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Comanaging fresh produce for nature conservation and food safety

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In 2006, a deadly *Escherichia coli* O157:H7 outbreak in bagged spinach was traced to California's Central Coast region, where >70% of the salad vegetables sold in the United States are produced. Although no definitive cause for the outbreak could be determined, wildlife was implicated as a disease vector. Growers were subsequently pressured to minimize the intrusion of wildlife onto their farm fields by removing surrounding noncrop vegetation. How vegetation removal actually affects foodborne pathogens remains unknown, however. We combined a fine-scale land use map with three datasets comprising ∼250,000 enterohemorrhagic *E. coli* (EHEC), generic *E. coli*, and *Salmonella* tests in produce, irrigation water, and rodents to quantify whether seminatural vegetation surrounding farmland is associated with foodborne pathogen prevalence in California's Central Coast region. We found that EHEC in fresh produce increased by more than an order of magnitude from 2007 to 2013, despite extensive vegetation clearing at farm field margins. Furthermore, although EHEC prevalence in produce was highest on farms near areas suitable for livestock grazing, we found no evidence of increased EHEC, generic *E. coli*, or *Salmonella* near nongrazed, seminatural areas. Rather, pathogen prevalence increased the most on farms where noncrop vegetation was removed, calling into question reforms that promote vegetation removal to improve food safety. These results suggest a path forward for comanaging fresh produce farms for food safety and environmental quality, as federal food safety reforms spread across ∼4.5 M acres of US farmland.

agriculture | biodiversity | disease ecology | *E. coli* | foodborne pathogens

Disease outbreaks originating from fresh produce have rapidly emerged as a major public health concern. Fresh produce is now the leading cause of foodborne illnesses (46%) and hospitalizations (38%) in the United States (1), up from <1% of outbreaks in the 1970s (2). As a result, system-wide reforms have swept through produce supply chains (3, 4). Nowhere have reforms been more evident than in California's Central Coast region, where ∼70% of the leafy green vegetables produced in the United States are grown (5).

In 2006, a deadly multistate *Escherichia coli* O157:H7 outbreak in bagged spinach that sickened 205 people and killed 3 people was traced back to a farm in California's Central Coast region (6). Although the originating strain was isolated from multiple sources (6), no definitive cause of the outbreak could be determined (7); however, one identified source was feral pig feces, which contributed to strong industry and regulatory pressure on Central Coast growers to mitigate wildlife intrusion onto their farm fields. Numerous growers erected wildlife fences, deployed rodent traps, and cleared noncrop vegetation (8, 9). For example, food safety interventions likely resulted in degradation or destruction of 13% of the remaining riparian vegetation along the Salinas River and its tributaries between 2005 and 2009 (5).

Two groups of pathogens, enterohemorrhagic *E. coli* (EHEC) and *Salmonella enterica*, are largely responsible for the perceived conflict between food safety and nature conservation, as well as for the majority of bacterial outbreaks in fresh produce (2). Both pathogens are carried by domestic animals (e.g., cattle) and wildlife; however, whereas *S. enterica* is readily isolated from many wildlife hosts (10, 11), EHEC is generally more prevalent in cattle than in wildlife. In one study, for example, 37.9% of cattle vs. only 7.4% of wildlife samples obtained from California's Central Coast tested positive for EHEC (12). Prevalence can vary by location, however; for example, ∼12% of cattle shed the EHEC strain *E. coli* O157:H7 in the midwestern United States (13), whereas only 2.6–7.1% did so in California's Central Coast (12, 14). Similarly, whereas *E. coli* O157:H7 was detected in <2% of bird, deer/elk, and feral pig samples across 50 studies worldwide (15), detection rates were higher in the Central Coast region (22%, 3.4%, and 4.7%, respectively) (12). These higher rates suggest that wildlife could potentially vector *E. coli* onto farm fields (6).

