

Utilisation of plant functional diversity in wildflower strips for the delivery of multiple agroecosystem services

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Abstract

Increased plant diversity in cropping systems can play an important role in agriculture by enhancing arthropod-mediated ecosystem services, including biological control and pollination. However, there is limited research investigating the concurrent influence of plant functional diversity within cultivated systems on different arthropod functional groups, the provision of multiple ecosystem services, and crop yield. During a field experiment, repeated over 2 years, we measured the effect of increasing plant functional diversity on community structure of arthropod visitors, the abundance of multiple pests and induced crop damage, and fruit production in two varieties of tomato. Plant resources (floral and extra-floral nectar and pollen) were included within experimental plots in four levels, with each level increasing the plant functional group richness, based on floral morphology and availability of resources, in a replacement series. The presence of sown flower mixtures in experimental plots was associated with increased abundance and diversity of natural enemy functional groups and an enhanced abundance of bees (Hymenoptera: Apiformes). However, we only detected relatively small variability in arthropod visitors among types of mixtures, and increased abundance of natural enemies did not translate into stronger pest suppression or reduced crop damage. Lepidoptera pest damage was significantly higher in plots adjacent to wildflower strips, an ecosystem disservice, but a significantly higher crop productivity was recorded from these plots. Our results provide evidence that inclusion of non-crop plant resources in agroecosystems can improve the conservation of beneficial arthropods and may lead to increased crop productivity.

Introduction

Agricultural intensification is an important driver of declining biodiversity in agricultural systems (Benton et al., 2003; Tscharntke et al., 2005) and may be associated with the concomitant loss of biodiversity and ecosystem functions, including pollination and biological pest control, which are necessary to maintain agricultural yield. Nevertheless, there are options that increase crop yield while reducing harm to biodiversity and maximising the benefits obtained from ecosystem services (Cunningham et al., 2013). The use of sown wildflower strips that

increase within-field vegetation diversity is a good example of this, and they have been introduced as agrienvironmental measures in several European countries to improve insect conservation and favour pollination and biological pest control (Haaland et al., 2011).

Several groups of natural enemies of agricultural pests utilise non-pest resources such as nectar and pollen (Wäckers & van Rijn, 2012), and thus may benefit from the plant-derived food sources and suitable habitat for completing their life cycle in wildflower strips. This may increase natural levels of biological control in modern cropping systems. In a recent meta-analysis, herbivore suppression, natural enemy abundance, and crop damage suppression were all shown to be enhanced in crops with greater vegetation diversity (Letourneau et al., 2011). Vegetation diversity in cropping systems has also been shown to increase the abundance of pollinators (Blake

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et al., 2011; Nicholls & Altieri, 2013), and this in turn may result in increased crop production (Carvalho et al., 2012; Blaauw & Isaacs, 2014). The stability of pollination services was found to decrease with distance from semi-natural and natural habitats (Garibaldi et al., 2011). However, although both natural enemies and pollinators can be positively driven by the compositional complexity of agroecosystems (Shackelford et al., 2013), the influence of increased plant functional diversity on pollinators (Greenleaf & Kremen, 2006; Carvalho et al., 2012; Blaauw & Isaacs, 2014) and natural enemies (Masetti et al., 2010; Skirvin et al., 2011; Balzan & Moonen, 2014), and on the respective functions in horticultural crops, has often been treated separately.

As different arthropod groups require specific flower traits (Patt & Hamilton, 1997; Wäckers, 2005; Fontaine et al., 2006; Wäckers & van Rijn, 2012), it is common to design wildflower strips based on the needs of a specific arthropod functional group (Campbell et al., 2012). A concurrent research endeavour is to develop wildflower strip mixtures that are capable of conserving various insect groups for the realisation of multiple ecosystem services in agriculture (Carrié et al., 2012). Previous studies have indicated that flower functional diversity affects insect visitation. In a manipulative experiment carried out by Fontaine et al. (2006), syrphids were mainly attracted to open flowers, whereas bumblebees preferentially visited tubular flowers, even though they can also pollinate open flowers. Similarly, in Campbell et al. (2012), bumblebees were strongly associated with tubular flowers, whereas syrphid flies and parasitoids were strongly associated with short-corolla flowers, which may be attributed to the short mouthparts of most hymenopteran parasitoids and many predators that restrict their feeding to exposed nectar and pollen (Gilbert, 1981; Jervis et al., 1993; Wäckers & van Rijn, 2012). In a study investigating the plant characteristics associated with increased natural enemy abundance, the combined effect of maximum flower height, decreasing corolla width, floral area, and period of peak bloom was significantly associated with the increased abundance of natural enemies (Fiedler & Landis, 2007). In another study, the perennial wall-rocket, *Diploxys tenuifolia* (L.) DC, was attractive to both bees and hoverflies and performed better than wildflower mixtures of which species were previously shown to attract either of the two arthropod groups (Barbir et al., 2015). Wild bees in agricultural landscapes have been shown to have a wide trophic niche and can access different flower functional groups. Therefore, ensuring the presence of flowering species appears to be particularly important for increasing the abundance of wild bees and honey bees (Korpela et al., 2013; Balzan et al., 2014; Rosa García & Miñarro, 2014). Because

generalisation in flower visitor webs appears to be the norm for plants and insects (Waser et al., 1996; Petanidou et al., 2008), the provision of flowering plants would be expected to have impacts on crop productivity by enhancing natural pest control and pollination ecosystem services. Nonetheless, attempts to determine the effects of local habitat management on crop productivity to date have largely focused on single pests, crops, and ecosystem services, such as pollination or natural pest control (Otieno et al., 2011), and relatively few studies have considered the effects on crop damage, yield, or quality (Bianchi et al., 2006; Jonsson et al., 2008). These are clearly important measurements that influence the feasibility of agrienvironment schemes. There is, therefore, a need to elucidate the relationship between local habitat management and components of insect diversity that provide multiple ecosystem services and the biodiversity-ecosystem function (BEF) relationships that regulate the provision of ecosystem services.

Biodiversity-ecosystem function experiments have traditionally focused on the manipulation of plant species richness to measure the effect on an ecosystem function (Naeem et al., 1994; Tilman et al., 1996), and numerous studies have shown that species diversity can enhance ecosystem functions (Loreau & Hector, 2001; Duffy et al., 2007; Isbell et al., 2011). Results from these studies have been attributed to mechanisms that may be categorised into two groups: complementarity and sampling effects. Complementarity effects are local deterministic processes, such as niche differentiation and facilitation, which increase the performance of communities, whereas sampling effects refer to stochastic processes involved in community assembly, which are mimicked in experiments by random sampling from a species pool (Loreau & Hector, 2001). Often studies use species diversity measures to quantify BEF relationships. However, it has been argued that it is probably more important to use measures for the diversity of functional groups in order to link biodiversity to ecosystem functioning (Bengtsson, 1998; Moonen & Bàrberi, 2008). A functional group is defined as a group of species that are similar, and at least partially substitutable, in their contribution to a specific ecosystem service (Naeem et al., 2002) indicating that there may be some level of functional redundancy among species (Hooper et al., 2005; Balvanera et al., 2006; Letourneau et al., 2009).

