and pesticides and commercially harvested (Appendix S2).

Natural vegetation adjacent to the fields in this region is typically sprayed or tilled according to costs, accessibility and other farm considerations to reduce potential impact. Furthermore, Israel currently lacks agri-environmental programmes promoting field margins (Segre et al., 2019). To assess the effect of maintaining naturally regenerated field margins, we used a block design in which each field received the following three treatments (Figure 1, Appendix S1): (a) a vegetation treatment was established along 200 m of a field margin with natural vegetation; (b) a herbicide treatment was established along 200 m, continuing the vegetation treatment where possible, and included removal of the natural vegetation using herbicide application and cutting and (c) an adjacent crop treatment was established in another field edge bordering a cultivated field and was used to assess additional sources of arthropods and weeds in the focal fields. In wheat, this treatment was applied to nine fields where an adjacent crop was present. In tomatoes, the adjacent crop bordering one focal field was ploughed early in the season, leaving only two fields with seasonal resources necessary for arthropods. Therefore, we did not analyse arthropod measures in the adjacent crop treatment in tomatoes. Finally, weeds were not sampled in the herbicide treatments, since these reduce weed cover but do not affect the seed bank, which we expected would bias the results in an overly conservative direction.

Four sampling transects (100 m) were set up in each treatment parallel to the field edge: one transect (0 m) was located within the field margins (for the herbicide and vegetation treatment) or within the adjacent field (for the crop treatment) and three transects at 1, 10 and 50 m distances from the field edge (Figure 1). Herbicide transects were located at least 100 m from the vegetation transects to prevent spillover from the vegetation treatment.

2.2 | Sampling methods

We used 'Vortis' vacuum (Burkard Manufacturing Co. Ltd, Rickmansworth, UK) to sample arthropods from the vegetation along the four distances in the vegetation and herbicide treatments and the crop treatment in wheat alone. We sampled the wheat fields in February (early crop stage, before the heading stage of the crop) and April (late crop stage, before harvest) and the tomato fields in May (early crop stage, flowering stage) and June (late crop stage, before harvest). Arthropods were identified to the order/suborder or superfamily level. Orders/suborders/superfamilies were classified as potential pests if they include mostly species that potentially cause damage to the focal crops or potential natural enemies if they include mostly species that are known to be natural enemies (e.g. predators and parasitoids; Table S2). Important pests of wheat and tomatoes that are known to be monitored by farmers in this area and their known natural enemies were subsequently identified to the species or family level (Appendix S3, Table S2). The abundance of these known natural enemies and pests was low in the wheat fields; therefore, the analysis for the wheat fields was performed only at the total pest and natural enemy abundance level. In the tomato fields, important pests and natural enemies in each crop stage were analysed if the samples contained at least 30 individuals.

We assessed damage to the tomato crop by arthropod pests at the late crop stage (end of June), 2 weeks before harvest, in the vegetation and herbicide treatments along each transect inside the field (1, 10 and 50 m). In all, 20 leaves were randomly collected from different plants along each transect, and we counted the number of leaf mines, damaged leaflets and number of holes per transect related to several important tomato pests (Appendix S3). We also collected a sample of 100 fruits from random plants in each transect and counted the number of fruits with damage per transect related to important tomato pests (Appendix S3). The amount of crop pests and damage to the wheat during the experiment was very low; therefore, damage to wheat crops was not assessed.

Weeds were sampled along each transect inside the field (1, 10 and 50 m) in the vegetation and crop treatments. We used 50 m transect lines and recorded all species present within 10 cm of either side of the transect line and their cover. Weeds were sampled once for each crop at the late crop stage (end of March/June for wheat/tomato).

Rodents were sampled at the end of March in the vegetation and herbicide treatments in six wheat fields. In each treatment, ten 10 m transects were sampled at 10 m intervals from the field edge (1 m) to its centre (90 m). In each transect, five traps were evenly spaced and left overnight with a total of 50 traps per treatment (Appendix S3). For each distance from the field edge (1–90 m), we calculated the total capture proportion out of five traps.

We recorded crop yield for both tomatoes and wheat in the three transects inside the field (1, 10 and 50 m) in all three treatments