If it discourages wildlife vector movements onto farm fields, then vegetation removal could mitigate food safety risk. The influence of noncrop vegetation in farming landscapes on EHEC or *Salmonella* prevalence is unknown, however. Although some pathogens are sufficiently prevalent to enable investigation of the effects of surrounding landscape composition on pathogens (16), low pathogen prevalence generally constrains such investigations. One response to this situation has been to relate landscape features to indicators (e.g., generic *E. coli*) as a proxy for known pathogens (17, 18). Another approach has been to assume that exposures result primarily from contact with local livestock or

Significance

Fresh produce has become the primary cause of foodborne illness in the United States. A widespread concern that wildlife vector foodborne pathogens onto fresh produce fields has led to strong pressure on farmers to clear noncrop vegetation surrounding their farm fields. We combined three large datasets to demonstrate that pathogen prevalence in fresh produce is rapidly increasing, that pathogens are more common on farms closer to land suitable for livestock grazing, and that vegetation clearing is associated with increased pathogen prevalence over time. These findings contradict widespread food safety reforms that champion vegetation clearing as a pathogen mitigation strategy. More generally, our work indicates that achieving food safety and nature conservation goals in produce-growing landscapes is possible.

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contaminated waterways, to aggregate reported illnesses to a county or district level, and to correlate infection rates with land use patterns (19, 20).

Here we investigated direct associations between landscape composition and generic *E. coli*, EHEC, and *Salmonella* prevalence on fresh produce farms. We generated four predictions. First, we hypothesized that, owing to its higher prevalence in cattle compared with many wildlife species (15), EHEC would be detected regularly near grasslands, woodlands, and scrublands that are suitable for livestock grazing but rarely near nongrazed natural areas. Second, we predicted that EHEC prevalence would not decline on farms that had removed noncrop vegetation. Third, we expected that a high prevalence of *Salmonella* in wildlife (11) would cause an increase in *Salmonella* prevalence near both nongrazed and grazed seminatural areas. Fourth, we predicted that removing noncrop vegetation would reduce the incidence of *Salmonella* in fresh produce.

To test our predictions, we gathered three datasets from California's Central Coast: 237,306 EHEC and *Salmonella* tests in fresh produce at 74 farms from 2007 to 2013; 6,887 generic *E. coli* tests in reservoirs, wells, and waterways at 484 farms from 2007 to 2010; and 792 *Salmonella* tests in rodents at 9 farms from 2009 to 2010 (21). At each sampled location, we quantified the fraction of surrounding cropland, land suitable for livestock grazing, nongrazed riparian areas, and other nongrazed natural vegetation (defined as woodland, upland scrub, grassland, and meadow/marsh). Land cover fractions were calculated from both a fine-scale, 1,900-km^2 extent land use classification of the Central Coast (mapped in 2005 and 2012) and a 2010 map of "grazeable land" from the California Department of Conservation's Farmland Mapping and Monitoring Program, defined as "land on which the existing vegetation is suited to the grazing of livestock" (22). Grassland dominated grazeable land (65%), whereas nongrazed areas hosted a more even distribution of noncrop vegetation types: upland scrub (35%), grassland (25%), woodland (23%), and riparian areas (13%) (*SI Appendix*, Fig. S1).

Results

We found that EHEC prevalence in leafy green vegetables significantly increased in California's Central Coast region, from <0.1% of samples in 2007 to 2.5% in 2013 (Fig. 1). EHEC did not increase in other states and countries, and *Salmonella* increased only weakly across all counties, states, and countries. Both pathogens were most prevalent in the late summer (*SI Appendix*, Fig. S2). Around the same time (2005–2012), many growers replaced noncrop vegetation with bare ground buffers (Fig. 1). Within 50 m of agricultural fields in the Salinas Valley, we detected declines in riparian (9%), woodland (2%), scrub (13%), grassland (11%), and meadow/marsh (30%) vegetation between 2005 and 2012, along with a 30% increase in bare ground.

Despite analyzing ~250,000 pathogen tests, we found no evidence that generic *E. coli* in water and EHEC in fresh produce were more prevalent in areas surrounded by nongrazed riparian or other natural vegetation (Fig. 2). These findings were robust across 500-, 750-, 1,000-, 1,250-, and 1,500-m spatial scales (*SI Appendix*, Table S1). Aligning with our first prediction, however, EHEC was significantly more prevalent in fresh produce on farms with more surrounding grazeable land (Fig. 2 and *SI Appendix*, Table S1). Specifically, models predicted that EHEC was ~100 times more likely (~0.01% vs. ~1%) to be detected near grazeable land (60% grazeable land within 1.5 km) versus far from grazeable land.

