Agricultural practices for food safety threaten pest control services for fresh produce

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Summary

1. Over the past decade, several foodborne disease outbreaks provoked widespread reforms to the fresh produce industry. Subsequent concerns about wildlife vectors and contaminated manures created pressure on growers to discontinue use of manure-based composts and remove nearby semi-natural vegetation. Despite widespread adoption, impacts of these practices on ecosystem services such as pest control have not been assessed.

2. We used a landscape-scale field experiment to quantify associations between compost applications, semi-natural vegetation, pest control services and lettuce yields on organic farms throughout California's Central Coast, a region experiencing food safety reforms.

3. We found that farms with surrounding semi-natural vegetation supported a diverse arthropod assemblage, whereas a herbivore-dominated assemblage occupied farms in simplified landscapes. Moreover, predatory arthropods consumed more herbivores at sites with more surrounding non-crop vegetation and reduced aphid pest infestations in lettuce.

4. Compost improved lettuce yields by increasing soil nutrients and organic matter, but affected neither pest control nor *Escherichia coli* prevalence.

5. *Synthesis and applications.* Food safety concerns are prompting practices that simplify farms and landscapes. Our results demonstrate that two practices – elimination of manure-based composts and removal of non-crop vegetation – are likely having negative impacts on arthropod biodiversity, pest control and soil quality. Critically, our findings and previous research suggest that compost can be applied safely and that habitat removal is likely ineffective at mitigating food safety risk. There is thus scope for co-managing fresh produce fields for food safety, ecosystem services, and biodiversity through applying appropriately treated composts and stopping habitat removal.

Key-words: agriculture, agro-ecology, biological control, co-management, compost, food safety, foodborne disease, natural enemies, pest control, produce

Introduction

Foodborne illness originating from fresh produce has emerged as a major public health concern (Painter *et al.* 2013), triggering sweeping reforms to the produce industry (LGMA 2013, FDA 2014). Reforms have been especially pervasive in California's Central Coast, the origin of a deadly, multistate *Escherichia coli* O157:H7 outbreak in 2006. Concerns that animals might carry foodborne

illnesses created pressure on growers to reduce wildlife field intrusions by removing non-crop vegetation, perceived as wildlife habitat (Karp *et al.* 2015a). Following the outbreak, ~13% of the remaining riparian habitat along the Salinas River was degraded or destroyed (Gennet *et al.* 2013). Manures were targeted as another contamination source. Now, many organic growers apply liquid or heat-treated, pelleted fertilizers. The environmental consequences of these food safety practices are largely unknown (Karp *et al.* 2015a), but may affect ecosystem services such as pest control (Letourneau,

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Allen & Stireman 2012) and building healthy soils (Mader *et al.* 2002).

In the Central Coast, a diverse suite of insect pests affects lettuce growers. Aphid and lepidopteran pests are usually the most damaging and often motivate insecticide applications (Bugg *et al.* 2008). Synthetic pesticides are unavailable to organic growers (~15% of growers in the region), who instead use a limited set of approved pesticides and/or rely on predators to consume aphids and other lettuce pests (Bugg *et al.* 2008; Smith, Chaney & Bensen 2008; Nelson *et al.* 2012). Removal of predatory syrphid larvae from lettuce heads in one study caused aphid populations to explode, resulting in unmarketable plants (Smith, Chaney & Bensen 2008). Food safety-induced vegetation removal may disrupt pest control because syrphids and other predators rely on non-crop vegetation to complete their life cycles (Bugg *et al.* 2008). Generally, predator and parasitoid abundance, diversity and consumption rates are higher on farms with more surrounding non-crop vegetation (Chaplin-Kramer *et al.* 2011). For example, semi-natural vegetation near broccoli farms increased syrphids as well as their predation on aphid pests, resulting in lower aphid population growth and less severe infestations at harvest (Chaplin-Kramer & Kremen 2013; Chaplin-Kramer *et al.* 2013).

Discontinuing manure-based compost applications could similarly disrupt predator–pest interactions. Mulches and composts may benefit predatory arthropods (Riechert & Bishop 1990; Settle *et al.* 1996; Mathews, Bottrell & Brown 2004) if increases in organic matter enhance detritivore activity and thereby provide predators with a reliable food source (Settle *et al.* 1996). However, abundant detritivores could also satiate predators and decrease pest consumption (Mathews, Bottrell & Brown 2004).

We conducted a field experiment at 29 sites over two seasons in 2014 to evaluate how changing food safety practices may influence pests, soils and lettuce yields on organic farms in the Central Coast. We addressed four questions. First, how does surrounding semi-natural vegetation affect arthropods on produce farms? Secondly, does surrounding semi-natural vegetation provide a pest control benefit to growers? Thirdly, how does compost affect pests? Fourthly, would retaining semi-natural vegetation and/or applying compost improve lettuce yields?

Materials and methods

STUDY SITES

We studied impacts of food safety management in California's Central Coast. The region encompasses a mosaic of farms, estuaries, marshes and riparian areas. Oak woodlands, upland scrub and grasslands predominate in often-grazed, hillier areas. We utilized a natural gradient in this surrounding vegetation to study the effects of non-crop vegetation on pest control, crossed with an experimental manipulation of compost. We included sites in the San Juan (*N* = 8), Pajaro (*N* = 4), Northern Salinas (*N* = 12)

and Southern Salinas (*N* = 5) Valleys (Fig. 1). We conducted our experiment over two seasons: spring (*N* = 14 sites) and summer (*N* = 15) of 2014. All farms were certified organic (https://www.ams.usda.gov/rules-regulations/organic).

EXPERIMENTAL DESIGN

We established paired treatment plots (hereafter subplots) – receiving and not receiving compost – at farms along a gradient of surrounding semi-natural vegetation. Semi-natural vegetation occupied 2% to 56% (mean 29%) of the area within 1000 m of plots (Table S1 in Supporting Information). To quantify pest control, we surveyed arthropod communities, measured pest consumption rates and quantified lettuce yields. Specifically, we demarcated a 5 m × 10 m plot at each site, encompassing either four 2 m crop beds or eight 1 m beds (depending on the grower's planting design) near the field edge (Fig. S1). Planted lettuce plots were located within vegetable fields (lettuce: *N* = 19, broccoli: *N* = 7, celery: *N* = 3). Management of plots aligned with the surrounding host farm. Beyond the normal fertilization regime, we applied organic compost on half (5 m × 5 m) of each plot, 1–2 months prior to planting. Specifically, a cow, chicken and green manure blend were applied at 25 tonnes ha^{-1} (Gabilan Ag Services, Salinas, CA, USA). Prior to use, the compost was packed into windrows for 14–18 weeks, during which internal temperatures consistently reached levels necessary for inactivating pathogenic *E. coli* (55 °C–75 °C) (Jiang, Morgan & Doyle 2003). Likely in part a result of recent food safety concerns, compost is not regularly applied at most sites (*N* = 24), and no site applied compost in 2014. Instead, most growers used heat-treated, pelleted and/or liquid fertilizers (TRUE Organic Products, Inc., Spreckles, CA, USA).