In a field experiment, we have manipulated the functional diversity of flowering plants in wildflower patches to investigate the influence of floral functional diversity on the abundance of arthropod functional groups, pest damage, and crop yield in an organic tomato crop (*Solanum lycopersicum* L., Solanaceae). Tomato crop was chosen for

this study as it requires protection from multiple arthropod pests and, even though domesticated varieties of tomato are self-pollinating (Free, 1993; Delaplane & Mayer, 2000), bee pollination has been observed to increase crop yield significantly (Greenleaf & Kremen, 2006). In this study, we investigate whether increased plant species and functional diversity is associated with increased insect functional diversity, and whether this is associated with lower crop damage from multiple pests and increased productivity. We hypothesise that increased plant functional diversity – in various wildflower mixtures containing different combinations of functional groups – is positively related with natural enemies' functional diversity (H1) and the abundance of wild bees (H2). Moreover, we predict that increased plant functional diversity is associated with (H3) lower pest abundance and crop damage from tomato pests and (H4) enhanced crop productivity.

Materials and methods

Experimental design

Observations were made in plots of tomato grown organically in experimental fields at the Interdepartmental Centre for Agroenvironmental Research 'E. Avanzi' of the University of Pisa (43°40'N, 10°19'E), during the growing seasons of 2011 and 2012. The tomato plants were sown in peat in polystyrene seedling trays for 4 weeks prior to transplanting in experimental plots. Experimental plots followed *Vicia villosa* Mill., a winter cover crop (sown on 15 September 2010 and 31 October 2011, and incorporated into the soil on 15 May 2011 and 24 May 2012, respectively). The experimental layout consisted of 12 main plots (4 × 22 m), divided into two subplots (4 × 10 m) planted with either tomato cv. Roma or cv. Perfect Peel. The two subplots were separated by a wildflower strip (4 × 2 m). In each subplot, 42 plants of either Perfect Peel or Roma were grown (six rows of seven plants each, with distances of 1.5 m between rows and 0.8 m between plants on the same row). Main plots were separated by a distance of 8 m during the 1st year (2011). This distance was increased to 15 m during the 2nd year of the trial. Uncultivated inter-plot areas were kept weed-free through mechanical weed control (harrowing and hoeing), in order to avoid effects of naturally occurring flowering plants on pest–natural enemy dynamics. The flower mixtures and the position of tomato variety with respect to wildflower strip were randomised. During 2011, these plots were part of a larger (2.5 ha) experimental set-up investigating the influence of flowering resources, fertilisation strategy, and tomato variety on dynamics of pest damage and natural enemy abundance (Balzan, 2013). Only the *V. villosa* treatment of 2011 is

considered in this study as this was the most successful winter cover crop.

Vegetation diversity in wildflower strips was provided in four levels, consisting of floral mixtures of different combinations of plant functional groups. Each level adds three species in a replacement series (also termed substitutive design). In substitutive designs, alternate species replace some of the main plant species (level 1 wildflower strip) thereby reducing the sowing density of the latter in more diverse strips (Jolliffe, 2000). The first level was an experimental control, which was kept weed-free through mechanical control. Subsequently, each experimental level increased functional plant diversity, based on floral morphology. The choice of functional effect groups was based on the floral morphological characteristics of various plant species. Level 1 (L1) consisted of three Apiaceae species, whereas in level 2 (L2), three Fabaceae were added to the seed mixture. Finally, experimental level 3 (L3) was composed of a more diverse floral mixture and, in addition to the six species from the previous level, included three species characterised with a diverse floral morphology (Table S1; Balzan et al., 2014). Species that did not flower (*Anethum graveolens* L. and *Centaurea jacea* L.), flowered sparingly (*Lotus corniculatus* L.), or flowered too early (*Sinapis arvensis* L.) during the 1st year of the study were replaced with new species [*Pimpinella anisum* L., *V. villosa*, *Calendula officinalis* L., *Lobularia maritima* (L.) Desv.] in 2012. Wildflower strips were sown on two separate dates (6 and 21 June 2011, 13 and 17 June 2012) to increase the duration of flowering of species within the sown strips.

Insect diversity in sown wildflower strips

Surveys of arthropod visitors to wildflower strips were carried out every 2 weeks through standardised aspiration 2× along the whole length of the plot, excluding the control plots (1 min per plot using a mechanical aspirator). Pitfall traps filled with 90% alcohol were placed at the centre of each wildflower strip, including control strips, to determine the influence of floral strips on ground-dwelling arthropods. Rain covers were positioned ca. 10 cm above each trap. Traps were set up soon after the flowering of sown strips and were sampled on a weekly basis up to the harvest date. The abundance of Hymenoptera parasitoids [Ichneumonoidea (Braconidae and Ichneumonidae), Chalcidoidea, Platygastroidea, Proctotrupioidea, Cynipoidea, Diaprioidea, Chrysoidea], honey bees (*Apis mellifera* L.), and other bee pollinators (Hymenoptera: Apiformes, Apidae) visitors was calculated. Similarly, the availability of non-target prey was calculated by measuring the abundance of sap-sucking Hemiptera bugs. However, some of these species are

secondary pests of tomato. Heteroptera (Hemiptera) bugs collected from the sown strips were identified to species level to investigate the hospitability of these strips to these pests. The abundance of ground-dwelling predators was calculated by adding the abundance of Carabidae and Staphylinidae (both Coleoptera), Formicidae (Hymenoptera), Opiliones, and Araneae families (Letourneau et al., 2009). Each recorded taxon was assigned to a particular functional group based on its trophic position and feeding habits (Table S2).

Crop yield measurements for cvs Perfect Peel and Roma

The crop was harvested when a threshold level of 80% of the fruits were ripe (5–9 September 2011, 5–6 September 2012). Five plants per plot ($n = 240$) were sampled, and for each plant, the total number of marketable (ripe), green, and discarded fruits were recorded, plus the fresh weight of all ripe and green fruits. Total crop yield was recorded as the number of marketable fruit, and all fruits collected from these plants were classified with respect to the type of pest damage [Noctuidae (Lepidoptera), *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae), or sucking bugs]. Data were subsequently aggregated at the plot level. Of four ripe fruits per plant ($n = 20$ per plot), the fresh weight and biomass (by oven-drying at 60 °C to constant weight) were determined.

Crop damage surveys for cv. Perfect Peel during the crop cycle

Within the study area, pests of tomato include the aphids *Myzus persicae* Sulzer and *Macrosiphum euphorbiae* Thomas (Hemiptera: Aphididae) and the sucking bugs *Nezara viridula* L. (Hemiptera: Pentatomidae) and *Lygus* spp. (Hemiptera: Miridae) (Sannino & Espinosa, 2009). Moreover, several Noctuidae species are known to feed on tomato, namely *Helicoverpa armigera* (Hübner), *Heliothis virescens* Hufnagel, and *Heliothis peltigera* Denis & Schiffmüller (Balzan, 2013). The recently introduced *T. absoluta* has also become an important cause of yield loss. Surveys of characteristic damage by Lepidoptera pests and sucking bugs (Sannino & Espinosa, 2009) and leaf aphid abundance were carried out for five random fruits and two leaves from a plant located in each row of a particular plot ($n = 30$ fruits per plot, including green fruits larger than 2.5 cm in diameter plus pink and red fruits, and $n = 12$ upper-canopy leaves per plot). Pest damage on fruits was classified into three categories (Noctuidae, *T. absoluta*, and sap-sucking bugs). Damage from Noctuidae pests and *T. absoluta* was recorded per leaf, and numbers of aphids and parasitised aphid mummies were recorded. This survey was carried out in all subplots with Perfect Peel (total of 360 fruits and 144 leaves per sampling occasion) and was repeated 4× in 2011 and 3× in 2012, from the

beginning of flowering till crop harvest. Sampling on plant material was not destructive, and this survey allowed for the inclusion of temporal variation within the statistical analysis.