Aligning with our second prediction, we also did not find that removing riparian or other natural vegetation decreased EHEC prevalence over time (Fig. 3 and *SI Appendix*, Table S2). Instead, farms on which cropland expanded and natural vegetation was removed were significantly more likely to experience an increase in EHEC prevalence over time. Riparian vegetation removal did not affect EHEC prevalence at any spatial scale.

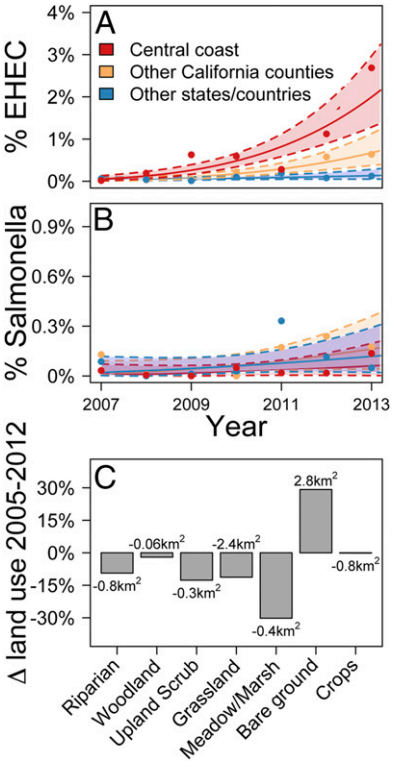

Fig. 1. (*A*) EHEC prevalence in leafy green vegetables increased significantly from 2007 to 2013 (likelihood ratio test: $n = 21$ region-years/482,208 tests, $\chi^2 = 16.8$, $P < 0.001$). The rate of increase was marginally lower in California counties outside the Central Coast region and much lower in other states and countries (interaction: $\chi^2 = 10.7$, $P = 0.005$). (*B*) *Salmonella* increased marginally over time ($\chi^2 = 2.75$, $P = 0.10$) across all states and countries (interaction: $\chi^2 = 0.47$, $P = 0.79$). Solid lines represent predicted pathogen prevalences from linear mixed models; dotted lines, prediction intervals. Points are observed percentages of infected samples in each year and region. (*C*) Percent change in Salinas Valley land cover from 2005 to 2012 within 50 m of cropland. Numbers represent absolute changes.

Contrary to our third prediction, no land cover significantly predicted *Salmonella* prevalence in rodents or leafy green vegetables at any spatial scale (*SI Appendix*, Fig. S3 and Table S3). Moreover, changes in cropland and nonriparian natural vegetation were not associated with changes in *Salmonella* prevalence between 2007–2008 and 2010–2012 (*SI Appendix*, Fig. S4 and Table S2). Riparian vegetation removal was significantly associated with increased *Salmonella* prevalence at large scales (1,000, 1,250, and 1,500 m), however *SI Appendix*, Table S3).

Discussion

Although *Salmonella* and EHEC displayed distinct spatial and temporal prevalence patterns, our results strongly suggest that vegetation removal does not mitigate the risk of contamination of fresh produce by either pathogen. While the prevalence of *Salmonella* in fresh produce increased only marginally over the last decade, the prevalence of EHEC increased dramatically, despite significant efforts to reduce pathogen prevalence, including measures to prevent wildlife intrusions (5, 8, 9). We also found no evidence that any pathogen was more prevalent near nongrazed natural areas. Rather, removal of riparian and other natural vegetation was associated with increased *Salmonella* and EHEC prevalence, respectively.