We planted sites from March 5–28 (spring) and May 30 to July 5 (summer). Each plot was planted with Romaine lettuce, either
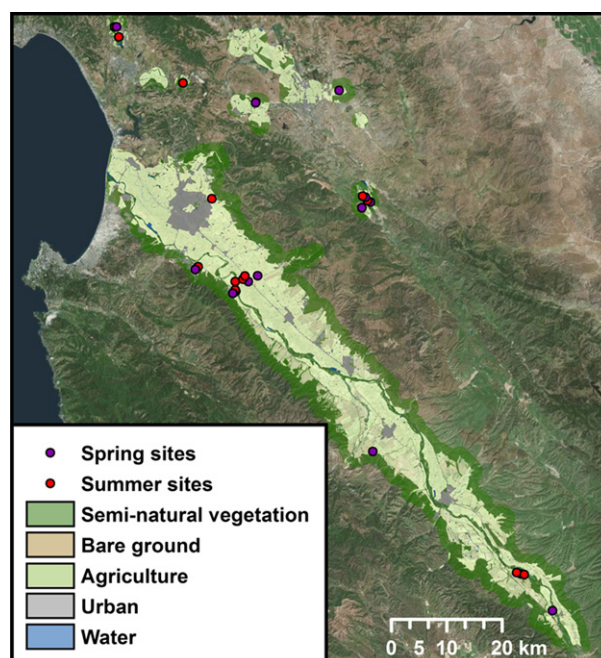

Fig. 1. Study site map. Our experiment encompassed 14 sites in spring (purple dots) and 15 in summer (red dots).

through direct seeding ($N = 20$; Rio Bravo variety; Syngenta Seeds Co, Minnetonka, MN, USA) or transplanting ($N = 9$; Salvius variety; Johnny's Selected Seeds Co., Fairfield, ME, USA) depending on grower preference. Plots that received transplants did not differ in any measured pest control metric from direct-seeded plots (all $P > 0.05$). Seeds and seedlings were planted in 2 lines per 1 m bed or 4–5 lines per 2 m bed and were subsequently thinned following industry standards.

ARTHROPOD SAMPLING

We used a combination of survey methods to sample arthropod assemblages: pan traps (captured volant pests and enemies), pitfall traps (epigeal predators and detritivores) and collecting entire lettuce heads (pests and enemies that directly affect lettuce marketability). Sites were sampled twice: once at the seedling stage (~25 or ~7 days after direct seeding or transplanting, respectively) and once when the lettuce was mature (~60 or ~42 days).

For each sample round, we deployed 3 pitfall and 2 pan traps per subplot. Pitfall traps were constructed from 7.5 cm diameter plastic cups, buried so that tops were flush with the soil, and filled with soapy water (~0.5 tbsp Blue Dawn/L; Procter & Gamble Co., Cincinnati, OH, USA). Traps were sheltered with Styrofoam bowls, suspended 5 cm above the ground. Pan traps were 15 cm plastic bowls, spray-painted fluorescent yellow or blue. Each subplot received 1 yellow and 1 blue pan filled with soapy water. Pitfall and pan traps were collected after 48 h.

We also haphazardly collected three lettuce heads per subplot on the second site visit. Lettuce heads were cut at the base of the plant and transferred immediately into Ziploc bags. Bags were filled with water and drained through an arthropod funnel. Then, lettuce leaves were pulled off and rinsed above the funnel. RM identified 98% of all 38 418 arthropods captured to a family level. Known lettuce pests were identified to species, and RM, DSK and SVJ assigned families to primary feeding guilds (see Appendix S1).

PREDATION RATES

We used a combination of sentinel pest (Meehan *et al.* 2012) and exclosure experiments (Chaplin-Kramer & Kremen 2013) to quantify predation rates. Our focus was on lepidopteran and aphid pests, important categories of lettuce pests (Bugg *et al.* 2008).

At seedling and mature lettuce phases, we placed live corn earworm eggs (*Helicoverpa zea*) and 2nd–3rd instar beet armyworm larvae (*Spodoptera exigua*) in our plots and monitored predation rates. Both pests were obtained from a commercial insectary (Benzon Research Inc., Carlisle, PA, USA). We affixed 5 larvae and 25–70 (mean: 40) eggs to separate waterproof paper cards (~3.5 cm × ~1.5 cm; JL Darling LLC, Tacoma, WA, USA). Larvae were adhered to cards at the posterior end of their bodies with hot glue to allow movement. Eggs were affixed by gluing small sections of their fabric substrates to cards. We used a microscope to count the initial number of eggs per card. During each visit, three each of egg and larvae cards were deployed in each subplot. After 48 h, we collected all cards and counted the number of remaining eggs and larvae that had escaped predation.

We also conducted an exclosure experiment to quantify predation rates on potato aphid (*Macrosiphum euphorbiae*). Potato aphids were collected from lettuce plants at our study sites and reared in a greenhouse on Romaine lettuce. Once lettuce plants were mature, we first selected three lettuce plants at each subplot. Secondly, we removed all insects from each plant by visually inspecting leaves and removing encountered insects. Thirdly, we washed the plant with water and performed a second inspection. Fourthly, we removed ~2 cm of topsoil to exclude insects that fell off the plants and onto the soil during inspection. Fifth, we constructed bamboo frame, fine-meshed netted cages around each plant (0.4 mm × 6 mm mesh, 7250NSW, Bioquip Products, Inc., Rancho Dominguez, CA, USA). Each 40 cm × 40 cm × 40 cm cage was buried ~10 cm into the soil. Two of the three plants per subplot received control cages with no netting on two sides to allow natural enemies to forage and to ensure that all plants would experience similar microclimates (Chaplin-Kramer & Kremen 2013). The third plant was completely enclosed.

Finally, we inoculated the caged plant and one control plant with 50 aphids each. The other control plant did not receive aphids and was used to monitor aphid colonization. Aphids were selected to reflect the colony's age structure, but alate (winged) aphids were excluded to prevent emigration (Chaplin-Kramer & Kremen 2013). After 2 weeks, plants were bagged and washed through a filter to collect all arthropods.