Statistical analysis

Influence of plant functional group richness on arthropod diversity. To investigate the influence of functional floral diversity on arthropod groups, generalised linear mixed-effect models (GLMM) were used. A top-down strategy was utilised for model selection. A beyond optimal model was fitted on all explanatory variables [flowering resources (L), time from sowing of strips in number of days (T), and year (YR)] and all possible interactions. Within these GLMMs, L and YR were considered factorial variables with four and two experimental levels, respectively, whereas T was considered a continuous variable. The Akaike information criterion with a 2nd-order correction (AICc) values were used in order to select the optimal random structure of the model (Anderson & Burnham, 2002). Subsequently, the most parsimonious model was selected by backward elimination. The significance of the interactions between variables was tested using a Poisson error distribution (Bates et al., 2013). This approach aims at selecting the least complex model without losing important information on interactions between the experimental factors, time, and spatial autocorrelation. A similar approach was used to determine the effect of enhanced plant diversity on the abundance and diversity of natural enemies. Natural enemy richness (S) was calculated at the family level for each flowering strip per sampling occasion. This analysis was conducted at the family level because of the lack of identification keys to identify all species to a more precise level, similar to other studies that measured the diversity of natural enemy groups (Noordijk et al., 2010; Carrié et al., 2012; Poveda et al., 2012). Organisms that could not clearly be assigned to a trophic group were included in the diversity analysis with total number of families and diversity, but not in the analysis of the various functional groups.

Effect of wildflower strips on aphid abundance and crop damage throughout growing season. Measured yield loss parameters for pest damage and aphid abundance during the growing season were analysed in relation to the sown flower strip mixtures for cv. Perfect Peel, as other studies have reported an important effect of timing of planting on pest abundance and crop damage in tomato (Letourneau et al., 1996; Balzan, 2013). A beyond optimal model, containing all explanatory variables (L, YR, and T) and their interactions, was fitted on the data. A top-down strategy was used for the selection of the minimum

adequate model (MAM). The significance of each independent variable was assessed by elimination from the full model, and an ANOVA was performed to compare the two models. The MAM was then used for parameter estimation of each measured variable. If the dependant variable was expressed as count data, such as with aphids and *T. absoluta* leaf galleries, a Poisson error distribution was used, whereas if the dependent variable consisted of proportion data (e.g., of damaged leaves or fruit) a binomial error distribution was used.

Effect of flower morphological diversity on crop damage and yield at harvest. As crop damage count data are likely to be influenced by the total number of fruits per sampling point, crop production was included as an additional fixed variable within the GLMM and a Poisson error distribution was utilised (Bates et al., 2013). The influence of flower mixtures on crop yield was assessed using year and experimental level as fixed effects and plot as random variable, and a top-down strategy was used for model selection.

Results

Influence of flower functional diversity on insect diversity in wildflower strips

In total, 19 838 individuals were collected from the sown wildflower strips, of which 10 869 individuals were

collected from periodical suction sampling of floral visitors, whereas the rest were collected from pitfall traps. The most abundant groups were Hemiptera bugs, which made up a total of 31.2% of above-ground arthropods, Diptera (27.5%), and Hymenoptera (20.2%). Parasitoids were the most important Hymenoptera group, accounting for 89.0% of this order, followed by Apiformes (8.1%) and Formicidae (2.6%). Only a small fraction of the bees recorded were honey bees (0.04%). Carabidae were the most abundant ground-dwelling natural enemy group, representing 17.4% of arthropods collected from pitfall traps. Staphylinidae and Formicidae made up 6.0 and 9.3% of the sample, respectively. Araneae made up a total of 10.5% of the sample collected from pitfall traps, and the most important families were Lycosidae (53.6%) and Linyphiidae (27.8%).

The inclusion of wildflower strips significantly increased the abundance of ground-dwelling natural enemy groups (Table 1). Nevertheless, increased plant functional group richness in L2 and L3 strips, when compared with L1 strips, was not associated with an enhancement of the abundance of most arthropod groups recorded from pitfall traps (Figure 1). Control (L0) strips had a significantly lower abundance and functional group richness of ground-dwelling natural enemies in comparison with baseline L1 (Apiaceae) strips (Table 1).

The presence of various plant functional groups in wildflower strips has been shown to influence flower-visiting

Table 1 Parameter estimates using GLMMs with a Poisson error distribution for abundance (no. individuals) data and a Gaussian distribution for richness data of three groups of natural enemies within the flowering strips (L0–L3) according to growing season (YR) and time (T). The most parsimonious model (lowest Akaike information criterion with a second-order correction, AICc) for each variable was selected as the best model

| | Ground-dwelling natural enemies | | | | Flower-visiting natural enemies | | | | Wild bees | |
|--------------------|---------------------------------|----------|------------|----------|---------------------------------|----------|----------------|---------|--------------|---------|
| | Abundance | | Richness | | Abundance | | Richness | | Abundance | |
| | Estimate | z | Estimate | t | Estimate | z | Estimate | t | Estimate | z |
| Intercept | 2.85 | 16.17*** | 2.86 | 11.66*** | 2.80 | 17.18*** | -0.47 | 0.58ns | -0.07 | -0.26ns |
| L2 | 0.08 | 0.40ns | 0.05 | 0.15ns | 0.21 | 1.15ns | 0.85 | 2.14* | -0.39 | -1.05ns |
| L3 | -0.22 | -1.01ns | -0.25 | -0.74ns | -0.10 | -0.49ns | -0.23 | -0.59ns | 0.01 | 0.03ns |
| L0 | -1.60 | -6.22*** | -1.34 | -3.83*** | - | - | - | - | - | - |
| T | - | - | - | - | 0.21 | 1.31ns | 0.08 | 6.90*** | - | - |
| YR _B | 0.11 | 1.16ns | 1.10 | 4.74*** | - | - | 1.62 | 4.63*** | -1.35 | -2.19* |
| L2*YR _B | - | - | - | - | - | - | - | - | 0.13 | 0.14ns |
| L3*YR _B | - | - | - | - | - | - | - | - | 2.16 | 2.98** |
| d.f. | 8 | | 8 | | 7 | | 7 | | 9 | |
| AICc | 2145.19 | | 806.4 | | 1189.33 | | 467.44 | | 365.75 | |
| ΔAICc | 4.83 | | 2.02 | | 4.31 | | 4.45 | | 6.59 | |
| Model | ln(Y) ~ L + YR | | Y ~ L + YR | | ln(Y) ~ L + T | | Y ~ L + T + YR | | ln(Y) ~ L*YR | |

‘-’ indicates that this variable was not included in the model.