There are several possible explanations for these findings. First, replacing natural vegetation with bare ground buffers may not deter wide-ranging wildlife, such as feral pigs, from entering

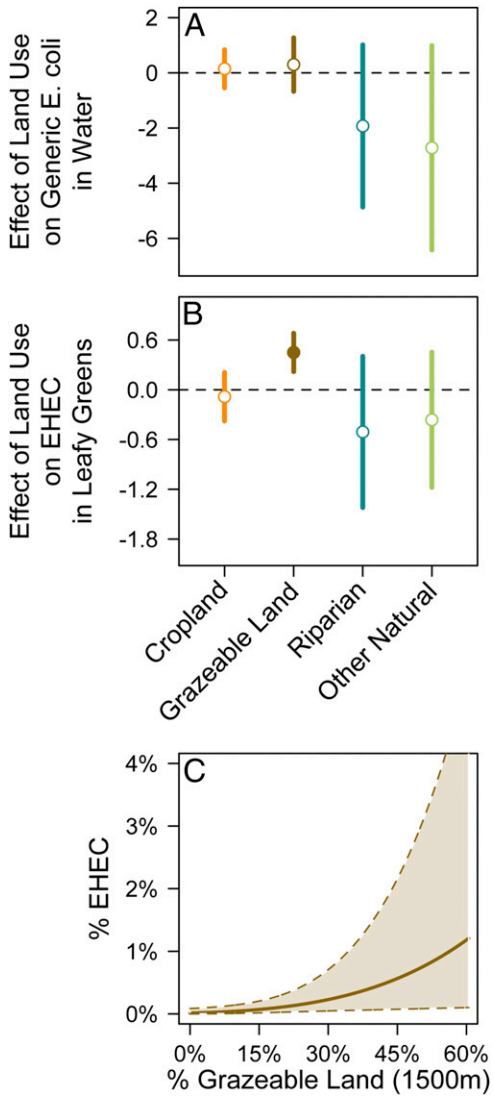

Fig. 2. (*A*) Surrounding land cover did not significantly predict changes in the prevalence of generic *E. coli* in water (*SI Appendix*, Table S1). (*B* and *C*) Although EHEC was more prevalent in leafy greens at sites with more surrounding grazeable land (model averaging: n = 236,522 tests across 57 farms, Z = 3.8, P < 0.001), we found no evidence that riparian or other nongrazed natural vegetation increased EHEC prevalence (*SI Appendix*, Table S1). Points and lines in *A* and *B* are model-averaged estimates and confidence intervals of land cover effects on pathogen prevalence (filled circles; P < 0.05). The solid line in *C* relates surrounding grazeable land to pathogen prevalence; dotted lines represent prediction intervals.

farm fields (23). Second, removing vegetation could increase risk if persisting wildlife species are efficient disease vectors. Indeed, one study found that the prevalence of foodborne diseases was higher in low-diversity rodent communities dominated by deer mice compared with biodiverse rodent communities (the "dilution effect") (21). Third, *E. coli* may survive longer in agricultural soils than in soils from riparian areas, and thus replacing noncrop vegetation with crops could increase disease incidence (24). Fourth, removing vegetation could increase pathogen prevalence in runoff from adjacent hill slopes, given that noncrop vegetation is known to sequester many pathogens, including *E. coli* (25, 26).

Nonetheless, our results do indicate that produce farms located near land suitable for livestock grazing may be at increased risk for EHEC contamination (Fig. 2). Previous work also has shown that generic *E. coli* (18), *E. coli* O157:H7 (27), *Salmonella* (28), and *Listeria* (29, 30) are positively associated with livestock density or proximity to livestock. Similarly, studies that have aggregated reported EHEC illnesses to county or district levels have generally observed higher EHEC infection rates in counties with higher cattle densities, although this approach infers rather than directly links cases and exposures (19, 20).