YIELDS AND SOIL ANALYSES

We calculated the average fresh weight (g) of harvested plants from a 1 m × 1 m quadrat within each subplot (5–15 plants, mean = 7.5). In spring, we also collected soil samples to determine soil properties and pathogenic *E. coli* prevalence. We used a 1.25 cm diameter soil probe to collect 1.4 L of soil to a depth of 10 cm per subplot. A commercial laboratory quantified concentrations of nitrate (mg kg^{-1}), phosphorous (mg kg^{-1}) and potassium (mg kg^{-1}), as well as pH, % organic matter and % sand (Soiltest Farm Consultants Inc., Moses Lake, WA, USA).

Samples were also tested for indicator and pathogenic (STEC) *E. coli*. From each sample, four 25 g subsamples were inoculated into 225 mL of buffered peptone water (BPW), shaken for 15 min and allowed to settle for 5 min. One mL and 0.1 mL aliquots of BPW from each subsample were spread-plated onto separate 150 mm violet-red bile agar with VRB-MUG plates. The VRB-MUG plates and remaining BPW mixture were incubated overnight at 37 °C. The red, fluorescent colonies on VRB-MUG were presumptively identified as *E. coli*, and three colonies per soil sample were then subjected to TSI, oxidase and indole tests. All colonies yielding typical *E. coli* reactions to these tests were counted and banked. After counting, swabs were used to sweep the VRB-MUG plates and were stored in buffered glycerol at −20 °C. All saved *E. coli* isolates were screened for shiga-toxins – the disease-causing agent present in some *E. coli* strains – using PCR. The PCR used multiplexed primers directed against markers stx1, stx2, eae and fliCH7 (Olsvik *et al.* 1991; Gannon *et al.* 1997).

HABITAT CLASSIFICATION

We contracted an Anderson Level II terrestrial land-use/land-cover map to calculate the extent of semi-natural vegetation in the Salinas, San Juan and Pajaro Valleys (Total area: 1906 km^2; Aerial Information Services, Redlands, CA, USA). Land cover was hand-classified into 16 categories from 1 m^2 resolution National Agricultural Inventory Program imagery, taken in the

summer of 2012. Due to the large spatial extent of our study area, only cropland and riparian features larger than 0·2 ha were hand-classified (minimum mapping unit); the minimum mapping unit for other land-cover classes was 0·4 ha. We combined non-crop vegetation into one layer encompassing all semi-natural vegetation including: 'Riparian Forest & Woodland', 'Southwestern North American Riparian Scrub', 'California Forest & Woodland', 'Upland Scrub', 'Mediterranean Grasslands & Forbs', and 'Meadow and Marsh'.

We developed an index to quantify the extent of surrounding semi-natural vegetation, recognizing that regions located closer to study sites were likely to have greater influence than those further away. First, we quantified the amount (m^2) of semi-natural vegetation in 20 concentric rings, with inner radii at distances distributed uniformly on an exponential scale between 50 m and 1500 m. Next, we used a Gaussian function to assign weights to each ring, with farther rings given lower weightings than closer rings. Using a different decay function (*e.g.* exponential decay) did not influence our results. Specifically, each ring was assigned weight *W*, given by:

$$W = \exp(-I^2/(2 * d^2)) \qquad \text{eqn 1}$$

where *I* is the inner edge distance of the ring and d is the decay rate that specifies how quickly weightings decrease with increasing distance. In order to determine the most predictive scale for subsequent analyses, we assessed several decay rates. We calculated the weighted sum of the area of semi-natural vegetation by summing across the 20 concentric rings the amount of semi-natural habitat within each ring, multiplied by that ring's weight. We standardized this index across study sites by subtracting the mean value and dividing by the standard deviation. Because the semi-natural vegetation index was highly negatively correlated with a similar index of cropland extent (Fig. S2), we focus only on the effects of semi-natural vegetation on pest control.

We found the most predictive decay rate to be β = 250 (Fig. S3; Appendix S2). The amount of surrounding semi-natural vegetation less often predicted pest control variables when it was calculated with larger decay rates (β = 1000 and 5000) that increased the importance of areas further from the study site (Appendix S2). We subsequently utilized β = 250 in our analyses.

STATISTICAL ANALYSES OF ARTHROPOD COMMUNITIES

We assessed the effects of semi-natural vegetation and compost on arthropod abundance, family richness and biocontrol metrics with linear mixed-effects models (Zuur *et al.* 2009). Mixed-effects models were used so that site and region could always be included as random effects. We first aggregated arthropod censuses to a subplot level, creating lists of all the arthropods captured in pitfall traps, pan traps or lettuce heads during each visit to each subplot. If traps were lost or broken (<2% of traps deployed), an alternate trap in the same subplot and visit was counted twice (1·3% of insects sampled).

We next evaluated whether to use generalized or linear mixed-effects models. Simulations of null hypotheses (no effect of explanatory variables) suggested that evaluating significance using generalized linear mixed-effects models was anticonservative, with

a type-I error rate of ~0·5 for a nominal *P*-value of 0·05 (Ives 2015). In contrast, linear mixed-effects models yielded low type-I error rates (~0·05). Simulations were performed by randomly permuting values of semi-natural habitat and then comparing models with and without the predictor via likelihood ratio tests. The fraction of (1000) randomizations with *P* values <0·05 was taken as the type-I error rate.

Separate linear mixed-effects models were created for arthropods surveyed in lettuce heads, pitfall traps or pan traps and for different response variables. Response variables of total arthropod, natural enemy, herbivore, aphid, non-aphid pest, syrphid fly and detritivore captures were log-transformed to ensure normality and heteroscedasticity. Because residuals were normally distributed, it was not necessary to transform family-level richness of all arthropods, natural enemies and herbivores, or Pielou's evenness and Simpson diversity, except for pitfall traps (square-root transformation). To assess the relative abundance of enemies vs. herbivores, we divided total enemy captures by the total captures of enemies and herbivores and square-root transformed the result. The same approach was used for the relative abundance of enemies vs. aphids and enemies vs. non-aphid pests.

The effects of compost and semi-natural vegetation on each response variable were assessed in two steps. To investigate main effects, we created a first set of models with compost treatment, semi-natural vegetation (Gaussian-weighted index), season (spring or summer) and lettuce life stage (seedling or mature plant) as explanatory variables. Statistical significance of each predictor was evaluated via likelihood ratio tests that compared the full model to a reduced model without the variable (Zuur *et al.* 2009). Not all sites were included in each analysis: early harvests and mammalian herbivory caused some sites to be excluded (Table S2).