*0.01 < P < 0.05, **0.001 < P < 0.01, ***P < 0.001; ns, P > 0.05; P values obtained from Wald z-statistics for each parameter.

insect groups (Balzan et al., 2014). Our results indicate that L2 strips were the most effective at increasing the abundance of predators and parasitoids (Figure 2). L2

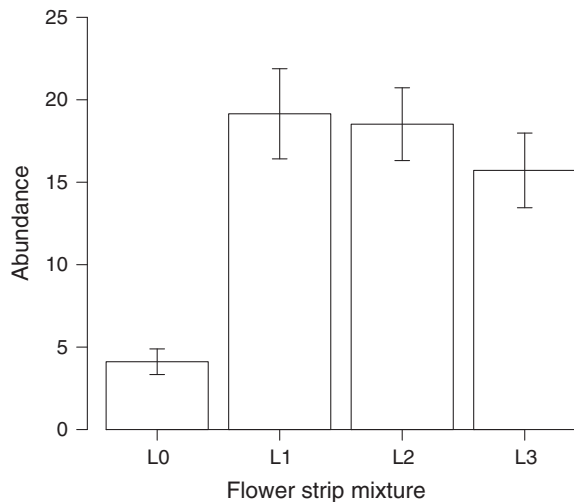


Figure 1 Mean (\pm SE) abundance (no. individuals per plot) of ground-dwelling predators in wildflower strips with increasing plant functional group richness.

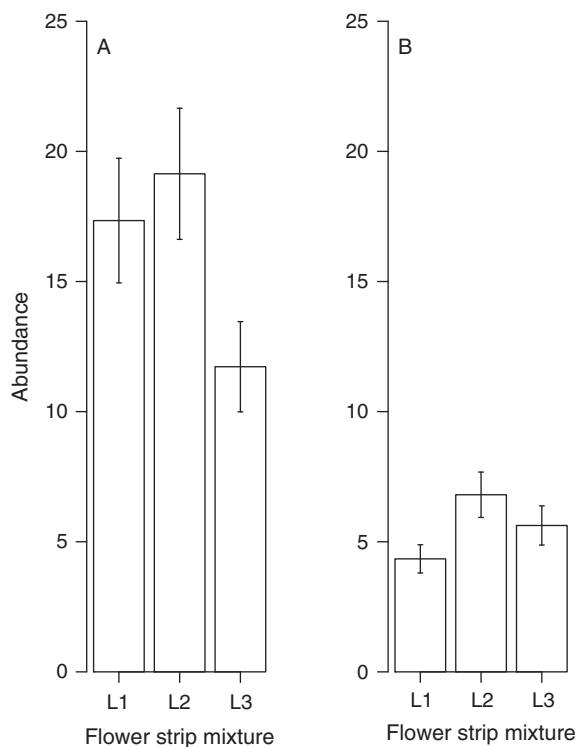


Figure 2 Mean (\pm SE) abundance (no. individuals per plot) of flower-visiting (A) parasitoids (Hymenoptera) and (B) predators in wildflower strips with increasing plant functional group richness.

strips had a significantly higher natural enemy group richness in comparison to baseline L1 strips, but natural enemy abundance was not significantly different between flower strip mixtures. The diversity of flower-visiting natural enemies increased with time, whereas no significant trend was observed for natural enemy abundance (Table 1). The abundance of wild bees was only significantly increased in L3 strips during the 2nd year of the study (Figure 3B). During the 1st year, a higher initial abundance of wild bees was recorded in L3 strips, which flowered earlier, but subsequently declined within this experimental level (Figure 3A). The abundance of bees in L1 and L2 strips increased exponentially with time as these flowered later.

The abundance of sap-sucking herbivores from flowering strips was significantly lower in L3 strips in 2011 but this was not confirmed subsequently (Table 2). The secondary pests *Lygus gemellatus* Herrich-Schäffer, *Lygus italicus* Wagner, *Lygus rugulipennis* Poppius, and *Lygus pratensis* L. were recorded, of which the latter was the most abundant. Increased plant diversity in L2 and L3 wildflower strips was associated with higher abundance of the polyphagous pests *Lygus* spp. and *N. viridula*.

Effects of flower functional diversity on crop damage and yield at harvest

Tomato productivity was significantly affected by the presence of adjacent flowering strips. However, there are some differences between tomato varieties and years. During the first year of the study (2011), crop productivity, in terms of fruit number (Figure 4) and biomass (Figure 5), was increased for cv. Roma adjacent to L1 strips. The MAM for average fruit fresh weight did not include the interaction between experimental treatment and year and indicates that L1 strips were associated with increased fruit fresh weight throughout the study (Table 3). During 2012, no effect on biomass and total number of fruit was recorded from L1 strips, possibly due to the relatively weak flowering of Apiaceae in 2012. A positive effect on total fruit number was observed in plots with Roma adjacent to L2 and L3 strips during 2012. Crop productivity was similarly higher in plots planted with cv. Perfect Peel and adjacent to L1 strips during 2011, and an enhanced fruit biomass and fresh weight were recorded (Table 3). Contrastingly, L3 strips were associated with a reduced number of fruit for the Perfect Peel crop. L1 strips were also associated with reduced fresh weight and biomass for Perfect Peel during 2012.

When crop damage was measured using the number of galleries for each pest per plant, a significant effect of crop productivity (number of fruit per plant) and wildflower strips was recorded (Table 4). Plots with cv. Roma

Figure 3 Abundance of bees (no. individuals per plot) according to the experimental level for wildflower strips used in (A) 2011 and (B) 2012. Curves indicate the fit of a generalised linear model with Poisson error distribution on plot data.

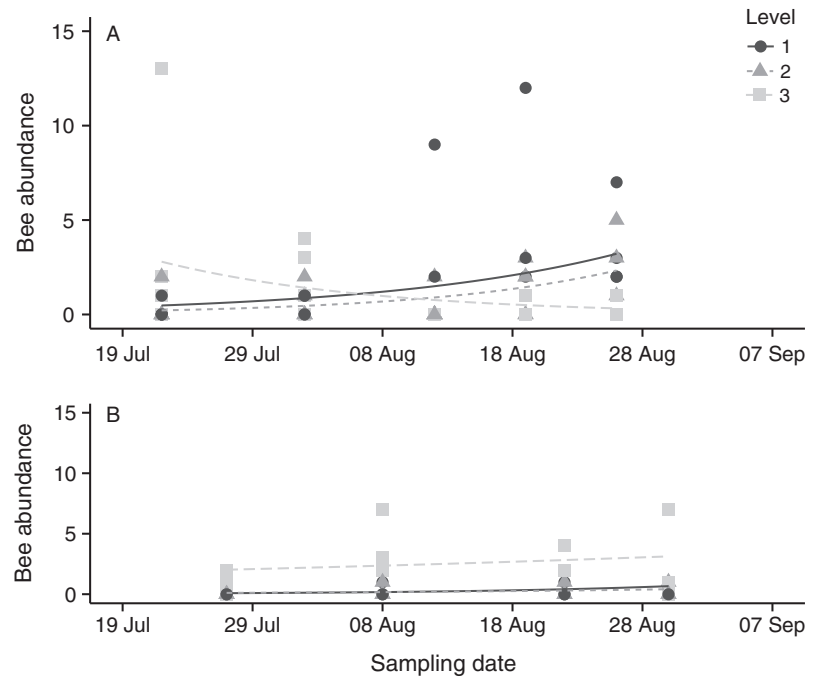


Table 2 Minimum adequate model (MAM) investigating the influence of experimental wildflower strips (L), growing season (YR), and time from the sowing of the strips (T) on the abundance of two pests of tomato (*Lygus* spp. and *Nezara viridula*) and sap-sucking hemipteran bugs in the flowering strips

