

Research



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Landscape context shifts the balance of costs and benefits from wildflower borders on multiple ecosystem services

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In the face of global biodiversity declines driven by agricultural intensification, local diversification practices are broadly promoted to support farmland biodiversity and multiple ecosystem services. The creation of flower-rich habitats on farmland has been subsidized in both the USA and EU to support biodiversity and promote delivery of ecosystem services. Yet, theory suggests that the landscape context in which local diversification strategies are implemented will influence their success. However, few studies have empirically evaluated this theory or assessed the ability to support multiple ecosystem services simultaneously. Here, we evaluate the impact of creating flower-rich habitats in field margins on pollination, pest control, and crop yield over 3 years using a paired design across a landscape gradient. We find general positive effects of natural habitat cover on fruit weight and that flowering borders increase yields by promoting bee visitation to adjacent crops only in landscapes with intermediate natural habitat cover. Flowering borders had little impact on biological control regardless of landscape context. Thus, knowledge of landscape context can be used to target wildflower border placement in areas where they will have the greatest likelihood for success and least potential for increasing pest populations or yield loss in nearby crops.

1. Introduction

Presently, 40% of the earth's terrestrial surface is used for agricultural production [1] and the continued transition of natural habitat to agricultural use is one of the primary drivers of biodiversity loss worldwide [2]. Balancing the demand for agricultural productivity with biodiversity conservation is one of the greatest challenges facing global humanity. However, agricultural intensification can undermine the very biodiversity and ecosystem services that would otherwise benefit crop production [3–5]. Diverse biological communities support many ecosystem services to agriculture, provide resilience to disturbances, and maintain the capacity to adapt to future changing environments [6,7]. Agricultural intensification at both local and landscape scales reduces the spatial and temporal availability of resources required by beneficial organisms, such as pollinators and natural enemies [8], while crop pests often benefit from a concentration of host plants [9].

To increase agricultural sustainability, strategies are needed that reduce conflicts between biodiversity conservation and crop production. Ecological intensification capitalizes on the biodiversity within agroecosystems to achieve sustainable increases in crop yields by actively managing communities of ecosystem service providers [10,11]. Yet, a major hurdle to the widespread adoption of ecological intensification strategies is a framework for predicting the contexts in which they will be successful. Variable effectiveness of these practices may be due to the landscape context in which they are implemented [12–14]. The intermediate landscape complexity hypothesis predicts that local management strategies will be most effective at improving biodiversity and ecosystem services

when established in landscapes that are dominated by agriculture but with at least some natural habitat remaining [9,12]. In landscapes with high natural habitat cover, beneficial organisms continuously colonize agricultural habitats. Alternatively, in landscapes with very little natural habitat remaining, source populations of beneficials are too depauperate to recruit from. However, in landscapes with intermediate amounts of remaining natural habitat, regional source populations are present, but agricultural habitats are not continuously colonized. Therefore, ecological intensification in these intermediate landscapes is expected to produce the greatest effects and early findings from Europe support these patterns with respect to enhancing biodiversity [15–19]. Whether these findings are also reflected in the delivery of multiple ecosystem services and crop yield remains unresolved.

Multiple ecosystem services are expected to benefit from increases in local habitat diversity. For example, local management with flowering strips has been shown to increase the abundance of pollinators and natural enemies of pests in adjacent cropland [19–21]. However, few studies have evaluated the effect of local habitat management on multiple services simultaneously [22–24], and only one has evaluated their combined effects on crop yield [25]. Consequently, our understanding of the potential interactions between yield-supporting ecosystem services and ecological intensification strategies that can simultaneously support them is limited.

Pests can also benefit from natural habitats at the local and landscape scale [24,26,27], thus management strategies aimed at increasing ecosystem services may fail to improve pest control or crop yield [28]. In these cases, although biodiversity may be locally improved, yield gaps may trigger the transition of natural lands to agriculture elsewhere leading to a net loss for both biodiversity and ecosystem services. The planting of flower-rich crop borders is subsidized by policies in both the USA and EU and many governments and intergovernmental agencies have recently called for agricultural management practices that support biodiversity and ecosystem services on farms (White House Pollinator Protection Task Force 2016, IPBES 2017) making the need to ensure efficient placement and effectiveness more critical than ever.

Here, we evaluate the benefits and potential costs of a commonly implemented ecological intensification strategy, the planting of native perennial wildflowers in field margins. We explore the effect of wildflower borders on crop visitation by bees, biological control, pest abundance, crop damage, and crop yield using a paired design in strawberry plantings with and without a wildflower border on 12 farms across a landscape gradient. Following the predictions of the intermediate landscape hypothesis, we expect that wildflower margins will improve ecosystem services and crop production to a greater extent when implemented in landscapes with intermediate amounts of natural habitat cover.