Next, we developed a second set of models to investigate whether effects of semi-natural habitat on response variables varied by season (summer vs. spring) and life stage (seedling vs. mature). To do so, we created four binary variables indicating whether the census took place in: (i) seedling stage/spring, (ii) mature stage/spring, (iii) seedling stage/summer and (iv) mature stage/summer. Each variable was allowed to interact with semi-natural habitat. With this parameterization, models could be compared via likelihood ratio tests with and without each interaction to determine whether semi-natural habitat significantly influenced response variables in each season–life stage combination. All other fixed effects (compost treatment, season main effect and lettuce life stage effect) were included in these models. For analyses of detritivore abundance only, we additionally included interactions between compost treatment and season and life stage.

ANALYSES OF NATURAL ENEMY ACTIVITY

To assess landscape effects on enemy activity, we modelled associations between surrounding semi-natural habitat and predation rates on *H. zea* eggs, *S. exigua* larvae and *M. euphorbiae* colonies. First, we aggregated data from egg and larvae cards to subplots, calculating the total number of eggs (or larvae) deployed and the fraction consumed. After calculating the proportion of eggs and larvae consumed at each plot, we modelled effects of surrounding semi-natural habitat as above. Egg and larvae proportion data were square-root transformed to ensure normality of residuals.

To quantify aphid predation from the exclosure experiment, we developed a biocontrol index (BCI) defined as:

$$BCI = \log([E + C]/O) \qquad \text{eqn 2}$$

where E is the final count of non-alate aphids in the exclusion treatment (closed to predation, received 50 initial aphids), C is the count in the colonization treatment (open to predation, no aphids), and O is the count in the control treatment (open to predation, 50 aphids). The colonization treatment was added to the exclusion treatment to account for aphids that colonized the open treatment during the experiment. Ignoring the colonization treatment and re-calculating BCI as the ratio of aphids in predator exclosures vs. controls did not change results. Higher values of BCI indicate more natural enemy suppression of aphids. Effects of semi-natural habitat on BCI were assessed using the same model structure as arthropod community analyses.

YIELD ANALYSES

We assessed changes in lettuce yields relative to compost addition and landscape context by calculating the average lettuce weight per subplot. To determine whether herbivores affect lettuce yields, we calculated an index of average herbivore abundance per subplot by: (i) quantifying total herbivores captures in lettuce heads, pan traps and pitfall traps at each subplot; (ii) scaling total captures across subplots for each capture method by subtracting the mean and dividing by the standard deviation; and (iii) calculating the average of the lettuce head, pan trap and pitfall trap scaled values at each subplot. We then implemented linear mixed-effects models of average weight with season, compost, an interaction between semi-natural vegetation and season, an interaction between herbivore abundance and season, and the number of days between planting and collection as explanatory

variables (3 weeks were added to transplants to account for greenhouse growth). Lettuce weight was log-transformed to satisfy model assumptions.

SOIL ANALYSES

We quantified effects of compost on soil properties and effects of soil properties on lettuce weights. We modelled effects of compost on nitrate, phosphorous and potassium concentrations and on pH, per cent organic matter and per cent sand. Next, we created models to predict changes in lettuce weights, including as fixed effects elapsed days past planting and soil properties (in separate models). Lettuce weights were log-transformed, and significance was assessed with likelihood ratio tests. All analyses were conducted in R version 3.2.2 (R Development Core Team 2010), using the 'lme4' package (Bates *et al.* 2015).

Results

We captured a total of 38 418 arthropods across 21 orders and 128 families (Fig. S4; Appendix S1). Dominant guilds included herbivores ($N = 24\ 670$), detritivores ($N = 8183$) and natural enemies ($N = 3015$). 23% of herbivores were pests, mostly aphids (~90%). Plots surrounded by lettuce yielded more insect captures ($\chi^2 = 3\cdot72$, $P = 0\cdot05$), aphids ($\chi^2 = 6\cdot36$, $P = 0\cdot01$) and non-aphid pests ($\chi^2 = 4\cdot80$, $P = 0\cdot03$) than plots surrounded by other crops. Correspondingly, predation of *M. euphorbiae* and *S. exigua* larvae was lower in plots surrounded by lettuce ($\chi^2 = 6\cdot03$, $3\cdot84$; $P = 0\cdot01$, $0\cdot05$,
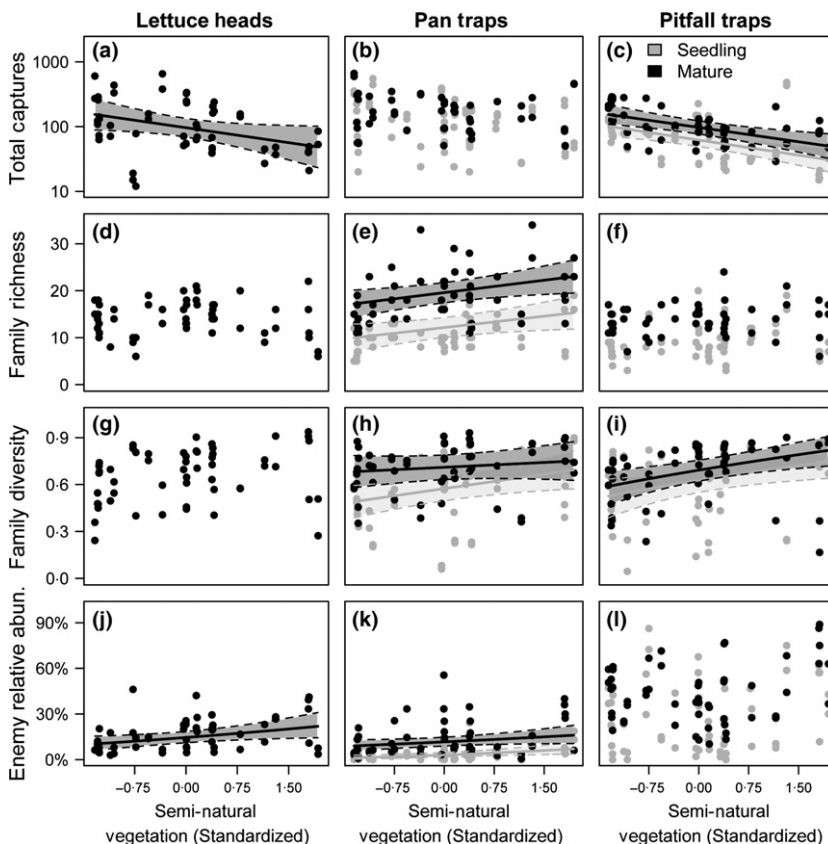

Fig. 2. Effects of surrounding semi-natural vegetation on arthropod assemblages. Captures in lettuce heads (a) and pitfall traps (c) declined at sites with more surrounding semi-natural vegetation. Captures marginally declined in pan traps (b). Family richness in pans (e) but not lettuce (d) or pitfalls (f) increased at sites with more semi-natural vegetation. Family-level Simpson diversity also increased in pans (h) and pitfalls (i) but not lettuce heads (g). Sites with semi-natural vegetation had more enemies relative to herbivores in lettuce heads (j) and pans (k) but not pitfalls (l). In j, k and l, enemy relative abundance is calculated as enemy captures divided by enemy plus herbivore captures. Model predictions are presented for significant effects – solid lines are slopes and dotted lines are 95% confidence intervals. Points are raw data at subplots. Light grey shading corresponds to samples obtained at the lettuce seedling stage; darker shading indicates mature lettuce. Panels a-c are on a log scale.

respectively). Semi-natural vegetation did not differ between plots surrounded by lettuce vs. other crops ($F = 1.24$, $P = 0.28$).