If infected livestock are responsible for the observed association between EHEC prevalence and surrounding lands suitable for livestock grazing (rather than the wildlife that cohabit grazeable land), then coordinating management practices among feedlot operators, ranchers, and produce growers might reduce this risk (Fig. 4). For example, feedlot operators could vaccinate their livestock against *E. coli* O157:H7 (31). Feedlot operators and ranchers also could reduce *E. coli* and *Salmonella* in runoff by >90% with secondary treatment wetlands, which would provide additional conservation benefits (32). Similarly, ranchers could mitigate cross-contamination risk by fencing waterways that eventually pass through produce fields to prevent entry of livestock and wildlife or by attracting livestock away from field crops or streams with water, food supplements, and food troughs (33). Rather than removing vegetation, ranchers and growers could sequester pathogens by maintaining and/or installing vegetated buffers between crop fields and grazeable lands (25, 26). Other alternatives include planting produce that is not eaten raw in areas adjacent to grazeable lands and reducing application of agrichemicals (i.e., herbicides and fungicides), which can increase EHEC through decreasing predatory and competitor bacterial abundance (34).

Since 2006, there has been considerable tension between the need to manage produce farms to respond to concerns about conservation and the need to ensure food safety (5, 8, 9). Despite the lack of explicit regulatory language calling for its removal (4), a significant amount of the Salinas Valley's noncrop vegetation has been cleared (5). Instead, this vegetation removal likely was related in part to pressure exerted by buyers on growers through auditors to mitigate perceived food safety risks (8). Likewise, the recent Food Safety Modernization Act—the largest overhaul to food safety regulations of the past 70 y (3)—does not call for vegetation removal. Nonetheless, after the extension of food safety regulations to 4.5 M acres of US farmland, buyer pressure to remove vegetation may continue to spread, because regulations may be interpreted as a floor, rather than a standard or a ceiling, for on-farm practices to ensure food safety.

Our data indicate that removing noncrop vegetation does not improve produce safety. Vegetation removal is economically costly, and ecosystem-service losses (e.g., pollination, pest control) may compound costs (35, 36). Harmonizing nature conservation and produce production may be possible by realizing that noncrop vegetation can be a benefit, not a threat, to growing safe and sustainable produce.

Methods

Pathogens in Fresh Produce. Since October 2, 2006, an organic farming operation with numerous fields spread across California's Central Coast region has consistently tested all of the leafy green vegetables that it produced or acquired for foodborne pathogens. At harvest, vegetables were packed into boxes and loaded into pallets, with each 40 × 48 × 78 in pallet holding ~600 lb of product. The pallets were transported to centralized packing centers and sorted into production units (four pallets per production unit). Sterilized forceps were used to grab 60 "pinches" of fresh leafy greens (~150 g) from each production unit. Samples were placed into sterile plastic bags and transported to an in-house molecular laboratory operated by a third-party company. Unique farm names were associated with each vegetable sample, and records of spatial farm locations were obtained from food-safety staff at the larger farming operation.

Although established methods for detecting EHEC and *Salmonella* are readily available (11, 12, 21), the specific methods used by the third-party company were not disclosed. Generally, however, the company's pathogen testing procedure consists of DNA preparation, amplification, and detection.

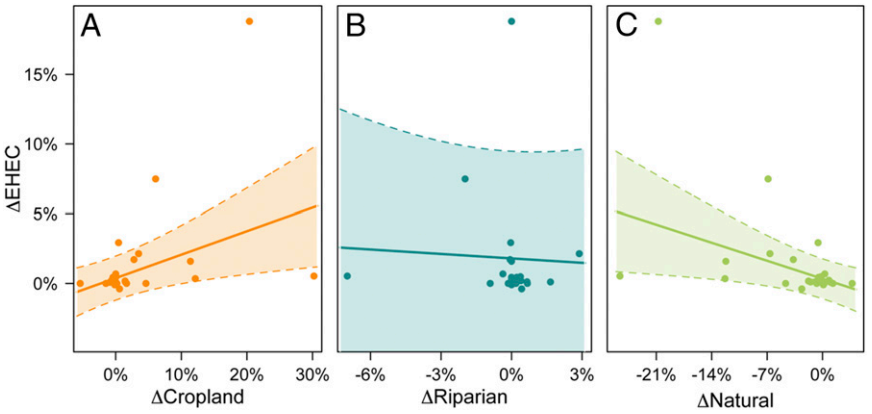

Fig. 3. (*A*) EHEC prevalence in leafy greens increased on farms that replaced nonriparian natural vegetation with crops between 2005 and 2012 (likelihood ratio test: $n = 28$ farms, $\chi^2 = 4.22$, $P = 0.04$). (*B* and *C*) In contrast, EHEC did not change when riparian vegetation was removed (n = 28, $\chi^2 = 0.07$, $P = 0.79$) (*B*) and increased when other natural vegetation was removed (note the negative scale of the *x*-axis; $n = 28$, $\chi^2 = 4.55$, $P = 0.03$) (*C*). Solid lines depict predicted effects on EHEC from linear models, dotted lines are prediction intervals, and points are farms.