2. Methods

(a) Experimental design

We identified 12 farms within the Finger Lakes region of central New York State that varied in landscape composition (18–61% natural land cover; electronic supplementary material, figure S1). On each farm, we established two 10 × 15 m plots consisting of five rows of strawberry (var. 'Jewel') in the spring of 2012. Plots were separated by a minimum of 200 m and were randomly

assigned to either a control border or a native perennial wildflower border. The distance separating plots represents a compromise between the relatively small foraging ranges of the insect communities relevant to strawberry [29] and ensuring that plot pairs within a farm were within the same landscape contexts. Composition and management of control borders were representative of field edge management practices in the region. Control borders consisted primarily of orchard grass and were regularly mown over the growing season. Wildflower borders were approximately 4 m wide by 10 m long and ran parallel with the crop border consistent with standard implementations of this management strategy in terms of size and orientation. Plantings consisted of the following nine US native perennial species *Zizia aurea*, *Penstemon digitalis*, *Coreopsis lanceolata*, *Potentilla fruticosa*, *Veronicastrum virginicum*, *Agastache neptoides*, *Silphium perfoliatum*, *Lobelia siphilitica*, and *Solidago canadensis*. These species were selected based on their attractiveness to bees and natural enemies [13,20,30–32] and provide overlapping bloom periods, so that flowers are present throughout the growing season. When possible, every effort was made to grow plants from local ecotypes. Both border types were established in the autumn of 2012. Plots were managed organically or involved limited use of pesticides for weed or fungal pathogen management. Each year, straw mulch was applied to all plots in the autumn and raked into the row middles in the spring consistent with standard horticultural practices for strawberry in the northeast. In 2015, one wildflower strip was accidentally destroyed leaving only 11 site replicates in that year.

At four plots, it was necessary to prevent damage from large mammalian herbivores by erecting temporary plastic fencing. Fence gaps were wide enough (3 × 3 cm) to allow access to even the largest pollinators (H Grab 2014, personal observation). In each case, both the control and wildflower treatment plots on the same farm were fenced.

(b) Landscape

Landscape complexity was characterized using the National Agricultural Statistics Service Cropland Data Layer for New York [33] for each year of the study (2013–2015) in ArcGIS 10.1. The region is characterized by a mix of row crops, fruits and vegetables, orchard, dairy, old-field habitats, and forest. We quantified the cover of natural and semi-natural habitats at four radii from the centre of each plot (500, 750, 1 000, and 1 250 m). Land cover values were averaged between paired plots in each farm to generate a single landscape value for each farm in each year. We fitted separate nonlinear models for each response variable and scale and determined that 750 m was the scale at which the cover of natural area provided the best fit to the data (based on AICc values, see electronic supplementary material, table S1). Previous studies of the pollinators, parasitoids, and pests in this system have found strong responses to this landscape metric at similar scales [29,34,35].

(c) Pollinator surveys

The community of pollinators visiting strawberry is dominated by a diverse fauna of wild bees with honeybees comprising only 7% of the pollinator community [29]. In the 3 years following plot establishment (2013–2015), the visitation rate of bees to strawberry flowers was estimated by conducting visual surveys on four dates per plot spanning the duration of crop bloom. Surveys were carried out between 10:00 and 15:30 on sunny days with temperatures above 16°C. Visitation rate was assessed using standardized 10 min transects through each plot recording each bee visit to a strawberry flower. The number of open strawberry flowers per square foot was estimated for each plot by averaging counts of flowers in 1 ft² quadrats in each of the five rows. Visitation rates per plot were calculated by dividing the

total number of visits recorded during the 10 min transects by the average number of open flowers per square foot.

To better understand the relative importance of the planted wildflower species, we monitored pollinator visitation rates to each plant species as well as visits to flowering weeds within the borders throughout the season in 2015. All flowering plants within the border were observed for 10 min and total number of visits per plant species was recorded.

(d) Pest surveys

The primary pest of strawberry in the region is *Lygus lineolaris* (Hemiptera: Miridae), a generalist herbivore that feeds on the seeds of developing strawberry fruits. From 2013 to 2015, the abundance of *L. lineolaris* was estimated in each plot immediately following strawberry flowering by tapping individual strawberry inflorescences until a total of 24 nymphs were collected or all inflorescences in the plot were sampled. We chose a target of 24 nymphs per sample because this number allowed us to accurately estimate parasitism rates using the protocols described below. Nymph densities were calculated by dividing the number of nymphs collected by the total number of inflorescences tapped.