Arthropod assemblages changed predictably across the vegetation gradient. First, fewer arthropods were captured on lettuce heads and in pitfall traps at sites with more surrounding semi-natural vegetation (Fig. 2; Table 1). Pan trap captures declined marginally ($P = 0.09$). Secondly, while total captures declined, the number of arthropod families captured either remained constant (lettuce heads and pitfall traps) or increased (pan traps). As a result, sites with more surrounding semi-natural vegetation hosted more diverse assemblages (Tables 1 and S2).

Higher arthropod diversity in landscapes with more semi-natural vegetation could be characterized by an increase in natural enemies relative to herbivores. Enemy richness in pan traps was higher at sites with more

semi-natural vegetation (Table S3). Moreover, herbivore captures were lower in landscapes with more semi-natural vegetation under each survey method, while enemies were unaffected (Table S3). Therefore, the relative abundance of enemies vs. herbivores in lettuce heads and pan traps was significantly higher at sites with more surrounding semi-natural vegetation, especially when lettuce plants were at the seedling stage (Fig. 2; Table 1). The one exception was pitfall traps, where both enemies and herbivores were less abundant at more vegetated sites.

Some pests (*i.e.* aphids) were also less abundant at sites with more nearby semi-natural vegetation (Fig. 3; Table 2). Correspondingly, the relative abundance of natural enemies vs. aphids was higher in areas with more surrounding semi-natural vegetation. Non-aphid pests, however, exhibited no clear response to surrounding landscape composition (Fig. 3; Table 2).

Table 1. Effect of semi-natural vegetation on arthropods. Significance was assessed with likelihood ratio tests (LRT), comparing models with and without predictors (see Methods). Because lettuce heads were not sampled at the seedling stage, no life stage interactions are included. Transformations to ensure normality and heteroscedasticity are noted in parentheses. Significant effects are bolded

Response	Predictor	Lettuce heads			Pan traps			Pitfall traps		
		β	χ^2	P	β	χ^2	P	β	χ^2	P
Total arthropod counts (log)	Intercept	4·78			4·65			4·14		
	Habitat	**−0·35**	**4·66**	**0·03**	−0·16	2·97	0·09	**−0·32**	**14·36**	**<0·01**
	Compost	−0·05	0·24	0·62	0·05	0·19	0·66	−0·06	0·38	0·54
	Summer	−0·32	1·06	0·30	0·11	0·39	0·53	0·08	0·27	0·61
	Mature Plant				**0·31**	**6·38**	**0·01**	**0·44**	**17·97**	**<0·01**
	Habitat: spring seedling				−0·27	2·47	0·12	**−0·42**	**8·68**	**<0·01**
	Habitat: spring mature	−0·40	2·72	0·10	0·13	0·63	0·43	**−0·40**	**7·79**	**0·01**
	Habitat: summer seedling				−0·23	2·63	0·10	**−0·26**	**5·07**	**0·02**
	Habitat: summer mature	−0·31	2·25	0·13	−0·23	2·51	0·11	**−0·25**	**4·66**	**0·03**
Arthropod family richness (log)	Intercept	13·92			11·60			8·44		
	Habitat	−0·09	0·02	0·90	**1·71**	**7·73**	**0·01**	0·31	0·58	0·45
	Compost	0·56	0·82	0·37	0·38	0·30	0·58	−0·43	0·65	0·42
	Summer	−0·11	0·01	0·93	0·68	0·36	0·55	**2·06**	**5·81**	**0·02**
	Mature Plant				**7·43**	**72·02**	**<0·01**	**4·60**	**53·39**	**<0·01**
	Habitat: spring seedling				1·90	3·19	0·07	1·00	1·76	0·19
	Habitat: spring mature	−1·09	1·02	0·31	1·21	1·32	0·25	0·16	0·04	0·83
	Habitat: summer seedling				1·46	2·82	0·09	−0·26	0·17	0·68
	Habitat: summer mature	0·59	0·46	0·50	**2·21**	**6·03**	**0·01**	0·03	0·35	0·55
Simpson diversity (none but pitfalls which were squared)	Intercept	0·63			0·52			0·37		
	Habitat	0·04	2·17	0·14	**0·04**	**5·11**	**0·02**	**0·09**	**8·36**	**<0·01**
	Compost	0·00	0·00	0·94	0·01	0·26	0·61	0·00	0·00	0·97
	Summer	0·04	0·63	0·43	**0·08**	**5·36**	**0·02**	0·05	1·01	0·32
	Mature Plant				**0·14**	**19·38**	**<0·01**	**0·09**	**6·54**	**0·01**
	Habitat: spring seedling				**0·10**	**6·62**	**0·01**	**0·12**	**6·05**	**0·01**
	Habitat: spring mature	−0·01	0·02	0·90	−0·02	0·25	0·61	**0·10**	**4·39**	**0·04**
	Habitat: summer seedling				0·04	1·88	0·17	0·05	1·82	0·18
	Habitat: summer mature	0·08	3·23	0·07	0·05	2·87	0·09	**0·09**	**4·61**	**0·03**
Relative abundance of enemies vs. Herbivores (square root)	Intercept	0·33			0·11			0·35		
	Habitat	**0·05**	**6·09**	**0·01**	**0·04**	**11·20**	**<0·01**	0·03	2·28	0·13
	Compost	0·02	0·50	0·48	0·02	0·95	0·33	0·00	0·02	0·90
	Summer	**0·07**	**4·15**	**0·04**	**0·10**	**16·23**	**<0·01**	**0·25**	**29·32**	**<0·01**
	Mature Plant				**0·17**	**50·49**	**<0·01**	**0·17**	**33·28**	**<0·01**
	Habitat: spring seedling				**0·06**	**5·85**	**0·02**	**0·07**	**3·82**	**0·05**
	Habitat: spring mature	0·03	1·12	0·29	0·00	0·00	1·00	0·02	0·30	0·58
	Habitat: summer seedling				**0·04**	**4·80**	**0·03**	0·01	0·11	0·74
	Habitat: summer mature	**0·06**	**5·83**	**0·02**	**0·06**	**7·56**	**0·01**	0·02	0·66	0·42

Exclusion experiments suggested that enemies consumed a significant fraction of pests. Excluding enemies for 2 weeks caused a 4·7-fold increase in aphid captures, from ~40 to ~170 aphids/plant when enemies were present vs. excluded (Fig. S5; χ^2 = 54, P < 0·001). This estimate is likely conservative, as cages did not completely exclude predators. Still, at the conclusion of the experiment, significantly more enemies were found in the open vs. caged treatment (~8 vs. ~4 enemies/plant) (χ^2 = 33, P < 0·001).