| | <i>Lygus</i> spp. | | <i>N. viridula</i> | | Sap-sucking bugs | |
|--------------------|--|---------|--------------------|----------|------------------|----------|
| | Estimate | z | Estimate | z | Estimate | z |
| Intercept | 1.12 | 1.28ns | -2.33 | -4.56*** | 3.27 | 26.41*** |
| L2 | -1.11 | -1.01ns | 0.13 | 0.18ns | 0.02 | 0.11ns |
| L3 | 1.76 | 1.76ns | 1.73 | 3.18** | -0.34 | -2.48* |
| YR _B | -2.39 | -2.68** | - | - | -0.43 | -2.42* |
| T | -0.02 | -1.65ns | - | - | - | - |
| L2*YR _B | 1.89 | 2.43* | - | - | 0.62 | 2.57* |
| L3*YR _B | 1.76 | 2.32* | - | - | 0.60 | 2.49* |
| L2*T | 0.03 | 1.79ns | - | - | - | - |
| L3*T | -0.01 | -0.79ns | - | - | - | - |
| YR _B *T | 0.03 | 2.57* | - | - | - | - |
| d.f. | 11 | | 7 | | 9 | |
| MAM | ln(Y) ~ L + YR + T + L*YR + L*T + YR*T | | ln(Y) ~ L | | ln(Y) ~ L*YR | |

— indicates that this variable was not included in the model.

*0.01 < P < 0.05, **0.001 < P < 0.01, ***P < 0.001; ns, P > 0.05; P values obtained from Wald z-statistics for each parameter.

adjacent to L1 and L2 strips were characterised by a significantly higher abundance of fruit galleries caused by *T. absoluta* (Table 4). Increased crop productivity in the plots with wildflower strips was also associated with a higher

gallery count in cv. Perfect Peel. Results indicate a significant three-way interaction (L*YR*N) for the experimental plots with Perfect Peel, suggesting that the effect of the wildflower strips on *T. absoluta* and Noctuidae pest dam-

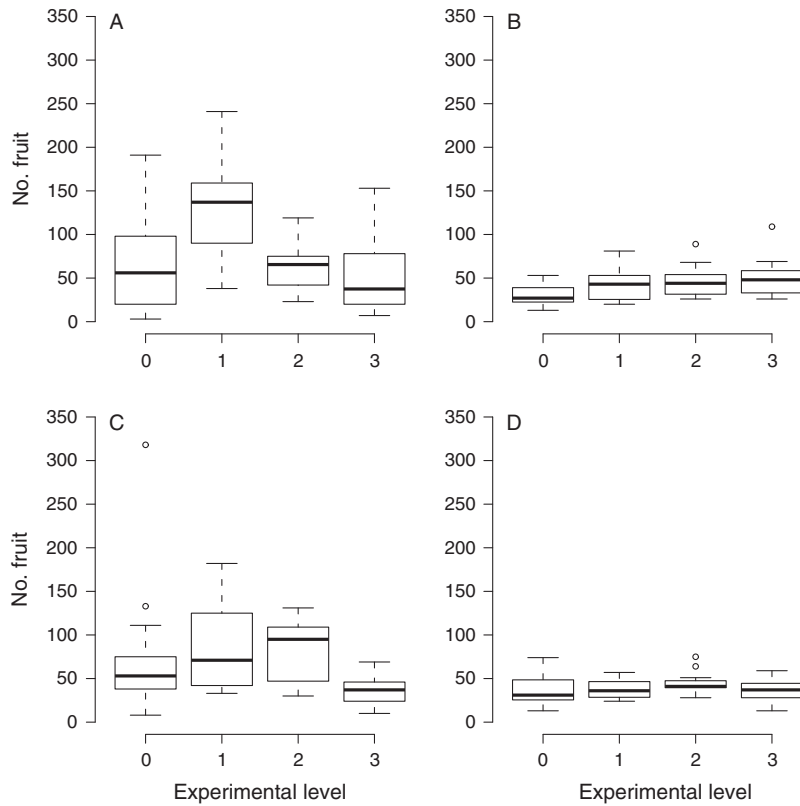


Figure 4 Boxplots of fruit production (no. of fruits per plant) for tomato cvs (A, B) Roma and (C, D) Perfect Peel during (A, C) 2011 and (B, D) 2012, with experimental levels 0–3, indicating flower mixtures with increasing plant functional group richness. The thick horizontal line represents the median, the boxes represent the 25th and 75th percentiles and indicate the spread of the data, the whiskers indicate 1.5× the spread, and the dots are potential outliers (n = 240).

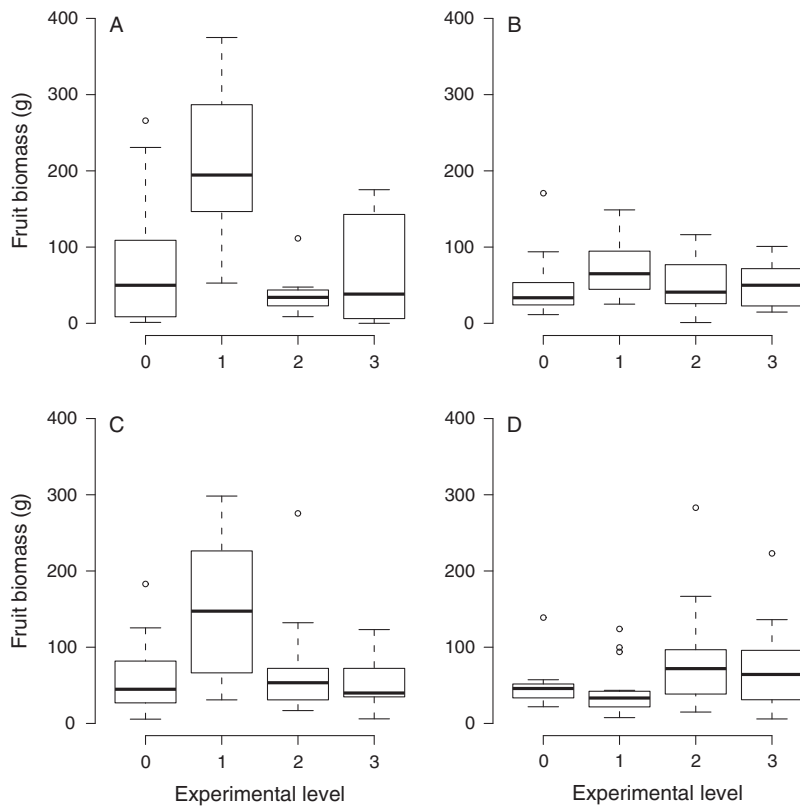


Figure 5 Boxplots of fruit dry biomass (g) for tomato cvs (A, B) Roma and (C, D) Perfect Peel during (A, C) 2011 and (B, D) 2012, with experimental levels 0–3, indicating flower mixtures with increasing plant functional group richness. The thick horizontal line represents the median, the boxes represent the 25th and 75th percentiles and indicate the spread of the data, the whiskers indicate 1.5× the spread, and the dots are potential outliers (n = 240).