Because wildflower borders may harbour pest populations that can spill over into the crop, we estimated the abundance of *L. lineolaris* in the wildflower borders compared to the control borders for an entire growing season in 2015. The abundance of *L. lineolaris* adults and nymphs was estimated for each flowering species present in the wildflower borders by vacuuming (Echo ES 230 Shred 'n Vac, Lake Zurich, IL, USA) 25 inflorescences of each plant species once a week from May to October. Plants were sampled at the bud, flowering, and seed head phases, so that our estimate for each species accurately reflected the broad feeding preferences of *L. lineolaris*. After sampling a particular species, all *L. lineolaris* were returned to the host plant they were collected from to ensure that the effects of sampling in one week had little impact on samples in the subsequent weeks. Sampling also included any weedy flowering species that had invaded the perennial borders. As some plant species had fewer than 25 inflorescences on any particular sampling date, the total number of *L. lineolaris* collected was divided by the number of inflorescences vacuumed for each sample. The order of sampling was randomized for species blooming on a given date. An equivalent number of vacuum samples were obtained from the grassy margins of control borders for each wildflower species sampled from its paired wildflower treatment plot.

(e) Parasitism rates

In the study region, the primary natural enemies of *L. lineolaris* include a complex of native and introduced parasitoid wasps in the genus *Peristenus* [36]. Three species, *Peristenus digoneutis* (introduced), *Peristenus pallipes* (native), and rarely *Peristenus relictus* (introduced), are known to attack *L. lineolaris*; however, parasitism rates are reduced in landscapes with a high proportion of agricultural land cover [35]. Diagnostic PCR assays were used to simultaneously estimate parasitism rates and parasitoid species identity, as they are faster and more accurate than rearing or dissection [37,38]. Random samples of 24 nymphs from each sampling period at each site were selected for parasitism assays. In some cases, fewer than 24 nymphs were collected in a sampling period. In these cases, all collected nymphs for the period were processed. In three instances, no nymphs were collected on a farm in a particular year; therefore, these instances resulted in only 32 site by year replicates. DNA from nymphs was extracted using an abbreviated chloroform: isoamyl alcohol protocol developed by Tilmann & Hoffmann [39]. DNA extractions along with negative controls were amplified using *Peristenus* species-specific primers as in [40]. Using this method, species-specific forward

primers are combined with a genus-specific reverse primer to amplify a region including ITS1 and ITS2.

(f) Fruit damage and yield

A typical strawberry inflorescence is comprised of a single primary fruit (king berry), a pair of secondary fruit, and four tertiary fruit. Strawberries are an aggregate accessory fruit comprised of as many as 300 achenes on a primary fruit and 200 on a secondary fruit [41]. Each achene must be fertilized for the surrounding tissue to develop and an average of four visits per flower is required to achieve full pollination [42]. *Lygus lineolaris* nymphs and adults feed on developing achenes leading to developmental failure of the surrounding tissues. Fruit weight is highly correlated with the number of developed undamaged achenes [41]. Fruits with a high percentage of damaged achenes, either from poor pollination or *L. lineolaris* feeding, develop with major malformations that reduce overall yield and marketability [43].

To measure the impact of wildflower borders on crop yield at each site, 30 flowers were marked and the resulting fruits from each plot were harvested when ripe and weighed. Owing to sample processing errors, fruit data are unavailable for one site in 2013 and one site in 2014. The percentage of poorly pollinated and damaged achenes was estimated for each fruit. Secondary fruits were used, as they are less prone to frost damage than primary fruit and due to their later development are highly susceptible to damage from *L. lineolaris* nymph feeding.

(g) Statistical analysis

To evaluate whether wildflower borders had differential effects across the landscape gradient, we first pooled individual measures for each variable (ex. pollinator visitation, *L. lineolaris*, parasitism, malformations, or weights per individual fruit) by plot and year averaging over all surveys within a plot in each year. Because the primary objective of the study was to determine the effectiveness of the plantings under varying landscape contexts, we calculated an index of wildflower border effectiveness for each variable. In this way, we are able to control for the overall variation that occurs across the landscape gradient and isolate the variation due to the wildflower border. Absolute values for each variable on control and wildflower planting across the landscape gradient are presented in electronic supplementary material, figure S2. The effectiveness index was calculated by subtracting the average value observed on the plots with a wildflower border minus the control divided by the control $((\text{Wildflower} - \text{Control})/\text{Control})$ of each farm in each year. The effectiveness index therefore represents a quantitative measure of the relative effectiveness of the wildflower planting. Positive values indicate an increase in the variable of interest on the plot with a wildflower planting compared to the control and negative values indicate the measured variable was higher on control plantings. We then constructed linear and nonlinear mixed effects models for each index (GLMER, R package lme4 [40,44]) with Gaussian error structures. Fixed effects in each model included year and proportion of combined natural and semi-natural habitat cover as well their interaction. We constructed linear, logistic, and polynomial models for each variable and selected the best fit model based on AICc values. Farm was included as a random effect in each model to account for the paired experimental design and repeated measures across years. Additionally, we tested whether site-level covariates including the distance between the wildflower and control plot, the total number of flower plant species, and the total number of native perennial species that established had an effect on each of the index variables. Each of these site-level covariates was evaluated in a mixed effects model that included the linear and polynomial natural habitat cover terms with site as a random effect. The majority of covariates did not explain a