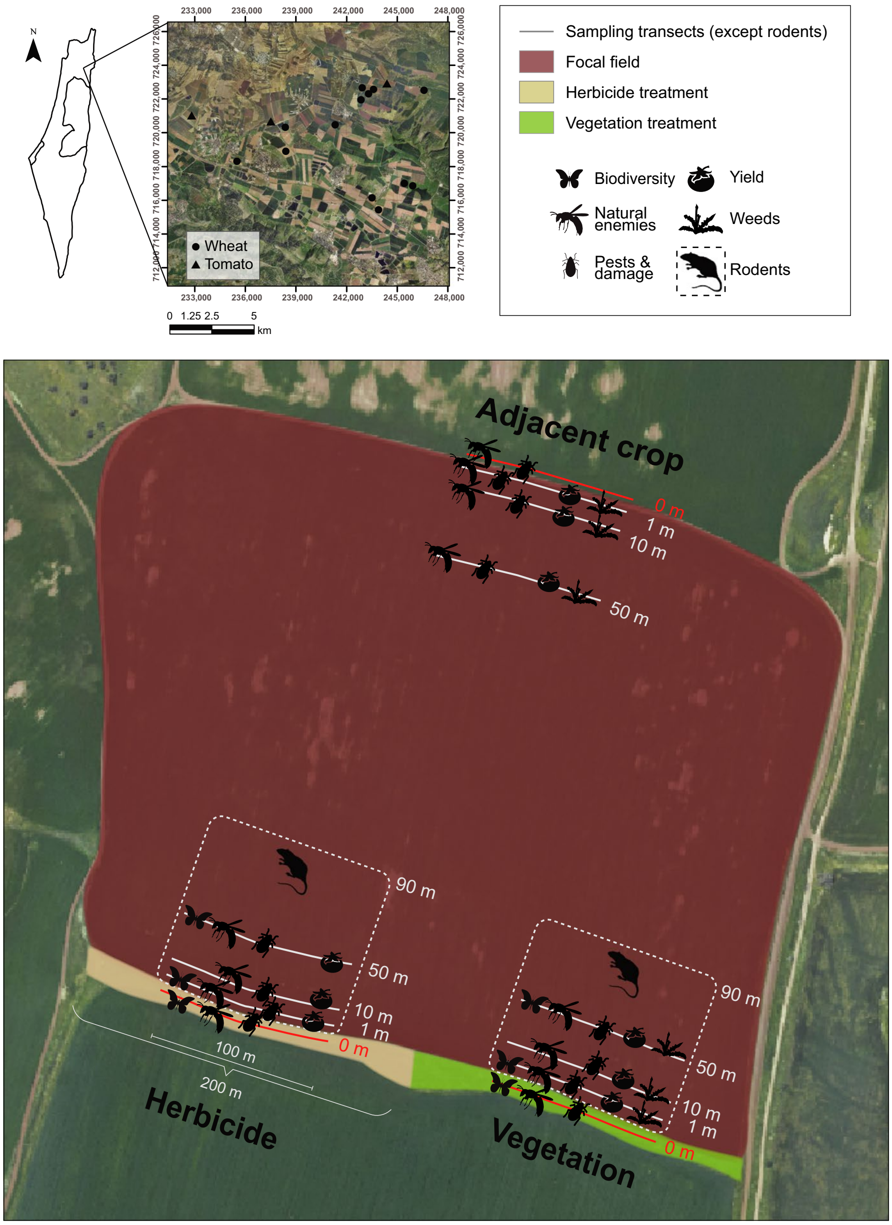

FIGURE 1 Map of the study area and a schematic representation of the experimental design. Lines indicate sampling transects of arthropod pest control, weed control, yield and biodiversity measures in the treated field margins or the adjacent crop (0 m) and 1, 10, 50 m into the field. Dashed quadrats indicate location of 10 evenly spaced transects of rodent traps (1–90 m inside the field)

using five evenly spaced 1 m × 1 m samples in each 100 m transect. We recorded wheat dry biomass in late March and tomato fruit biomass in July (Appendix S3). All five samples per transect were averaged to determine the mean weight or dry weight per 1 m^2.

Butterflies were sampled in the vegetation and herbicide treatments within field margins (0 m) and inside the field at 1–5 and 50 m distances, sampling 2.5 m from each side of the observer using Pollard walk (Pollard, 1977; Appendix S3). Each field was visited twice during March–June, and all transects in the field were sampled consecutively. Butterflies are not pests or natural enemies in tomato and wheat crops in the region.

Vegetation in the field margins was sampled in late February. We recorded all species in four evenly spaced 10 m × 1 m quadrats along a 100 m transect and all woody species that were present in a 20 m radius around the transect.

2.3 | Data analysis

Statistical analyses were performed using R software (R version 3.3.3). We used Linear and Generalized-linear mixed-effect models to assess the effect of the treatment (vegetation, herbicide or crop) and the distance from the field edge in wheat and tomato fields separately, using the field as a blocking factor (R packages 'NLME', 'LME4'). The significance of fixed effects was assessed using a likelihood-ratio chi-squared test. Non-significant interaction terms were removed from the models, and significant interactions were followed by multiple comparisons between treatments at each distance. We used principal component analysis of plant composition (R package 'STATS') to classify field margins and then used the most predictive PC-axes as explanatory variables in our models (Appendix S2). We used this method to model the treatment