Table 3 Parameter estimates for the fixed effects in the final model for fruit production data for tomato cvs Roma and Perfect Peel using a GLMM with Poisson errors for count data (no. of fruits per plant) and Gaussian errors for fruit biomass (dry weight and fresh weight data). Minimum adequate models were selected through backward elimination

| | Roma | | | | | | Perfect Peel | | | | | | | | | | | |
|--------------------|-----------------|-----------|--------|------------------------------------|-------|---------|--------------------------------------|----------|--------|-----------------|--------|---------|------------------------------------|---|--|--------------------------------------|---|--|
| | No. fruit/plant | | | Fruit biomass (g dry weight/plant) | | | Fruit biomass (g fresh weight/plant) | | | No. fruit/plant | | | Fruit biomass (g dry weight/plant) | | | Fruit biomass (g fresh weight/plant) | | |
| | Estimate | z | t | Estimate | t | | Estimate | t | | Estimate | z | t | Estimate | t | | Estimate | t | |
| Intercept | 4.00 | 19.04*** | 79.42 | 3.74*** | 40.37 | 9.93*** | 4.07 | 30.57*** | 54.74 | 3.89*** | 34.45 | 8.03*** | | | | | | |
| L1 | 0.68 | 2.07* | 89.80 | 2.40* | 14.07 | 2.18* | 0.14 | 0.73ns | 85.74 | 3.17** | 22.08 | 2.89** | | | | | | |
| L2 | 0.23 | 0.69ns | -24.31 | -0.65ns | -1.64 | 0.78ns | 0.29 | 1.66ns | 26.62 | 0.98ns | 8.45 | 1.11ns | | | | | | |
| L3 | -0.60 | -1.70ns | -25.55 | -0.70ns | 4.37 | 0.74ns | -0.36 | -2.04* | -22.27 | -0.82ns | 7.52 | 0.97ns | | | | | | |
| YR _B | -0.94 | -14.07*** | -80.19 | -4.20*** | 6.40 | 2.21* | -0.36 | -7.19*** | -13.98 | -0.73ns | 11.09 | 2.72** | | | | | | |
| L1*YR _B | 0.14 | 1.40ns | 10.60 | 0.33ns | | | | | -67.89 | -2.15* | -17.08 | -2.48* | | | | | | |
| L2*YR _B | 0.88 | 2.28* | 98.98 | 2.13* | | | | | 21.02 | 0.59ns | 8.04 | 0.84ns | | | | | | |
| L3*YR _B | 1.41 | 3.26* | 77.46 | 1.59ns | | | | | 52.24 | 1.44ns | 1.68 | 0.17ns | | | | | | |
| d.f. | 9 | | 10 | | 7 | | 6 | | 10 | | 10 | | | | | | | |
| MAM | L*YR | | L*YR | | L+YR | | L+YR | | L*YR | | L*YR | | | | | | | |

*0.01<P<0.05, **0.001<P<0.01, ***P<0.001; ns, P>0.05; P values obtained from Wald z- or t-statistics for each parameter.

Table 4 Parameter estimate from minimum adequate models for Lepidoptera-caused pest damage (no. galleries per plant) for the tomato cvs Perfect Peel and Roma at harvest, using a GLMM with Poisson errors. Total fruit production (N), wildflower strips (L), and year (YR) are used as fixed variables, whereas plot identity was included as a random effect

| | Noctuidae | | | | <i>Tuta absoluta</i> | | | |
|-----------------------|--------------|----------|----------|---------|----------------------|---------|----------|---------|
| | Perfect Peel | | Roma | | Perfect Peel | | Roma | |
| | Estimate | z | Estimate | z | Estimate | z | Estimate | z |
| Intercept | 1.20 | 8.64*** | 0.933 | 0.002** | -1.17 | -2.14* | -1.34 | -2.04* |
| L1 | -0.01 | -0.02ns | -0.57 | -1.34ns | 1.73 | 2.07* | 1.97 | 2.33* |
| L2 | 0.11 | 0.26ns | 0.51 | 1.34ns | -0.63 | -0.49ns | 2.07 | 2.59** |
| L3 | -0.68 | -1.67ns | -0.03 | -0.08ns | -0.16 | -0.01ns | 0.80 | 0.93ns |
| YR _B | -2.83 | -4.93*** | - | - | 0.06 | 0.11ns | -0.01 | -0.03ns |
| N | 0.00 | 3.38*** | 0.00 | 8.55*** | 0.00 | 0.41ns | 0.01 | 5.43*** |
| L1*YR _B | 1.81 | 2.36* | - | - | 0.32 | 0.37ns | - | - |
| L2*YR _B | 3.40 | 3.94*** | - | - | 3.57 | 2.45* | - | - |
| L3*YR _B | 3.80 | 4.77*** | - | - | 17.63 | 0.01ns | - | - |
| L1*N | 0.01 | 2.63*** | - | - | 0.00 | 0.42ns | - | - |
| L2*N | 0.00 | 0.61ns | - | - | 0.01 | 0.94ns | - | - |
| L3*N | 0.02 | 3.30*** | - | - | 0.00 | 0.00ns | - | - |
| YR _B *N | 0.05 | 4.97*** | - | - | 0.03 | 3.38*** | 0.01 | 3.08** |
| L1*YR _B *N | -0.02 | 1.60ns | - | - | -0.00 | -1.66ns | - | - |
| L2*YR _B *N | -0.06 | -4.12*** | - | - | -0.04 | -2.94** | - | - |
| L3*YR _B *N | -0.07 | -4.52*** | - | - | -0.01 | -1.06 | - | - |
| d.f. | 17 | | 6 | | 17 | | 8 | |
| MAM | L*YR*N | | L + N | | L*YR*N | | N*YR + L | |

‘-’ indicates that this variable was not included in the model. The minimum adequate models presented here were obtained from Table S3. *0.01<P<0.05, **0.001<P<0.01, ***P<0.001; ns, P>0.05; P values obtained from Wald z-statistics for each parameter.

age depends on the effect of crop productivity which depends on the effect of the year. Model parameter estimates suggest a lower *T. absoluta* and Noctuidae pest damage in tomato plants with a higher number of fruit produced and adjacent to L2 and L3 strips in the 2nd year of the study (Table 4).

Influence of wildflower strips on pest damage during the crop cycle

GLMM results for crop damage surveys carried out on cv. Perfect Peel throughout the growing seasons do not indicate a direct effect of sown wildflower strips on reducing pest damage and associated yield loss (Table S4). Cumulative pest damage generally increased throughout the season (Figure 6), but no reduction in aphid abundance or the rate of increase of crop damage with time was observed for plots adjacent to wildflower strips.

Discussion

Effect of increasing plant functional group richness on arthropod community

A comparison of the abundance of ground-dwelling arthropods collected from control (L0) strips to that in wildflower strips (L1, L2, L3) indicates that the latter are

associated with increased natural enemy diversity, supporting our initial hypothesis (H1). However, greater plant functional group richness was not associated with a corresponding increase in the abundance and diversity of ground-dwelling natural enemies. This supports previous observations that vegetation cover in agroecosystems increases the abundance of ground-dwelling predators, including Carabidae, Lycosidae, and Linyphiidae (Hummel, 2002; Yardim & Edwards, 2002; Balzan et al., 2014). Contrastingly, flower visitors are known to differentially utilise floral resources based on their suitability and the ability to detect and access available resources (Wäckers, 2005). In a previous study, we only found a limited effect of the wildflower strip mixtures on the abundance of arthropod groups collected by suction sampling (Balzan et al., 2014). In this study, the L2 strips were significantly better at enhancing natural enemy richness within this study. The lack of major significant effects of experimental levels on the abundance of insect visitors may be partly explained by the efficacy of temperate Apiaceae in attracting large number of flower visitors (Olesen et al., 2007). The provision of simple wildflower strips is likely to improve the conservation of multiple arthropod groups responsible for the delivery of key agroecosystem services.