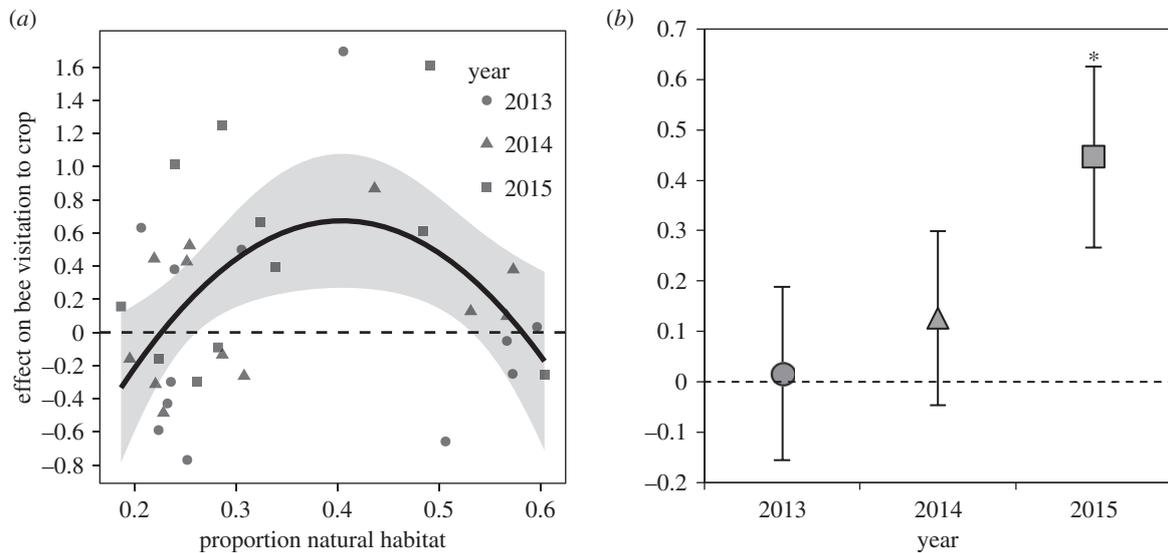


Figure 1. Effectiveness of wildflower (WF) borders relative to control (C) plots $((WF - C)/C)$ for bee visitation to strawberry flowers (a) in relation to the proportion of natural land cover in a 750 m radius around each site across all 3 years of the study and (b) in each of the study years following wildflower establishment in 2012. In (a), shaded areas represent 95% confidence intervals. Asterisk in (b) indicates values different from 0 at $p < 0.05$ based on *post hoc* contrast tests.

significant portion of the variation in any index and were not included in the final models.

Differences in *L. lineolaris* numbers and bee visits to wildflower and weedy flowering species within the plot margins were assessed with generalized linear mixed effects models with Poisson error distributions. For both variables, plant species was included as a fixed effect and farm was included as a random effect. For overall *L. lineolaris* abundance in wildflower compared to control borders, an index was computed similar to those described above. Fixed effects included year and proportion of combined natural and semi-natural habitat cover as well their interaction.

The contribution of *L. lineolaris* feeding versus poor pollination to fruit damage was assessed using a generalized linear mixed effects model with a Poisson error structure. Fixed effects include year, average bee visitation, and average *L. lineolaris* abundance, as well as, the two-way interactions between year and bee visits, and year and *L. lineolaris* abundance. In all models, p -values and degrees of freedom are calculated based on the Satterthwaite approximation as implemented in the package *lmerTest* [45].

3. Results

Wildflowers bloomed from April to November each year beginning in 2013. On average, seven of the nine wildflower species became established at each site, but no site had fewer than six species (electronic supplementary material, table S3). In the 3 years following establishment (2013–2015), a total of 5 684 bee visits to strawberry were recorded and 1 307 bee specimens were collected. Wild bees were the dominant visitors, representing 95.8% of the community while managed bees (honeybees) made up only 4.2% of recorded visits. In total, 99 species were recorded based on net collected specimens.

Following the expectations of the intermediate landscape hypothesis, the effect of wildflower borders on bee visitation to the strawberry crop across the landscape gradient was best described by a second-order polynomial function ($AIC_{c_{poly}} = 63.86$, $AIC_{c_{log}} = 73.86$, $AIC_{c_{linear}} = 73.89$; Poly: $F_{1,21} = 7.33$, $p = 0.01$). Wildflower borders increased bee visitation to strawberry relative to controls only in landscapes with intermediate amounts of natural habitat (figure 1a). On average,

wildflower borders had little effect on bee visitation in the first 2 years after establishment, but had positive effects in 2015 ($t_{1,21} = 2.48$, $p = 0.02$; figure 1b).