TABLE 1 Summary of chi-squared test on generalized and linear mixed-effect models for all measures affected by field margins treatment and distance from field edge (χ^2 and sig. level). Non-significant terms are marked by (–). Significance levels: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, $^{(.)}p < 0.1$. Measures that were sampled in two crop-stages are shown separately for the early and late sampling. Butterfly model results refer to both visits. Models were run only if enemy/pest abundances were >30. PC, Plant composition (PC-axis in superscript). R^2, marginal R^2

		Early					Late				
Crop	Measure	Treatment	Distance	Treatment × distance	PC	R^2	Treatment	Distance	Treatment × distance	PC	R^2
Tomato	Enemy abundance	*n* = 24					*n* = 24				
	Total	4.37*	13.26**	7.17$^{(.)}$		0.41	13.35***	8.00*		8.30**$^{(1)}$	0.62
	Braconidae						–	–	–	6.28*$^{(1)}$	0.31
	Nesidiocoris tenuis						5.02*	25.79***	–	10.82**$^{(1)}$	0.64
	df	1	3	3			1	3	3	1	
	Pest abundance	*n* = 24					*n* = 24				
	Total	–	24.30***	–		0.51	–	17.77***	–		0.38
	B. tabaci	–	8.13*			0.29	–	–	–	9.62**$^{(1)}$	0.31
	df	1	3	3			1	3	3	1	
	Damaged fruit						*n* = 18				
	Thrips						2.86$^{(.)}$	–	–		0.06
	Tuta absoluta						4.45*	8.00*	–		0.31
	df						1	2	2		
	Damage to leaves						*n* = 18				
	T. absoluta						2.82$^{(.)}$	8.41*	–		0.39
	Leafminers						–	16.35***	–	6.11*$^{(2)}$	0.63
	df						1	2	2	1	
	Weeds						*n* = 18				
	Cover (%)						4.35*	20.38***	–		0.56
	Richness						–	19.58**	–		0.54
	df						1	2	2		
	Butterfly	*n* = 36									
	Abundance	3.56$^{(.)}$	5.91$^{(.)}$	–		0.24					
	Richness	–	–	–		0.02					
	df	1	2	2							
	Yield						*n* = 135				
	Weight						9.17*	75.25***	–	13.28***$^{(3)}$	0.42
	df						2	2	4	1	

(Continues)

TABLE 1 (Continued)

		Early					Late				
Crop	**Measure**	**Treatment**	**Distance**	**Treatment × distance**	**PC**	R^2	**Treatment**	**Distance**	**Treatment × distance**	**PC**	R^2
Wheat	Enemy abundance	*n* = 101					*n* = 91				
	Total	19.49***	87.39***	13.84*	45.86***(3)	0.89	—	66.97***	—	3.94*(3)	0.44
	df	2	3	6	1		2	3	3	1	
	Pest abundance	*n* = 101					*n* = 91				
	Total	7.66*	—	61.31***	7.19**(3)	0.43	19.98***	72.88***	—		0.36
	df	2	3	6	1		2	3	3		
	Weeds						*n* = 66				
	Cover (%)						2.90(.)	—	—	10.69**(1)	0.18
	Richness						—	—	5.70(.)	12.86***(1)	0.16
	df						1	2	2	1	
	Rodents	*n* = 120									
	Captures	—	—	—		<0.01					
	df	1	1	1							
	Butterfly	*n* = 108									
	Abundance	—	12.90**	7.51*		0.12					
	Richness	—	17.42***	—	3.13(.)(1)	0.17					
	df	1	2	2	1						
	Yield						*n* = 415				
	Weight						9.40**	51.78***	18.41**	5.49*(2), 6.66**(3)	0.32
	df						2	2	4	1, 1	

effect on total pest abundance, total natural enemy abundance, abundances of important crop pests and their natural enemies, all measures of damage to tomato fruit and leaves, weed cover and richness, rodent capture proportion, tomato and wheat yield, butterfly abundance and richness (see Appendix S4 for model specification). Full results of all models are presented in Table 1, and representative figures highlight the important results in the main text, while all graphs are shown in Figures S1–S10.

3 | RESULTS

3.1 | Arthropod natural enemies

Natural enemies were generally more abundant in the vegetation treatment than in the herbicide treatment for both crops, yet differences persisted throughout the entire agricultural season in tomato fields only. In tomatoes, total natural enemy abundance was higher in the vegetation treatment than in the herbicide treatment in both crop stages and decreased towards the field centre (Table 1; Figure 2a; Figure S1a, respectively), but the treatment effect in May was only significant in the field margins (0 m; Table 1, $t = 3.04$, $p < 0.001$, Figure S1a). The abundance of the generalist predator *Nesidiocoris tenuis* was positively affected by the vegetation treatment and by distance in June (Table 1; Figure 2b). Braconid parasitoid abundance was unaffected by treatment or distance in June (Table 1; Figure S3a). Abundance of both *N. tenuis* and braconid wasps was <30 individuals in May. The total natural enemy, *N. tenuis* and braconid abundances were all affected by the field margins vegetation composition in June (Table 1). In wheat fields, total natural enemy abundance was higher in the vegetation treatment than in the herbicide and crop treatments in the field margins (0 m) in February; it also decreased towards the field centre and was affected by vegetation composition (Table 1, $z = 3.60$, $p < 0.001$ and $z = 5.05$, $p < 0.001$, respectively, Figure 3a). In April, total natural enemy abundance was only affected by distance and vegetation composition (Table 1; Figure S2c).