Our data suggest that even simple wildflower mixtures provide benefits to several insect groups and may enhance the provision of multiple ecosystem functions in agroecosystems, namely pollination and biological control. Other recent studies have similarly observed positive effects of various wildflower strips on several arthropod groups important for the provision of agroecosystem services (Fiedler & Landis, 2007; Noordijk et al., 2010; Campbell et al., 2012; Carrié et al., 2012). In our study, wild bees were strongly associated with more functionally diverse (L3) strips (Table 1). This could have been caused by differential attractiveness of flowering species for this group, which suggests the need for habitat management that increases plant functional diversity in areas surrounding the crop. Wild bee abundance was initially high in L3 strips with early flowering of *S. alba* during the first year of the study, whereas L1 and L2 strips became more attractive later during the crop cycle. The profuse flowering of *F. esculentum* throughout the crop cycle in L3 strips, during the 2nd year of the study, was associated with increased abundance of wild bees. These results complement previous observations that wild bees in agricultural landscapes can access flower functional groups and that guaranteeing the presence of flowering species is more important for increasing their abundance (Korpela et al., 2013; Balzan et al., 2014; Rosa García & Miñarro, 2014).

The influence of plant functional group richness on pest damage and crop yield

Increased vegetation diversity at multiple scales has been recommended for restoring ecosystem functions in agricultural habitats (Gurr et al., 2003; Bianchi et al., 2006). Results from this experiment indicate that the wildflower strips were associated with an improved productivity of the adjacent crop. However, we have found no indication that increased plant diversity and enhanced abundance and diversity of natural enemies within the wildflower strips reduce pest damage in adjacent crops. This is in contrast to a recent study on tomato crop, where the flowering strips were shown to act as a potential trap crop to sap-sucking pests of tomato and to improve natural pest control (Balzan & Moonen, 2014). The inclusion of wildflower strips in two lettuce field experiments was associated with lower aphid abundance up to a distance of 10 m (Chaney, 1998; Skirvin et al., 2011), whereas in another study, higher parasitism of lettuce leafminers (Agromyzidae) was recorded even though this was not associated with a significant reduction of these pests (Masetti et al., 2010). In two recent reviews, vegetation diversification within agricultural habitats was consistently associated with enhanced biological control, measured in terms of abundance of natural enemies, herbivore suppression and

parasitism, and a reduction in crop damage (Letourneau et al., 2011; Iverson et al., 2014). Iverson et al. (2014) recorded a significant win-win scenario for biological control and per-plant primary crop yield in substitutive design experiments, which showed a 40 and 31% increase for yield and biocontrol metrics, respectively, in polycultures over monocultures. However, Letourneau et al. (2011) recorded stronger effects on enhancing enemy abundance and crop damage suppression in large-scale experiments, and yield reduction due to plant diversification was a strong outcome in small-scale experiments (<225 m²). The latter was partly attributed to the trade-off between using vegetation diversity to control pests and taking up space by that vegetation diversity that would have otherwise been used for crop production.

In our study, natural enemy conservation in sown wildflower strips was enhanced, but this did not translate into a lower pest abundance and crop damage in comparison to control plots. The lack of a suppression of crop damage may be caused by multiple factors, including the relatively late flowering of wildflower strips, a possible lack of spillover of natural enemies into the crop, an effect of wildflower strips on pest control levels of other plots nearby, negative interactions between natural enemy groups, and the use of the wildflower strips by Lepidoptera pests. Results presented here provide evidence that increased availability of flowering resources can lead to increased Lepidoptera-caused pest damage, indicating the importance of considering resource use by the pest species when planning the inclusion of plant species in wildflower strips (Géneau et al., 2012; Balzan & Wäckers, 2013). The pest *T. absoluta* was shown to derive fitness benefits when provided with floral resources (Balzan & Wäckers, 2013), whereas higher pest damage from *T. absoluta* and Noctuidae pests was also recorded in tomato crop adjacent to field margins with enhanced availability of flowering resources (Balzan, 2013; Balzan & Moonen, 2014).

Top-down control of pests can be (1) strengthened when natural enemies complement each other, (2) inhibited by negative interactions, (3) balanced by both previously mentioned factors, and (4) driven by single influential species (sampling effect). Higher natural enemy diversity was observed to lead to greater herbivore suppression in a recent meta-analysis. This suggests a stronger impact of positive, complementary interactions among natural enemies over negative, antagonistic interactions (Letourneau et al., 2009). In a recent study, Northfield et al. (2014) found that pairs of natural enemies (belonging to the following groups: true bugs and ladybeetles predators and parasitoids) in the community improved aphid suppression on *Brassica oleracea* L. In a study investigating aphid suppression in wheat, aphid suppression by