A total of 3 197 *L. lineolaris* nymphs were collected from the strawberry plantings over the 3 years of the study. The effect of wildflower borders on *L. lineolaris* abundance was also influenced by the landscape according to a second-order polynomial function ($AIC_{c_{poly}} = 127.7$, $AIC_{c_{log}} = 136.3$, $AIC_{c_{linear}} = 136.1$; Poly: $F_{1,18} = 3.71$, $p = 0.06$). Pest abundances on plots with a wildflower border were greater than controls in the landscapes with the least and most natural habitat cover (figure 2a). In intermediate landscapes, wildflower borders decreased pest pressure below the levels of control plots. The abundance of *L. lineolaris* on plots with a wildflower border differed across the years ($F_{2,18} = 7.88$, $p = 0.003$) and was greatest in 2014 ($t_{1,21} = 4.67$, $p < 0.001$; electronic supplementary material, figure S3).

Parasitism assays revealed an overall parasitism rate of 18%. Three parasitoid species were detected with the introduced *P. digoneutis* being the dominant natural enemy (96.7% of parasitism events) and the other two species, *P. pallipes* (native, 2.8%) and *P. relictus* (introduced, 0.05%), represented at low levels. The effectiveness of wildflower borders across the landscape gradient on parasitism largely mirrored the pattern observed for pest abundances (figure 2b). Again a polynomial function best fit the data ($AIC_{c_{poly}} = 117.7$, $AIC_{c_{log}} = 126.5$, $AIC_{c_{linear}} = 126.4$; Poly: $F_{1,16} = 4.06$, $p = 0.06$). However, parasitism rates followed a pattern across years similar to bee visitation; achieving the highest values on wildflower plots relative to controls in 2015 ($t_{1,18} = 2.48$, $p = 0.02$; electronic supplementary material, figure S4).

Sampling *L. lineolaris* within the plot margins themselves revealed that densities of *L. lineolaris* were higher in wildflower borders compared to control borders throughout the season (WF: $F_{1,10} = 30.47$, $p = 0.0003$). Although there were no differences in the number of *L. lineolaris* collected in control margins between the landscape types, wildflower margins in landscapes with intermediate natural habitat cover supported greater numbers of *L. lineolaris* relative to landscapes with either low or high proportions of natural habitat (figure 3a,

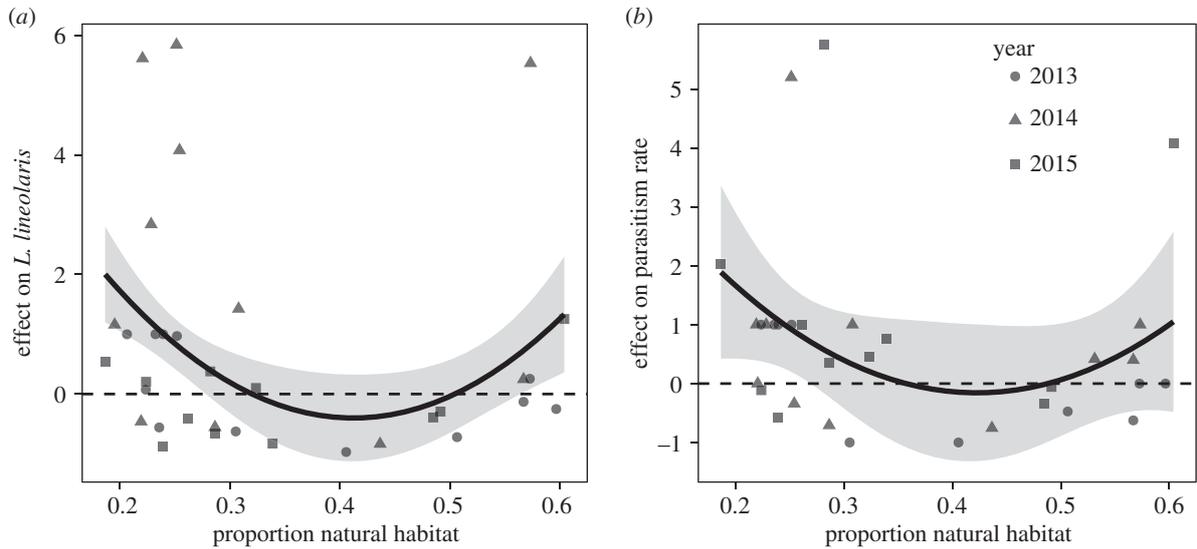


Figure 2. Effectiveness of wildflower (WF) borders relative to control (C) plots ((WF – C)/C) for (a) the number of *L. lineolaris* nymphs and (b) the parasitism rate of nymphs. Shaded areas represent 95% confidence intervals.