3.2 | Arthropod pests

The abundance of pest species demonstrated inconsistent patterns among crops, treatments and distances from the field edge. Total

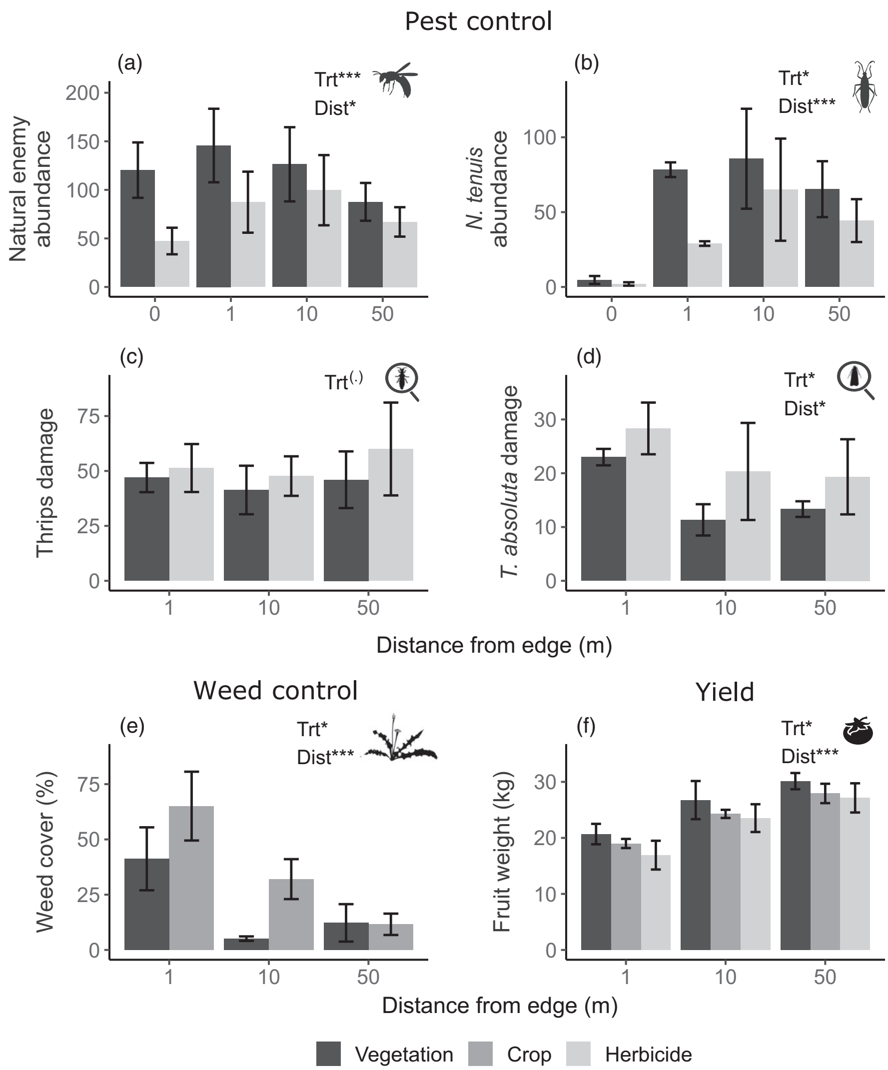

FIGURE 2 Pest control, weed control and yield measures in tomato fields in vegetation, herbicide and crop treatments at different distances from field edge ($M \pm SE$; 0 m is within the field margins/adjacent crop). (a) Total natural enemy abundance in June, (b) total abundance of the predator *Nesidiocoris tenuis* in June, (c) number of fruits damaged by thrips, (d) number of fruits damaged by the pest *Tuta absoluta*, (e) weed cover and (f) yield weight. Dist, distance; Trt, treatment (interaction was n.s.). Significance levels: $^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{(.)}p < 0.1$

pest abundance in tomato fields was not affected by the treatments but was affected by distance, with opposite trends in the early and late crop stages (Table 1; Figure S1b,d). The most dominant pest in tomato fields was the whitefly *Bemisia tabaci*. *Bemisia tabaci* abundance decreased towards the field centre in May, was affected by vegetation composition in June and showed a small non-significant decrease in the vegetation treatment in the margins (0 m) in both crop stages (Table 1; Figure S4).