First, samples were enriched, and bacterial DNA was extracted with a lysing procedure. Then samples were subjected to PCR, amplifying unique sequences from *E. coli* O157:H7, shiga toxin-producing *E. coli* (STEC), and *S. enterica*. PCR products were visualized on agarose gels with ethidium bromide, and positive bands were subjected to molecular confirmation, using four to six more multiplex reactions with and without magnetic bead separation, depending on the pathogen. Any sample that tested positive for *E. coli* O157:H7 or STEC was labeled as containing EHEC.

Between 2007 and 2013, a total of 482,208 samples originating from 295 farms were tested for *E. coli* O157:H7, STEC, and *Salmonella*. The farms were located in the United States (Arizona, California, Colorado, Nevada, and Oregon), Mexico (Baja California, Guanajato, and Sonora), and Chile. Samples were obtained from a variety of leafy green vegetables and cultivars (*SI Appendix*, Table S4).

Generic *E. coli* in Water. Irrigation water was sampled monthly by the leafy green agricultural industry across the California Central Coast region over a 4-y period (2007–2010). A commercial laboratory provided the blinded data, but sample collection locations were preserved using GPS coordinates. Samples were collected from on-farm wells and reservoirs and municipal water distribution systems by either contracted professionals or farm personnel at the points of distribution and application. Samples were captured in 250-mL Whirl-Pak bags and transported on ice (~4 °C) for microbial analysis.

The samples were analyzed for the presence of generic *E. coli* using a most probable number (MPN) technique; specifically, an enzyme substrate test typically performed using a commercially prepared quantification tray. In this test, 100 mL of sample water was added to a single tray and incubated at 35 ± 0.5 °C for 24–28 h. The presence of *E. coli* was determined by the presence of an enzymatic reaction that caused a color change in the substrate. Results were entered into an MPN calculator for final quantification, with lower and upper bounds of detection from 1 to 2,419.6 MPN/100 mL.

***Salmonella* in Rodents.** Fecal specimens were collected from 11 wild rodent species trapped in nine produce farms located in Monterey and San Benito Counties, California, between October 2009 and August 2011, as described previously (21). Trapping was carried out approximately once every 3 mo at each farm over the study period. Smaller-sized nocturnal rodents (e.g., *Peromyscus maniculatus*, *Peromyscus californicus*) were trapped using Sherman live