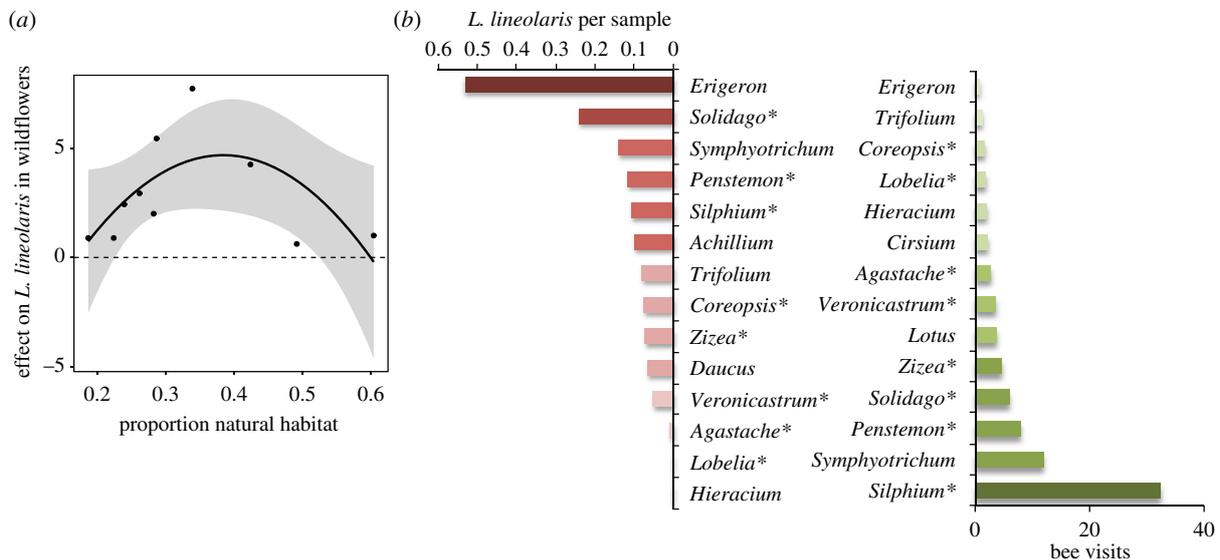


Figure 3. The average number of *L. lineolaris* nymphs collected within the wildflower borders (a) relative to control borders and (b) on various wildflower species (planted species with *) relative to the number of bees visiting each wildflower species.

$F_{1,10} = 5.42$, $p = 0.052$). In 2015, each wildflower species in the wildflower border was surveyed for its attractiveness to both bees and *L. lineolaris*. The number of *L. lineolaris* supported by different species of wildflowers varied ($F_{12,238} = 1.94$, $p = 0.03$) as did the number of bee visitors to each species ($F_{14,86} = 8.12$, $p = 0.0001$; figure 3b). While some species supported moderate numbers of both *L. lineolaris* and pollinators (ex. *Penstemon*), the most attractive species were different for pests (ex. *Erigeron*) and pollinators (ex. *Silphium*).

Both lack of pollination by bees and feeding by *L. lineolaris* cause malformations to developing strawberry fruit resulting in yield loss. The relative importance of *L. lineolaris* abundance versus bee visitation in predicting malformations varied across study years (*L. lineolaris* × year: $F_{1,11} = 36.03$, $p < 0.001$; bee × year: $F_{1,11} = 33.26$, $p < 0.001$). In both 2013 and 2014, *L. lineolaris* abundance was the only significant predictor of fruit malformations and increasing nymph abundance was associated with greater malformations (2013 *L. lineolaris*: $z = 2.98$, $p = 0.002$, bee: $z = 0.22$, $p = 0.823$; 2014 *L. lineolaris*: $z = 2.17$, $p = 0.029$,

bee: $z = -0.21$, $p = 0.829$). In 2015, both groups predicted malformations; although, bee visitation had a stronger effect in reducing malformations (bee: $z = -2.74$, $p = 0.006$; *L. lineolaris*: $z = 2.24$, $p = 0.025$; electronic supplementary material, figure S5) consistent with increasing positive effect of wildflowers on bees over the 3-year study.

The difference in fruit malformations on plots with a wildflower border compared to controls was best explained by a polynomial response to landscape ($AIC_{c,poly} = 65.83$, $AIC_{c,log} = 72.35$, $AIC_{c,linear} = 72.58$; Poly: $F_{1,19} = 3.48$, $p = 0.07$). Malformations caused by both poor pollination and *L. lineolaris* feeding were greatest on plots with a wildflower border relative to control plots in landscapes with the least natural land cover (figure 4a). Landscapes with intermediate cover of natural habitat had the greatest reduction in malformations relative to control plots.