Total pest abundance in wheat fields in February showed a mixed response; it was higher in the herbicide treatment than in the vegetation and crop treatments within the field margins (0 m; Table 1, $z = 6.78$, $p < 0.001$ and $z = 4.82$, $p < 0.001$, respectively, Figure 3b) but lower in the field centre (50 m; Table 1, $z = -3.30$, $p < 0.01$ and $z = -2.39$, $p < 0.05$, respectively, Figure 3b). In April, pest abundance in wheat fields was lower in the crop treatment than the vegetation and herbicide treatments, was negatively affected by distance and responded to vegetation composition (Table 1, $z = -2.88$, $p < 0.05$ and $z = -4.47$, $p < 0.001$, respectively, Figure S2d).

3.3 | Damage to fruit and leaves

In tomato fields, we found less damage from thrips (Thysanoptera; marginally significant) and the tomato leafminer *Tuta absoluta* in the vegetation treatment than in the herbicide treatment (Table 1; Figure 2c,d). Damage from the tomato leafminer decreased towards the field centre, while damage from thrips was not affected by distance (Table 1; Figure 2c,d). We found fewer leaf mines of *T. absoluta* in the vegetation treatment than in the herbicide treatment (marginally significant, Table 1; Figure S6a). The number of leaf mines of both *T. absoluta* and fly leafminers (*Liriomyza* spp.) decreased towards the field centre, and fly leafminers were also affected by vegetation composition (Table 1, Figure S6a,b).

3.4 | Weeds

The vegetation treatment was effective in decreasing weed cover in tomato fields but slightly increased weed cover in wheat fields. In tomato fields, weed cover was lower in the vegetation treatment than in the crop treatment and both weed cover and richness decreased towards the field centre (Table 1; Figure 2e; Figure S7a). In wheat fields, weed cover was higher in the vegetation treatment than in the herbicide treatment at all distances (marginally significant, Table 1; Figure 3c). Weed richness was also higher in the vegetation treatment than in the herbicide treatment but only 1 m from the field edge (Table 1, $z = 2.41$, $p < 0.05$, Figure S7c). Weed cover and richness in wheat fields were both affected by vegetation composition (Table 1). Table S4 presents the cover of the dominant species.

3.5 | Rodents

The proportion of rodent captures was not affected by treatment or distance (Table 1; Figure S8). The species captured most often were *Mus* sp. and *Meriones tristrami*, which are common pests in this area.

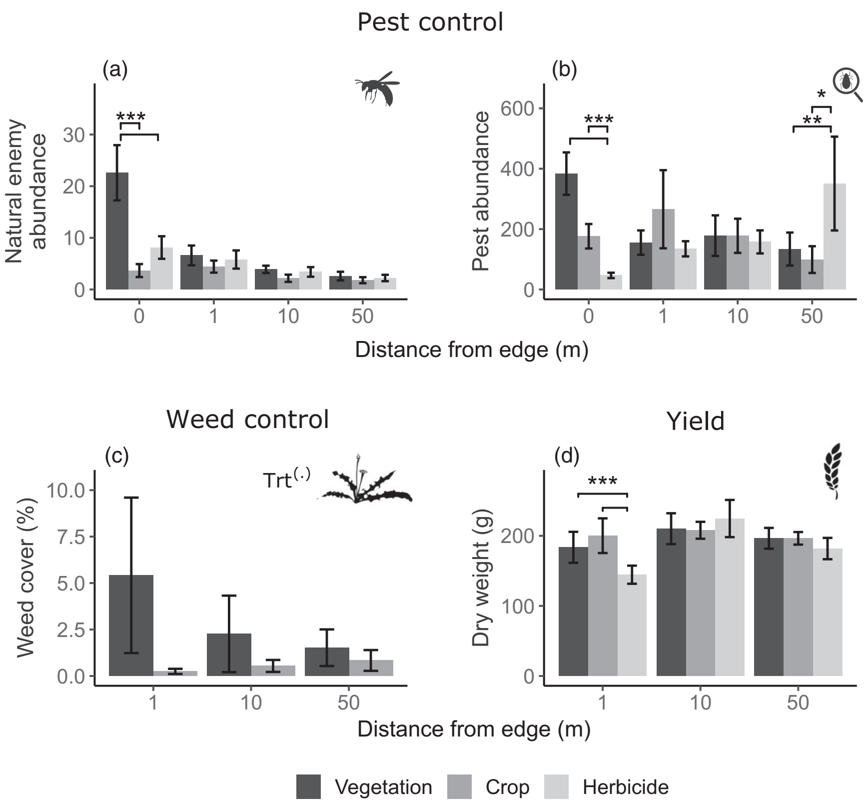

FIGURE 3 Pest control, weed control and yield measures in wheat fields in vegetation, herbicide and crop treatments at different distances from field edge ($M \pm SE$; 0 m is within the field margins/adjacent crop). (a) Total natural enemy abundance in in February, (b) total arthropod pest abundance in February, (c) weed cover and (d) yield weight. Dist, distance, Trt, treatment, otherwise brackets denote Tukey adjusted values where interaction was significant. Significance levels: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, $^{(.)}p < 0.1$