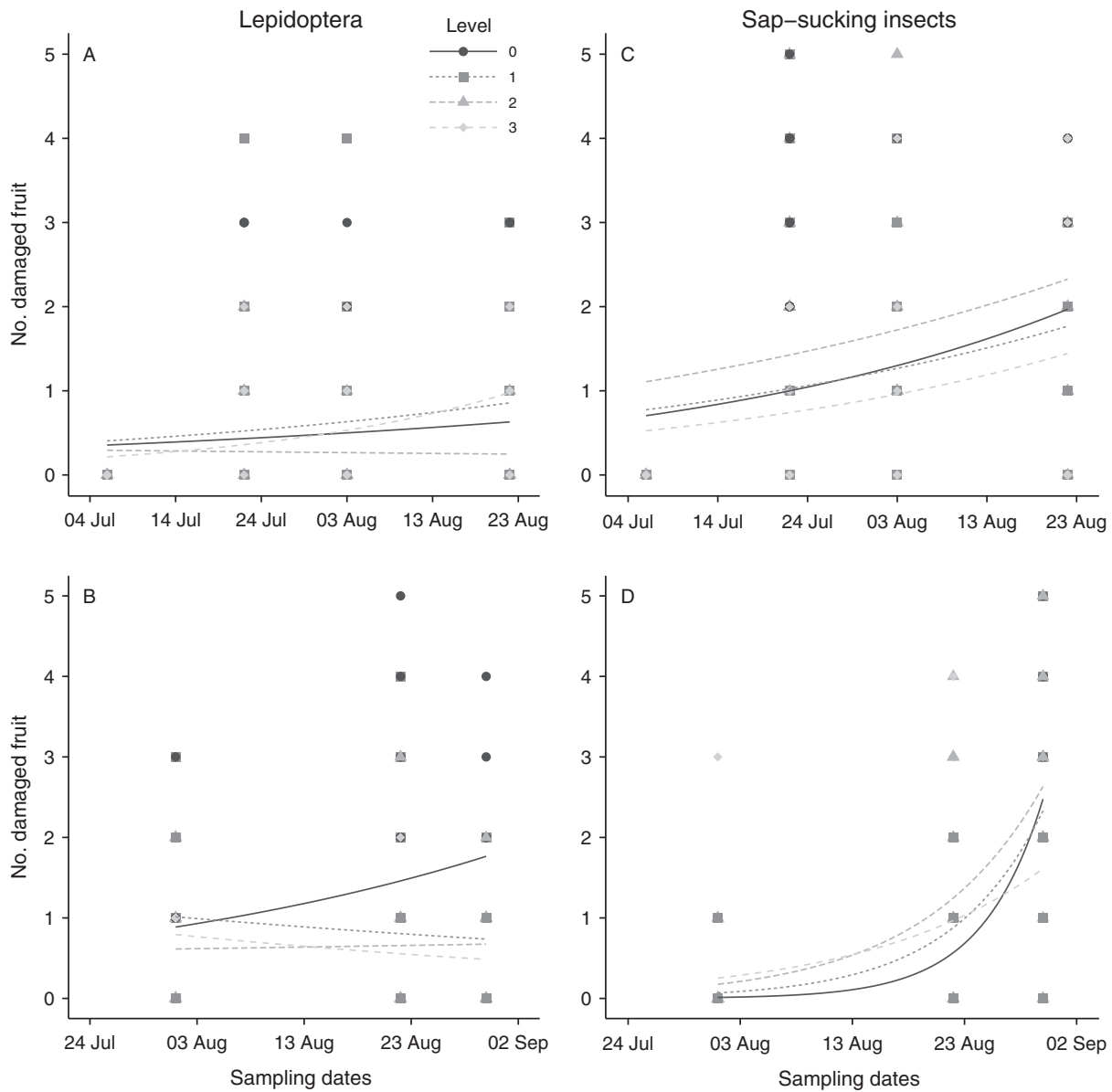


Figure 6 Cumulative tomato crop damage caused by (A, B) Lepidoptera and (C, D) sap-sucking pests for flowering strips used in (A, C) 2011 and (B, D) 2012. Lines indicate the fit of a generalised linear model with Poisson error distribution on plot data.

species-rich predator assemblages was greater than suppression by single-species monocultures. However, species-rich assemblages did not outperform all single-species compositions, suggesting an identity effect (Long & Finke, 2014). In another study, the trophic composition of predator assemblages was found to determine the impact of increased predator diversity on the occurrence of trophic cascades, and increasing the proportion of intra-guild predator species diminished herbivore suppression and reduced primary crop productivity (Finke & Denno,

2005). Increased habitat complexity, at the landscape scale, was associated with higher pest control, but also with the increased antagonistic interactions that constrain this same service (Martin et al., 2013). The outcome of interactions of natural enemies varies and depends on several factors that regulate predator-prey relationships. These include habitat complexity (Finke & Denno, 2002; Tylianakis & Romo, 2010), predator-prey relative size (Polis et al., 1989; Perdakis et al., 2014), diversity of prey communities, availability of intermediate prey (Tylianakis &

Romo, 2010; Lucas & Rosenheim, 2011; Perdakis et al., 2014), prey morphological and behavioural adaptations (Polis et al., 1989; Wilby et al., 2005), life-cycle complexity and abundance (Polis et al., 1989; Chacón & Heimpel, 2010; Tylianakis & Romo, 2010), predator diversity, and the spatiotemporal scale of the study (Tylianakis & Romo, 2010). Enhanced natural enemy diversity in wildflower strips used in our study did not result in a reduction in crop damage, which may indicate that top-down control of pests in adjacent crops was dampened by negative interactions between natural enemies. However, this cannot be determined because the abundance and diversity of natural enemies within the crop itself was not measured within this study. Intraguild interactions are common among generalist predators, and these may reduce top-down control (Sanders et al., 2011). Moreover, given that sown strips were the only habitat, other than the crop, available within the experimental fields, these were associated with a high density of generalist predators, which may enhance negative interactions (Chacón & Heimpel, 2010; Sanders et al., 2011). Furthermore, the relatively small scale of the study and hence the reduced microhabitat heterogeneity would also be expected to increase negative interactions (Tylianakis & Romo, 2010). Even though vegetation diversity in more complex flowering strips can mediate multipredator effects on herbivores, by providing microhabitats that dampen antagonistic interactions and provide access to alternative resources (Finke & Denno, 2002), we did not record significant differences between flower strip mixtures.

Experimental plots adjacent to sown flower strip mixtures were characterised by a higher crop yield (H3), in terms of number of fruit, and fruit fresh weight and biomass. Natural habitat has been shown to increase the abundance of pollinators of tomato and that these increase the production of field-grown tomato (Greenleaf & Kremen, 2006). During this study, we have recorded an increased abundance of wild bees in the sown strips, and tomato production was higher in experimental plots adjacent to these strips. Similarly, the inclusion of flowering resources and plant diversity within farmland was observed to increase crop productivity (Carvalho et al., 2012). This supports previous observations that polycultures can support higher crop yields in comparison to monocultures (Iverson et al., 2014) and suggests that increasing diversity at the local scale can provide multiple ecosystem services, that is, the conservation of natural enemies for biological control and pollinators for enhancing crop pollination. In general, there is little work showing how ecosystem services covary in response to vegetation diversity, especially with respect to crop yield (Shackelford et al., 2013; Iverson et al., 2014). Our results indicate that

the provision of vegetation diversity and flowering resources may enhance Lepidoptera pest fitness, an ecosystem disservice recorded through increased pest-induced fruit damage. However, this did not increase total yield loss and an increased crop production was recorded. The conservation of natural enemies and pollinators at the local scale is also enhanced by the presence of wildflower strips.

Our study adds to the growing evidence that increased floral diversity within agricultural habitats may enhance the provision of multiple ecosystem services, such as the conservation of arthropod functional diversity and maintaining crop yield (Campbell et al., 2012; Carrié et al., 2012; Balzan & Moonen, 2014). Although we have not observed any significant effects on natural pest control rates and crop damage suppression, the availability of non-crop habitats was associated with increased colonisation by natural enemies. This may be particularly important for annual crops, which depend on cyclic colonisation of the crop and surrounding habitat (Wissinger, 1997). The provision of simple flowering strips in arable crops has important conservation benefits for several functional groups of arthropods. Increased plant functional and species diversity within this study was particularly important for ensuring longer flowering and was also associated with increased abundance of Anthocoridae bugs and wild bees. These observations confirm the importance of maintaining plant diversity at the field scale. Moreover, these results imply that naturally occurring flowering annual plants may play an important role in maintaining ecosystem services within cropping systems (Bärberi et al., 2010), and that the maintenance of plant diversity in field margins within the study area can contribute to the maintenance of natural pest control and pollination services in arable fields (Balzan, 2013; Balzan et al., 2014). Habitat management at the local (field) scale should be combined with landscape management of natural and semi-natural habitats (Tschardt et al., 2005; Ricketts et al., 2008; Chaplin-Kramer et al., 2011), to effectively improve the conservation of biodiversity and maintain arthropod-mediated services in agroecosystems, thus enhancing the sustainability of horticultural crops.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1 Seed mixtures for different experimental levels of wildflower strips. Given that a substitutive design was used during this study, sowing rate for each species changed as a function of the number of sown species within each experimental level of wild flower strip. Dark grey squares indicate ‘peak/full bloom’, soft grey indicates flowers that were ‘in bloom’ while white cells indicate that the sown species did not flower.

Table S2 Taxonomic and functional groups used for arthropod visitors to flowering strips (p, pitfall traps; a, aspiration).

Table S3 GLMM fitting results for pest damage at harvest, measured in number of galleries per plant from Lepidoptera pests of tomato cvs Perfect Peel (PP) and Roma. Total fruit production (N) is included as a fixed effect given that this varied with experimental treatments and is inherently related to the magnitude of pest damage.

Table S4 GLMM fitting results for leaf aphid abundance and fruit damage throughout the growing season for the tomato cv. Perfect Peel.