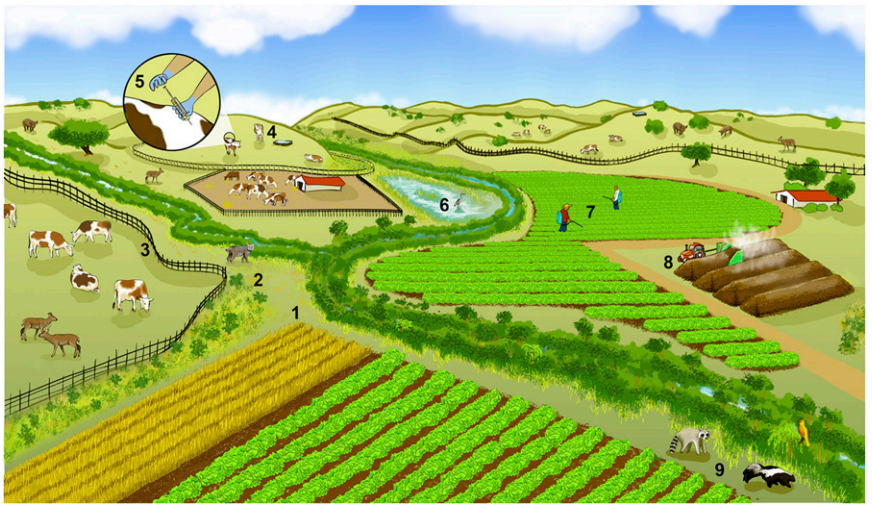

Fig. 4. Collaborative action among growers, ranchers, and feedlot operators could reduce food-safety risk while maintaining the conservation value of agricultural landscapes. Promising practices include (1) planting low-risk crops between leafy green vegetables and pathogen sources (e.g., grazeable lands); (2) buffering farm fields with noncrop vegetation to filter pathogens from runoff (25, 26); (3) fencing upstream waterways from cattle and wildlife; (4) attracting livestock away from upstream waterways with water troughs, food supplements, and feed (33); (5) vaccinating cattle against foodborne pathogens (31); (6) creating secondary treatment wetlands near feedlots and high-intensity grazing operations (32); (7) reducing agri-chemical applications to bolster bacteria that depredate and compete with *E. coli* (34); (8) exposing compost heaps to high temperatures through regular turning to enhance soil fertility without compromising food safety (4); and (9) maintaining diverse wildlife communities with fewer competent disease hosts (21).

traps, and California ground squirrels (*Spermophilus beecheyi*) were trapped using Tomahawk live traps. Fresh fecal pellets and bedding material were transported on ice to the University of California Davis for pathogen detection. All animals were handled humanely in accordance with the Institutional Animal Care and Use Committee's protocol no. 16376.

To detect *Salmonella*, an aliquot of each fecal sample (~0.025–0.10 g per rodent) was preenriched in 50 mL of buffered peptone water (BD Diagnostic Systems) for 20 h at 37 °C. Then 10 mL of preenrichment broth was transferred to 1 mL of Rappaport Vassiliadis medium (BD Diagnostic Systems) for 48 h at 42 °C. A loopful of broth was streaked for isolation onto xylose lysine desoxycholate agar (BD Diagnostic Systems). A pure isolated colony was confirmed biochemically using lysine, citrate, triple sugar iron, and urea (all from BD Diagnostic Systems).

Pathogen Prevalence over Time. We assessed whether the prevalence of EHEC and *Salmonella* changed over time with the leafy greens dataset. First, we calculated the number of detections and absences of each pathogen in each year. Then we modeled how the proportion of positive pathogen detections changed from 2007 to 2013, using linear mixed models with survey years as random effects (37). Proportions of EHEC and *Salmonella* detected were fourth root-transformed and square root-transformed, respectively, to satisfy model assumptions (e.g., normality, heteroscedasticity). To determine whether yearly dynamics differed among the California Central Coast, other counties in California, and other surveyed states/countries (see above), we included the following as fixed effects: ordinal survey year, an indicator variable demarcating the location of the pathogen test, and their interaction. We evaluated significance through backward model selection, comparing nested models with likelihood ratio tests (37).

We also assessed seasonal variation in pathogen prevalence at farms in the Central Coast region. First, we obtained the Julian day for which each sample was harvested. Then, for each day of the year, we calculated the fraction of samples that tested positive for EHEC and *Salmonella* (across all sites and years). Days with fewer than 100 pathogen tests were excluded. We then constructed linear models in which Julian date and Julian date^2 were included as fixed effects. As before, we assessed significance with backwards model selection.

Creating Land Cover Maps. To determine how landscape features influence pathogen prevalence, we created an Anderson level II terrestrial land use/land cover map of California's Central Coast region. Vegetation in 2005 and 2012 was mapped within a 1.5-km buffer of all agricultural areas in Monterey County's Salinas Valley (1,669.13 km^2). The maps also encompassed parts of the San Juan and Pajaro Valleys in Santa Cruz and San Benito Counties that were strategically chosen to encompass sites sampled for pathogens (2005: 81.33 km^2; 2012: 236.97 km^2). Vegetation was hand-classified into one of 16 possible categories from 1-m^2 resolution National Agricultural Inventory Program imagery, obtained in the summers of 2005 and 2012 (*SI Appendix*, Table S5).