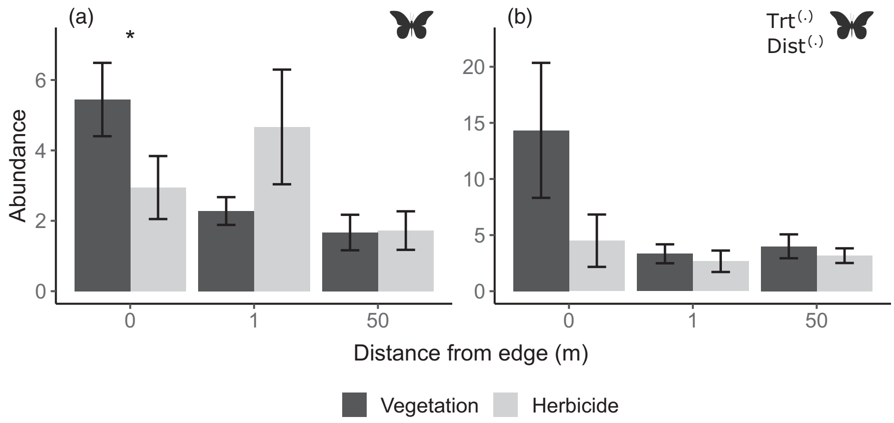

FIGURE 4 Butterfly biodiversity measures in tomato and wheat fields in vegetation and herbicide treatments at different distances from field edge ($M \pm SE$; 0 m is within the field margins). (a) Butterfly abundance in wheat fields and (b) butterfly abundance in tomato fields. Dist, distance, Trt, treatment, otherwise Tukey adjusted values are shown where interaction was significant. Significance levels: $^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{(.)}p < 0.1$

3.6 | Yield

Tomato yield was highest in the vegetation treatment, moderate in the crop treatment and lowest in the herbicide treatment at all distances from the field edge and increased towards the field centre (Table 1, vegetation-herbicide: $t = -3.32$, $p < 0.01$, Figure 2f). Wheat yield was lower in the herbicide treatment only 1 m from the field edge and was affected by vegetation composition (Table 1; Figure 3d).

3.7 | Butterfly biodiversity

The vegetation treatment had a small but positive effect on butterfly diversity. Butterflies were more abundant in the vegetation treatment than in the herbicide treatment within the field margins (0 m) in wheat fields and at all distances from the field edge in tomato fields (Table 1; Figure 4a,b). Butterfly richness in wheat fields decreased towards the field centre and was affected by vegetation composition (Table 1; Figure S10b,d).

4 | DISCUSSION

Ecological intensification can alter the way intensive agriculture is perceived, as it allows the promotion of biodiversity conservation and high-yielding agriculture. However, limited empirical evidence demonstrating these mutual benefits may hinder farmers from implementing ecological intensification practices (Bommarco et al., 2013). Ecosystem services and disservices may interact to affect crop yield and should be simultaneously studied to fully understand the mechanisms that facilitate ecological intensification (Garibaldi et al., 2018; Kremen & Miles, 2012). To address these knowledge gaps, we experimentally tested the dynamics and interactions between multiple ecosystem services and disservices provided by field margins and their effect on the yield of two crops. Overall, we identified pest and weed control processes that provide evidence for ecological intensification supporting increased yields in tomatoes but not in wheat accompanied by moderate benefits to biodiversity conservation (Figure 5). This result implies that in some cases, current farmer field margin management approaches of applying herbicides are not optimal and promoting uncultivated field margins can replace some anthropogenic inputs. However, establishing guidelines for farmers will require further corroboration since our sample size for tomatoes was small.

Field margins with natural vegetation increased the abundance of natural enemies, reduced pest damage and increased yield, adding to the recent evidence of ecological intensification (Pywell et al., 2015; Tschumi et al., 2016). The edge effect of pest abundance persisted in the herbicide treatment while maintaining the vegetation decreased pest populations and damage to crops by several pests. Although our sample size was relatively small for the tomato fields, our findings corroborate previous studies indicating that non-crop habitats promote biological control in tomato crops (Balzan & Moonen, 2014; Pease & Zalom, 2010). However, these studies focused on crop damage at the field edge, whereas our results further reveal that biological control associated with non-crop habitats increase yields and extends into the field centre. This is contrary to sharp declines in biological control from the field edge to the field centre reported by Boetzl, Krimmer, Krauss, and Steffan-Dewenter (2019), suggesting that some natural enemies may be effective in large crop fields (Segoli & Rosenheim, 2012). Specifically, Boetzl et al. (2019) surveyed ground dwelling arthropods, which may be less mobile than the flying natural enemies sampled in our study. The effect of pest control in wheat fields was smaller and persisted only in the early growing period. Later in the season, field margins introduced higher pest densities than the adjacent fields, suggesting that crop diversification may also restrict pest populations (Baillod, Tscharntke, Clough, & Batáry, 2017).