Predation rates also varied along the landscape gradient (Fig. 4; Table 3). For example, we found that the biocontrol index (see methods) of aphid consumption was significantly higher at sites with more surrounding semi-natural vegetation. *Helicoverpa zea* egg consumption was also higher in landscapes with more semi-natural vegetation, but only at the lettuce seedling stage. In contrast, *S. exigua* larval predation never changed across the land-use

gradient. These non-significant results may have been influenced by the difficulty of separating consumed larvae from those dehydrated from sun exposure. Additionally, larvae may have occasionally escaped.

Unlike semi-natural vegetation, we found no consistent effects of compost on any measure of arthropod abundance or diversity (Tables 1–3 and S3), including detritivore captures (Table S4). Compost did, however, increase lettuce yields without compromising food safety (Fig. 5; Table S5). No samples tested positive for shiga-toxin producing *E. coli* (STEC), and only two samples tested positive for generic *E. coli* (one of which was in a control subplot; thus, compost was not an *E. coli* source). Compost increased soil phosphorous, potassium and organic matter, all of which were positively correlated with lettuce weights (Fig. 5; Table S6). Compost, however, did not affect nitrates, which were also positively correlated with
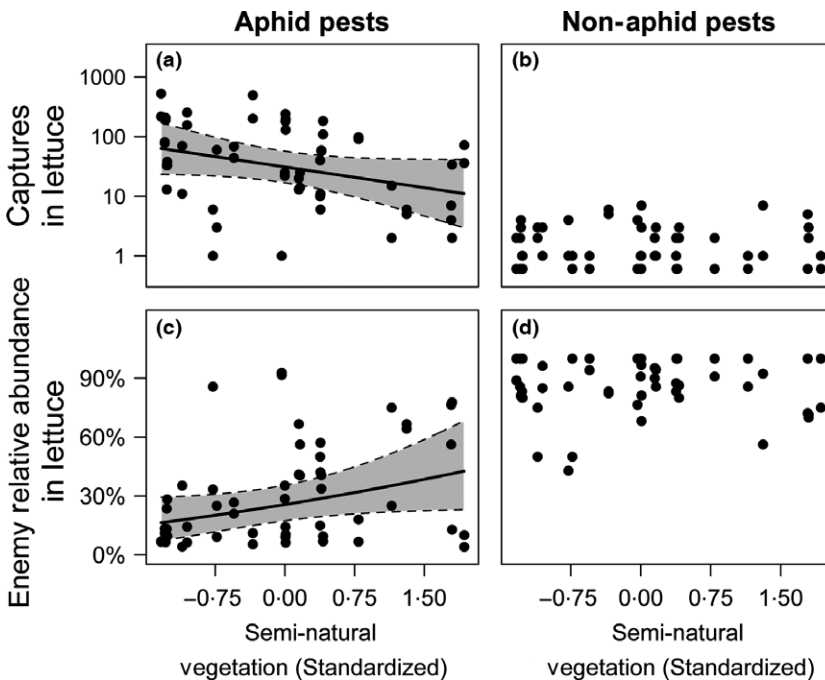

Fig. 3. Sites with more surrounding semi-natural vegetation were less infested with aphids (a) but not non-aphid pests (b). Similarly, enemy abundance relative to aphids (c), but not non-aphid pests (d), increased with semi-natural vegetation. In c and d, enemy relative abundance is calculated as enemy captures divided by enemy plus aphid (or non-aphid pest) captures. Points are subplots. For variables significantly affected by semi-natural vegetation, solid lines are model predictions and dotted lines are 95% confidence intervals. Panels a and b are on a log scale.

Table 2. Effect of semi-natural vegetation on pests on lettuce. Data transformations are indicated in parentheses. Significant effects are bolded

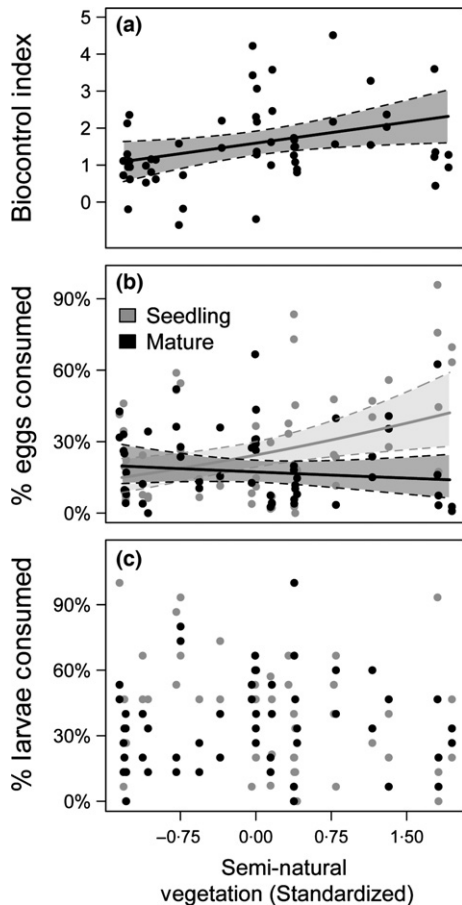| Predictor	Aphid count (log)			Non-aphid pest count (log)			Relative abundance of enemies vs. Aphids (square root)			Relative abundance of enemies vs. Non-aphid pests (square root)		
	β	χ^2	P	β	χ^2	P	β	χ^2	P	β	χ^2	P
Intercept	3·63			−0·46	1·34	0·25	0·49			0·91		
Habitat (overall)	**−0·52**	**3·90**	**0·05**	−0·56	2·73	0·10	**0·08**	**4·54**	**0·03**	0·01	0·60	0·44
Compost	−0·01	0·00	0·97	−0·46	1·34	0·25	0·01	0·07	0·79	0·01	0·16	0·69
Summer	−0·16	0·10	0·76	−0·56	2·73	0·10	0·03	0·18	0·67	0·00	0·04	0·84
Habitat: spring	−0·46	1·34	0·25	−0·46	1·34	0·25	0·05	0·79	0·37	**0·04**	**3·81**	**0·05**
Habitat: summer	−0·56	2·73	0·10	−0·56	2·73	0·10	**0·10**	**4·28**	**0·04**	−0·01	0·22	0·64

Fig. 4. Effects of semi-natural vegetation on enemy activity. Aphid growth was more suppressed (Biocontrol Index- BCI, see Methods) at sites with more surrounding semi-natural vegetation (a). Egg predation also increased with semi-natural vegetation, but only at the lettuce seedling stage (b). No landscape effects on larvae consumption were observed (c). Points are subplots. For significant models, solid lines are predicted slopes and dotted lines are 95% confidence intervals. Lighter shading indicates that samples were taken at the lettuce seedling stage; darker shading corresponds to mature lettuce.

lettuce weights. Similarly, compost did not alter soil pH or the fraction of sand in the soil. While soil pH yielded no effects, lettuce weights were highest in soils with intermediate levels of sand (~40% sand; Fig. 5).