For fruit weight, a polynomial function also best described the relationship between wildflower border effectiveness and landscape ($AIC_{c,poly} = -0.33$, $AIC_{c,log} = 7.42$, $AIC_{c,linear} = 8.52$; Poly: $F_{1,19} = 8.68$, $p = 0.008$). In the landscapes with the

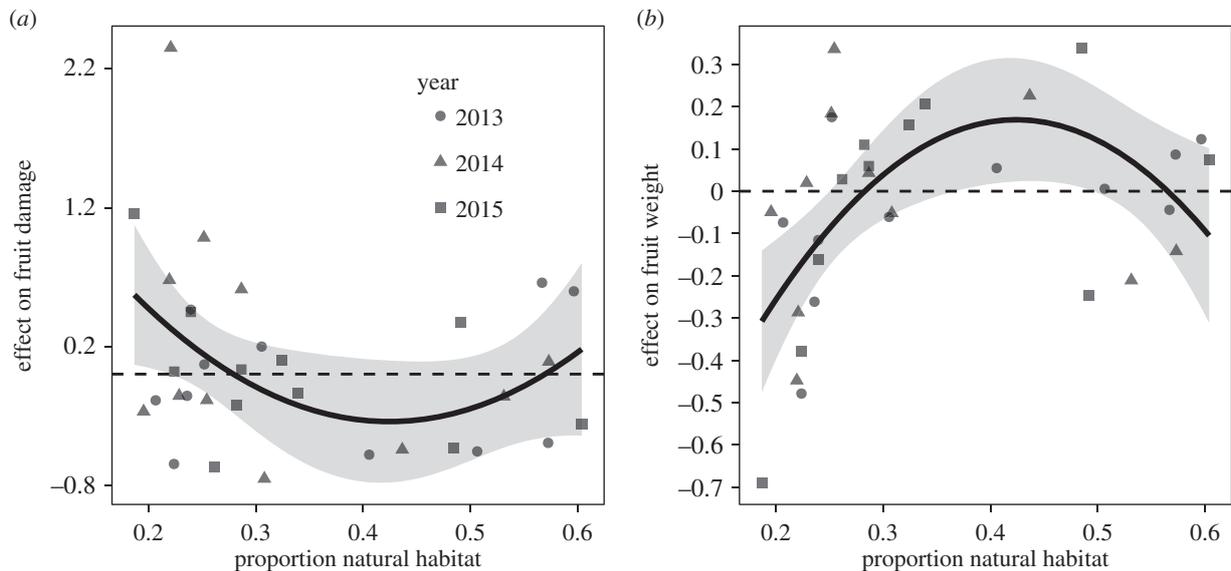


Figure 4. Effectiveness of wildflower (WF) borders relative to control (C) plots $((WF - C)/C)$ for (a) the malformations to and (b) the weight of strawberry fruits. Shaded areas represent 95% confidence intervals.

least natural cover, plots with a wildflower border had lower yields than control plots. By contrast, plots with a wildflower border had higher yields than controls in landscapes with intermediate amounts of natural land cover (figure 4b). This difference between wildflower and control borders decreased in landscapes with the most natural cover.

4. Discussion

Ecological intensification strategies including the creation of flower-rich habitats on agricultural lands have been promoted as a practice to support farmland biodiversity and encourage the delivery of ecosystem services (White House Initiative, EU Initiative, IPBES report 2016 [12,13,46–48]). In the USA, these practices are subsidized at a rate of \$57 million per year through the Conservation Reserve Program (CRP) and Environmental Quality Incentives Program (EQIP) [49]. Yet, few studies have evaluated the effectiveness of these practices across a gradient of landscape contexts or on multiple ecosystem services simultaneously, impeding our ability to effectively implement these practices. Here, we evaluate the impact of wildflower borders on pollination, pest control, and crop yield across a landscape gradient and find that while flowering crop borders can be successful in some contexts, landscapes that are the most agriculturally intensified will require larger scale more coordinated conservation approaches.

In terms of supporting crop pollination services, our findings support the prediction of the intermediate landscape hypothesis [9,12] with bee visitation to crop flowers increasing with the addition of local wildflower borders according to a polynomial function which peaked in landscapes with intermediate cover of natural habitats. Interestingly, the intermediate values of land cover that correspond with success of the wildflower borders in supporting ecosystem services are shifted strongly towards higher values of natural habitat compared to those originally proposed by Tscharrntke *et al.* [12] for supporting biodiversity in European landscapes. Tscharrntke *et al.* proposed that wildflower borders would have the strongest effects on biodiversity in landscapes with 1–20% non-crop habitat. In our study, wildflower habitats were the most successful at increasing the delivery of

ecosystem services in landscapes with 25–55% natural habitat cover. These differences in threshold values may reflect the differences in the composition of the current dominant natural habitat covers (grasslands in Europe, forest in the northeastern USA) or differences in the history of large-scale agricultural land use between the regions (thousands of years in Europe, hundreds in the northeastern USA). Alternatively, the shift in response curves may represent fundamentally different landscape optima for supporting ecosystem services compared to biodiversity with local management practices. One mechanism that may lead to this shift is that flowering crop borders continue to support increased abundance of functionally important species past the optima at which species richness is maximized. Delivery of ecosystem services has been shown to be driven by the abundance of functionally important taxa rather than community diversity [50,51]. Indeed, the effectiveness of supplementing floral resources for enhancing parasitism rates in California vineyards was greatest when landscapes contained 20–60% natural habitat [52], supporting the idea that a higher threshold of natural habitat is required for benefits to ecosystem services. These results imply that policies attempting to prioritize areas for either conservation or ecosystem services management need to be tailored, as the response curves may differ.