Biological pest control was probably driven primarily by specific natural enemies rather than by overall natural enemy densities (see also Letourneau, Jedlicka, Bothwell, & Moreno, 2009). The predatory bug *N. tenuis* was found in higher abundance in the vegetation treatment than in the herbicide treatment and dispersed from the field margins into the field centre, a trend that was accompanied by a reduction in pest damage. *Nesidiocoris tenuis* preys on several tomato pests, such as thrips, leafminers and *B. tabaci*, but it has proven most effective for controlling the oligophagous pest *T. absoluta* in trials of commercial applications (Shaltiel-Harpaz et al., 2016). This could explain why the reduction in *T. absoluta* damage was most pronounced, a trend that provides

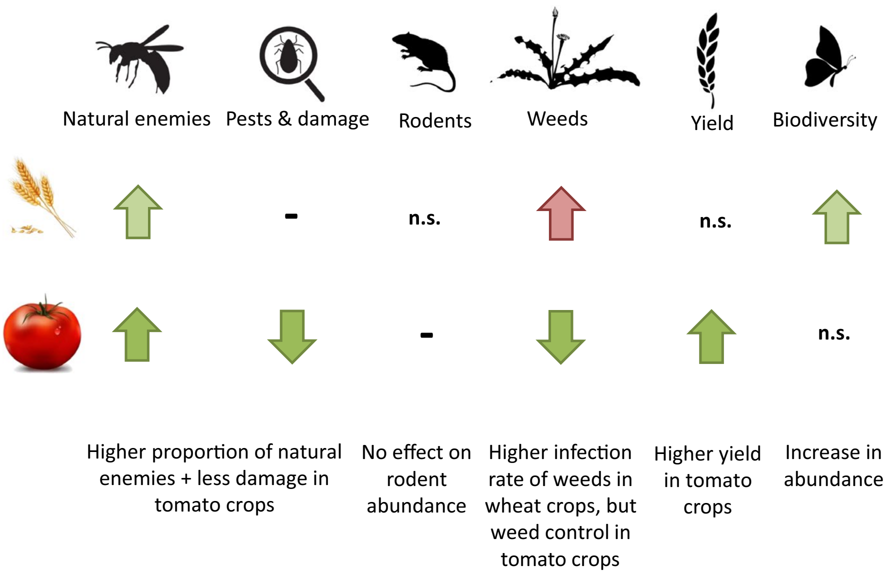

FIGURE 5 Qualitative overview of the main measures for ecological intensification (pest control, weed control and biodiversity). Arrow direction indicates increase or decrease in richness/abundance, arrow colour indicates ecological intensification (green) or damage (red). Dark arrows indicate strong evidence and light arrows indicate weak evidence. Non-significant effects are marked with n.s. and effects that were not tested are marked as (-)

important evidence that maintaining uncultivated field margins can control this economically important pest. The total abundance of natural enemies also increased in response to maintaining uncultivated field margins, yet it decreased towards the field centre. A plausible explanation for the low abundance in the field centre is that the most abundant natural enemies were parasitoid wasps (Table S2), which benefit from floral resources in the vegetation around the field and have low dispersion rates into the field centre (Landis, Wratten, & Gurr, 2000). Increasing non-crop habitats, which provide important resources, within large fields may thus enhance pest control by parasitoids and increase yields (Shapira et al., 2018). Indeed, natural enemies responded to vegetation composition. Although our experiment was not designed to assess the effect of specific plants, the results suggest that natural enemies were common in field margins with Umbelliferae species, for example, *Daucus* spp. and *Conyza* spp., which have been previously shown to attract parasitoids in Mediterranean regions (Kishinevsky, Keasar, Harari, & Chiel, 2017, pers. comm.).

Although weed management is a major obstacle to farmers' willingness to conserve vegetated field margins, studies rarely estimate weed control or weed damage (Holland et al., 2017; Mante & Gerowitt, 2009). Margins with natural vegetation reduced weed cover at all distances from the field edge in tomatoes and thus provided weed control. Most crop damage is attributed to a few dominant herbicide-resistant weeds (Petit et al., 2013). In tomatoes, these dominant weeds were found more often in the disturbed cultivated land than in the vegetated field margins (Tables S1 and S4), where they might be limited by competition with other species (De Cauwer, Reheul, Nijs, & Milbau, 2008). Accordingly, we did not detect an effect of field margins vegetation composition on weed cover in tomatoes.