Herbivores and surrounding vegetation were negatively correlated with lettuce weights (Table S5). Weights declined with herbivore abundance in summer but not spring. Instead, sites with more surrounding semi-natural habitat had lower yields in spring.

Discussion

If fresh produce continues to be a source of disease outbreaks, then pressure on growers to enforce sterile environments and remove semi-natural vegetation may escalate (Karp *et al.* 2015a). Recent work from the Central Coast of California, however, has demonstrated that foodborne pathogens do not increase on farms with more surrounding semi-natural vegetation (Karp *et al.* 2015b). Similarly, food safety risk from composts can largely be eliminated by subjecting pathogens to the high temperatures experienced inside windrows (Jiang, Morgan & Doyle 2003). Correspondingly, in this experiment, we did not observe elevated pathogen prevalence on composted plots or on plots surrounded by semi-natural vegetation. Our results do suggest, however, that removal of vegetation and cessation of compost could negatively affect growers through impacts on pests, soils and yields.
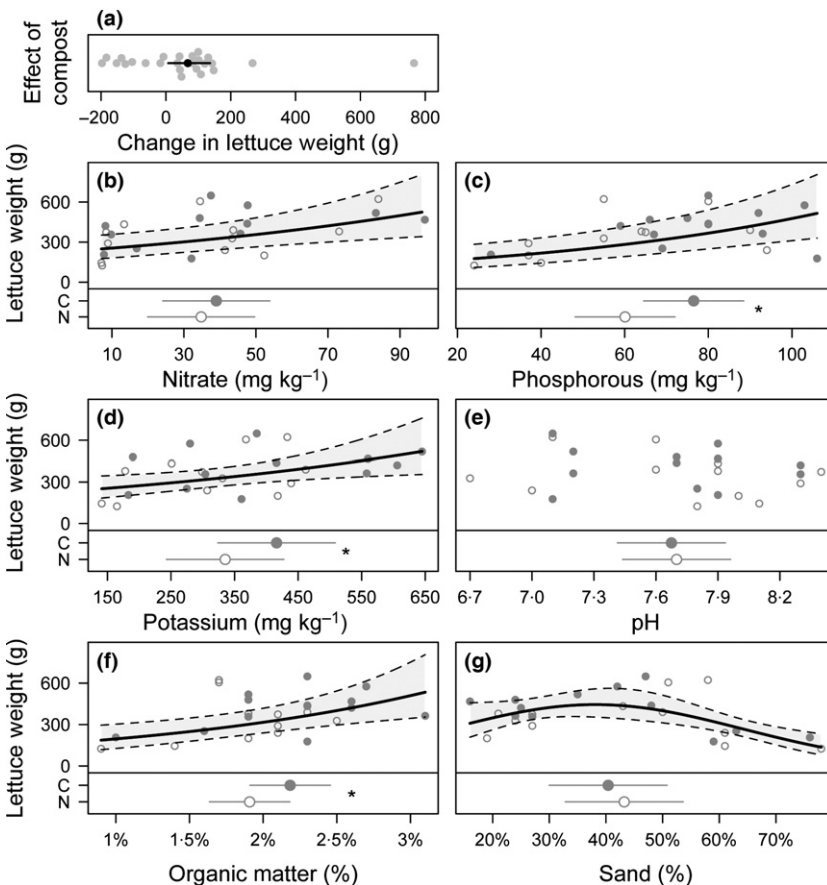
EFFECTS OF SEMI-NATURAL VEGETATION

We found that produce farms with more surrounding semi-natural vegetation had more diverse arthropod assemblages. In contrast, farms in more simplified landscapes hosted high abundances of fewer arthropod families, largely dominated by herbivores. Lettuce heads were also more infested with aphid pests on farms with less surrounding semi-natural vegetation. We likely observed these trends because we worked on organic farms – inorganic insecticides would likely lower arthropod abundances and mask trends.

Unlike herbivores, effects of semi-natural vegetation on enemies were unclear which was surprising given that enemies generally increase on farms with more surrounding semi-natural vegetation (Chaplin-Kramer *et al.* 2011). Indeed, other studies from the Central Coast have documented benefits of semi-natural vegetation for many of the enemies surveyed here (Letourneau, Allen & Stireman 2012; Chaplin-Kramer *et al.* 2013). One possibility is that enemies responded to fine-scale habitat elements (*e.g.* hedgerows) that were too small to be classified in our land-use map. Another explanation is that enemies colonize farms from semi-natural habitats early on (Costagmaga, Venables & Schellhorn 2015), but, over the season, enemies eventually equilibrate in population size across sites. Indeed, we observed that enemy captures and the relative abundance of enemies vs. herbivores were more positively associated with semi-natural vegetation at the seedling than at the mature lettuce stage. Herbivore suppression at the seedling stage may be critical for some crops; tomatoes, for example, are vulnerable to insect pests at the seedling stage but can later withstand pests (Drinkwater *et al.* 1995).