For pest pressure, the shape of the relationship between landscape and effectiveness of flowering crop borders is also predicted by the intermediate landscape hypothesis, yet the curve is shifted strongly above zero. This shift indicates a cost of wildflower borders not predicted by the intermediate landscape hypothesis. In landscapes with both the least and greatest natural habitat cover, plots with a wildflower border had greater pest abundances than those with a control border. Although flowering borders are intended to target beneficial insects, generalist pests like *L. lineolaris* are also able to take advantage of these additional resources [20,24,26]. We observed greater numbers of *L. lineolaris* in wildflower borders in moderately agricultural landscapes compared with more complex landscapes. This result likely reflects the lower propensity for *L. lineolaris* to disperse in agriculturally dominated landscapes [53] and may lead to increased spillover of pests from the wildflowers to the crop in the following spring.

The relationship between landscape and effect of wildflower borders on parasitism was the opposite of our predictions based on the intermediate landscape hypotheses. Rather, wildflower plots with the greatest increases in parasitism relative to controls were in the same landscape contexts that also had the greatest increases in pest abundances. In this case, parasitoid responses to wildflower borders may be obscured by density-dependent responses to host abundance [54]. However, other studies have found positive effects of wildflower borders on biological control of pests [20,55], particularly when the pest was not able to use the flowering crop border as alternative hosts. Effects of wildflower strips on parasitism rates may also have lagged behind effects on herbivores as *L. lineolaris* had the greatest increase in plots with a wildflower border in 2014 while parasitism increased most strongly in 2015.

The lag in time between the establishment of wildflower borders and the response of the beneficial insect community can influence the cost–benefit ratio for farmers implementing these borders with the goal of enhancing ecosystem services [31]. These lags are particularly important for annual crops or short-term perennial crops like strawberry, which are grown in the same field for only 2–5 years. In our study, increases in bee visitation and parasitism rates occurred in the third year following establishment. Although a number of studies report responses within the first year following establishment [19,20,32,56], the majority of these studies report on communities within wildflower plantings rather than in adjacent crop habitats [19,32] while others use annual plants in their borders [56]. These results suggest that other border types may be more appropriate for annual or rotating crops or that growers should establish flowering borders before the crop.

Ultimately, the benefits of ecological intensification practices like flowering crop borders can be measured in terms of increases in crop yields. Yet, while many studies evaluate the effects of wildflower borders on bee visitation or natural enemy communities, few assess the impact on crop damage and the final effect on yield (but see [25,31]). Regardless of crop border treatment, natural habitat cover had a generally positive effect on fruit weight. When comparing border treatments using the effectiveness index, wildflower borders reduced fruit damage and increased yield most strongly in landscapes with intermediate natural habitat cover, showing that ecological intensification practices can successfully improve crop productivity. However, in landscapes with either high or low natural habitat cover, wildflower borders tended to increase fruit damage and reduce yield. In these same landscapes, wildflower borders had little effect on bee visitation and increased pest abundances, suggesting that

the success of ecological intensification practices will be dependent on the context in which they are implemented.

Although flowering crop borders had positive yield effects at intermediate levels of landscape complexity, our study indicates that wildflower border management is not without costs imposed by increased herbivore pressure when implemented outside of the optimal landscape window. Yet, increases in herbivore pressure were only observed in landscapes where wildflower borders had the least success in improving bee visitation. In all landscape contexts, efforts should focus on selecting wildflower species that are not preferred by crop pests [21,57] and on managing weedy species that support high numbers of crop pests. Management practices that reduce these weedy species can also increase the establishment rates of planted species [58]. In simple landscapes where wildflower borders have few benefits, efforts should focus on the conservation of the remaining natural habitat and restoration of larger areas of natural habitat rather than on field-scale diversification strategies.

Because of the importance of landscape in mediating the success of ecological intensification practices like wildflower crop borders, we propose that landscape context should be explicitly considered in large policy initiatives that subsidize the creation of flowering habitats on farmlands. Ranking criteria that incorporate landscape along with other site-level criteria including slope, proximity to waterways or wetlands, and other factors will allow land managers and conservation practitioners to select appropriate conservation measures for a given site. By implementing these metrics, limited resources for establishing habitat for beneficial insect conservation can be targeted to areas where they will have the greatest likelihood for success with the least potential for increasing pest populations or yield loss in nearby crops.

Data accessibility. Data associated with this manuscript have been deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.425kd01> [59].

Authors' contributions. H.G., K.P., and G.L. designed experiments. B.D. provided materials for laboratory assays. H.G. collected data, conducted analyses, and wrote the first draft of the manuscript. All authors contributed substantially to revisions.

Competing interests. We declare we have no competing interests.

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