In wheat, contrary to tomatoes, the vegetated field margins increased infestation with weeds compared to the adjacent crop treatment, although yield loss was not recorded. The absence of impact on yield could have resulted from the fact that weeds showed low dispersal rates into the field centre, in accordance with previous studies (De Cauwer et al., 2008; Reberg-Horton et al., 2011). However, even small effects on yield that were not significant at the fine scale of this study could result in significant damage at larger scales. Indeed, in a previous survey we conducted, we detected a negative effect of uncultivated field margins on wheat yield at the whole-field scale (Segre et al., 2019), and previous studies have shown similar trends in other cereal crops (Wilcox et al., 2000). These negative effects may trade-off with ecosystem services provided by field margins. This highlights that only when studied together can the mechanisms underlying ecological intensification be properly understood (Dainese et al., 2017).

Rodents are among the major pests in arable crops and often dwell in non-crop habitats (Fischer et al., 2018). Here, we found no evidence that maintaining natural vegetation in field margins increased rodent densities in wheat crops. The high variability in rodent densities among wheat fields may have overridden our small-scale field margin intervention (although incorporating tillage into our models did not reduce variability, see Appendix S2). Factors such as field management practices (e.g. variations in irrigation and conservation tillage) and landscape composition have previously been reported as important in determining rodent densities (Fischer, Thies, & Tscharntke, 2011). These landscape properties and field management practices may be more important than small-scale interventions of ecological intensification for this taxonomic group.

We used butterflies as an indicator for biodiversity due to their high sensitivity to agricultural intensity (Pe'er, van Maanen, Turbé, Matsinos, & Kark, 2011). Butterfly abundance was significantly higher in the field margins but sharply declined towards the field centre, indicating that butterflies utilized the non-crop habitat and strongly avoided the cultivated land. This underlines the importance of non-crop habitats such as uncultivated field margins in maintaining high biodiversity in agricultural landscapes (Concepción et al., 2012). Despite their positive effect on abundance, field margins failed to increase butterfly richness. However, butterfly richness was slightly affected by vegetation composition, suggesting possibilities to improve the management of this resource. In the absence of agri-environmental programs, field margins experience frequent soil and herbicide disturbances and are dominated by few ruderal species. While simple greening measures such as non-managed field margins are beneficial for ecosystem services, increasing their conservation value may require targeted actions such as sowing nectar seed mixtures for insects and maintaining a low disturbance rate for plants (Boetzl et al., 2019; Meek et al., 2002).

The results should be interpreted cautiously. First, our sample size for tomatoes was small. Second, the high variability in the surrounding landscape, adjacent crops, field management and vegetation in the field margins have hindered the comparability of the different measures among fields. For instance, different adjacent crops may supply different resources to arthropods, whereas field margins composition affects weed measures in wheat fields. Despite the small sample size and high variability, the combination of manipulation-control block design allowed us to detect effects that may be masked in correlative studies. Furthermore, only field margins composition affected the services and disservices examined and did not change the main treatment effect (Appendices S1–S3). Another limitation is the 1-year manipulation for measures with long-term dynamics. For example, arthropods may overwinter in the litter layer, restricting the effectiveness of our herbicide treatment. In that sense, our estimated field margins effect can be considered conservative. Finally, sampling weeds only at the late crop stage probably gives a partial estimation of weed control services. Despite these limitations and the complexity of the study design, our results emphasize the importance of controlled experiments exploring multiple services and disservices together.

5 | CONCLUSIONS

Non-crop habitats can promote wildlife-friendly farming landscapes and have been suggested as a potential tool to facilitate ecological intensification and increase yields (Kremen & Miles, 2012). We show that even simple low-maintenance field margins provide multiple ecosystem services of pest and weed control, biodiversity and increase yields in an intensive vegetable crop. Examining the mechanisms underlying ecological intensification through multiple measures of pest and weed control shows that as often feared by farmers, field edges experience increased rates of arthropod pests and weeds. However, the common practice among farmers of removing the natural field margins using herbicides does not resolve the problem and sometimes may even exacerbate it. Ecological intensification of uncultivated field margins did not benefit both crops equally, and programmes intended to promote field margins in the agricultural landscape should consider specific crops across the landscape and their temporal rotation to maximize the benefits from this practice. Another fundamental issue for better designing ecological intensification practices is that sustainable farming and ecosystem services are not always synonymous with wildlife-friendly farming (Kleijn et al., 2015). While simple field margins can promote pest and weed control, biodiversity would benefit from field margins that are designed to provide resources for different species groups or other diversification practices (Kremen & Miles, 2012). Managing both biodiversity and sustainability goals is the path to true ecological intensification with higher value for both wildlife and farmers.

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AUTHORS' CONTRIBUTIONS

All authors conceived the ideas and designed methodology; H.S. and M.S. collected the data; H.S. and A.S. analysed the data; H.S. and A.S. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.np5hqbzqk (Segre, Segoli, Carmel, & Shwartz, 2020).

ORCID

Hila Segre https://orcid.org/0000-0002-3354-4675
Michal Segoli https://orcid.org/0000-0002-3728-4030
Yohay Carmel https://orcid.org/0000-0002-5883-0184

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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