Early enemy colonization from surrounding habitats may be responsible for suppressing later pest population growth and lowering aphid abundances in landscapes with more semi-natural vegetation (Costagmaga, Venables & Schellhorn 2015). Alternatively, because cropland and semi-natural habitat areas are negatively correlated, intensive farm management practices in more simplified landscapes may have reduced enemy activity and favoured pests (*e.g.* excessive pesticide applications and removal of floral resources). Regardless, our finding that 2 weeks of enemy exclusion caused a nearly fivefold increase in aphid population size supports the idea that

Table 3. Effect of semi-natural vegetation on pest consumption. Data transformations are indicated in parentheses. Significant effects are bolded

Predictor	Aphid growth (log)			% Eggs consumed (none)			% Larvae consumed (none)		
	β	χ²	P	β	χ²	P	β	χ²	P
Intercept	2·03			0·21			0·38		
Habitat (overall)	**0·38**	**4·37**	**0·04**	0·04	3·02	0·08	0·00	0·00	0·94
Predators in Cage	**−0·54**	**4·46**	**0·03**						
Compost	−0·29	0·68	0·41	0·01	0·06	0·81	−0·02	0·43	0·51
Summer	0·00	0·00	0·98	**0·15**	**10·50**	**< 0·01**	0·03	0·23	0·63
Mature Plant				**−0·09**	**8·06**	**< 0·01**	−0·02	0·32	0·57
Habitat: spring seedling				**0·14**	**11·69**	**< 0·01**	−0·02	0·12	0·73
Habitat: spring mature	0·25	0·89	0·35	−0·02	0·23	0·63	0·05	0·59	0·44
Habitat: summer seedling				0·06	2·80	0·09	−0·03	0·31	0·58
Habitat: summer mature	**0·47**	**3·98**	**0·05**	−0·01	0·16	0·69	0·00	0·00	0·95

Fig. 5. Effects of compost and soil properties on yields. Adding compost caused an increase in lettuce weight (a). Black point in panel a is the mean effect of compost addition, lines are 95% confidence intervals, and grey points are subplots. Lettuce weight increased in subplots with more soil nitrate (b), phosphorous (c), potassium (d) and organic matter (f). Lettuce weight peaked at intermediate levels of sand (g) and was unaffected by pH (e). In regression plots of panels b-g, points are subplots, solid lines are model predictions, and dotted lines are 95% confidence intervals. Compost increased phosphorous (c), potassium (d) and organic matter (f), but not nitrate (b), pH (e) or sand (g). For compost effects in panels b-h, points are mean values per treatment and lines are confidence intervals. Filled circles correspond to compost plots; open circles are controls.

enemy activity could have driven spatial trends in pests. Indeed, at sites with more surrounding semi-natural habitat, we detected stronger effects of enemy exclusion on aphids. We also observed more egg predation at the seedling stage at sites with more surrounding semi-natural vegetation.

We found no evidence, however, that enhanced pest control increased lettuce weights. Yield effects are difficult to document in landscape analyses of pest control (Bianchi, Booij & Tscharntke 2006; Chaplin-Kramer *et al.*

2011). Because agriculture may expand more rapidly in productive regions, areas where natural habitat remains may be more marginal for agricultural production. Indeed, in our study, while we observed lower lettuce weights at more vegetated sites in the spring, this may have been due to lower soil quality on farms near remaining habitat. The two sites with lowest lettuce weights were surrounded by semi-natural vegetation, but also had the lowest concentrations of soil nitrate, organic matter and phosphorous. Excluding either site caused semi-natural

habitat to no longer significantly affect lettuce weights ($P > 0.05$).

While yields are a key incentive for pest management, other biocontrol metrics may be equally important. Even without yield impacts, increased predation on aphids may improve profits, as small numbers of aphids can render lettuce plants cosmetically unmarketable (Smith and Chaney 2007, Nelson *et al.* 2012). Because aphid infestations declined in landscapes with more semi-natural vegetation, surrounding habitat could thus enhance lettuce marketability. Moreover, on farms with more surrounding vegetation and lower aphid infestations, growers could conceivably apply less insecticide, reducing costs and impacts on public health (Marks *et al.* 2010; Bouchard *et al.* 2011) and the environment (Anderson *et al.* 2003).

EFFECTS OF COMPOST

Paralleling other work from the region (Jackson *et al.* 2004), applying compost did not initiate a beneficial trophic cascade that increased pest control. On the one hand, previous studies that have shown compost-driven increases in detritivore and/or predator abundances have generally applied significantly more mulch (Riechert & Bishop 1990), compost (Bell *et al.* 2008) or both (Mathews, Bottrell & Brown 2004) than is typical for fresh produce growers in our region. On the other hand, some studies have found effects of compost on pest control at similar application rates to those used here (Settle *et al.* 1996). Consistent and multiyear compost applications may be necessary to sufficiently alter soil conditions before an effect on arthropods can be observed. Moreover, our plot size (5 m × 5 m) may not have been large enough to attract detritivores and initiate a trophic cascade.

Despite little evidence that compost affects pest control, we did find that lettuce weights were higher on plots treated with compost and that *E. coli* prevalence did not change. The positive effect of compost on lettuce yields may have resulted from increases in organic matter and soil nutrients (*e.g.* phosphorous and potassium) in compost-treated plots. Indeed, lettuce weights were significantly higher in plots with more phosphorous, potassium and organic matter in their soils. Especially because no substitute fertilizer was used on non-composted plots, it is unclear whether increases in lettuce weights would also be observed on conventional farms that apply synthetic fertilizers.

CONCLUSION

Food safety concerns have spurred pervasive reforms to produce management practices throughout the United States (LGMA 2013, FDA 2014). Our results demonstrate how two food safety practices – replacement of manure-based compost and removal of non-crop vegetation – may affect growers through impacting pests, soils and yields. Specifically, we observed a negative association between crop pests and surrounding semi-natural habitat, and higher lettuce yields and healthier soils on plots with compost. All plots had low levels of *E. coli*, regardless of landscape context and compost treatment. Indeed, emerging evidence suggests that non-crop vegetation can be maintained (Karp *et al.* 2015b) and compost applied (Jiang, Morgan & Doyle 2003) without compromising produce safety. Combined, our work suggests that growers may benefit from increased ecosystem services, without incurring food safety costs, by applying appropriately treated compost and maintaining semi-natural habitat. Co-managing fresh produce for food safety and conservation goals is possible and likely beneficial for nature and for growers.

Acknowledgements

Data accessibility

Arthropod surveys, exclosure experiments, sentinel pest experiments, lettuce weights, soil analysis and surrounding semi-natural habitat indices are archived in Dryad Digital Repository http://dx.doi.org/10.5061/dryad.37cc5 (Karp *et al.* 2016).

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Supporting Information

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

Figure S1. Study plot schematic.

Figure S2. Correlations between cropland and semi-natural vegetation.

Figure S3. Gaussian decay function used to develop semi-natural vegetation index.

Figure S4. Total arthropods by family and function guild.

Figure S5. Natural enemies consume potato aphids.

Table S1. Description of study sites.

Table S2. Sampling strategy.

Table S3. Effects of semi-natural habitat and compost on enemy and herbivore abundance and diversity.

Table S4. Effect of compost on detritivore captures.

Table S5. Effect of compost, vegetation, and herbivores on lettuce yields.

Table S6. Effects of soil properties on lettuce weight and of compost on soil properties.

Appendix S1. Arthropod captures by feeding guide.

Appendix S2. Effects of semi-natural habitat, quantified with varying decay rates, on pest control variables.