All cropland and riparian habitat was mapped with a 0.5-acre minimum mapping unit (MMU). Upland vegetation, urban areas, and other land use classes were mapped with a 1.0-acre MMU. To assess the effects of proximity to grazeable land, we overlaid spatial grazeable land data from 2010 on top of our land cover map, which was acquired from the California Department of Conservation (www.conservation.ca.gov/dlrp/fmmp/Pages/Index.aspx). Grazeable land was defined as "land on which the existing vegetation is suited to the grazing of livestock" and identified in collaboration with several organizations, including the California Cattlemen's Association and the University of California Cooperative Extension.

To determine how food safety concerns may have affected land cover, we compared the 2005 (preoutbreak) and 2012 (postoutbreak) land cover maps. We isolated agriculture-induced change rather than natural processes (such as riparian vegetation regeneration) by narrowing our focus to only land within 50 m of 2005 cropland (5). We quantified the changes in bare ground, cropland, riparian areas, and other natural vegetation across the Salinas Valley between 2005 and 2012 (*SI Appendix*, Table S5).

Landscape Associations with Pathogens. To model the effects of different land covers on pathogen prevalence, we calculated the fractions of cropland, grazeable land, riparian areas, and other natural vegetation classes (i.e., woodland, grassland, upland scrub, and meadow/marsh) around each pathogen survey site at multiple scales (within 500, 750, 1,000, 1,250, and 1,500 m of survey sites). We then assessed the effects of cropland, grazeable land, riparian areas, and other natural vegetation at each spatial scale with separate linear models. Recent studies have indicated that generalized linear mixed models (with Poisson, negative binomial, or binomial error structures) can have high type I error rates (38). Indeed, our preliminary analyses using generalized linear mixed models with binomial errors yielded type I error rates of >60%. Therefore, for all analyses, we used linear mixed models to quantify changes in the proportion of samples that were positive for each pathogen.

For analysis of generic *E. coli* in water, we first converted from an MPN to presence/absence (using a MPN of 1 as a threshold). We then calculated the fraction of samples that tested positive for generic *E. coli* across all years at each farm, square root-transforming proportions to satisfy model assumptions. Farms without at least 50 *E. coli* tests were excluded from the analyses, but our results were robust to varying this threshold. We next averaged the land cover values for all survey points within a given farm so that each farm was assigned one average value for each land cover type. Cropland, grazeable land, riparian areas, and other natural vegetation were included as fixed effects in each model, and closest city was included as a random effect to account for spatial autocorrelation.

For analyses of both EHEC and *Salmonella* in leafy greens, we first calculated the fraction of samples testing positive across all years at each farm, and then excluded farms without at least 100 pathogen tests. As before, our results were robust to varying this threshold. Proportion data were either fourth root-transformed (EHEC) or square root-transformed (*Salmonella*), so that resulting models would yield normally distributed residuals. For both pathogens, the four land cover types were included as fixed effects in all models, and "closest town" nested within "county" were included as random effects.

Finally, owing to fewer sampling locations, we quantified the fraction of rodent samples that tested positive for *Salmonella* in each year at each farm. Site-years without at least 10 samples were excluded from the analysis. As for the water dataset, we calculated average land cover values across all survey locations within each farm. The four land cover types were included as fixed effects in all models, and survey year was included as a random effect.

For each analysis, we used model averaging to assess the association of each land cover type (cropland, grazeable land, riparian vegetation, and other natural vegetation) with pathogen prevalence and reported nonshrinkage variance estimates. Nonshrinkage variance estimates for a fixed effect are estimated from a combination of model uncertainty and standard regression variance, using only the models that include that given fixed effect (39). All analyses were performed in R (40), using "lme4" for linear mixed models and "MuMIN" for model averaging.

Detecting Effects of Land Use Change. We assessed whether temporal changes in vegetation management practices were associated with temporal changes in EHEC and *Salmonella* prevalence in leafy green vegetables on the 28 farms that were regularly surveyed for pathogens and had their surrounding land cover mapped in 2005 and 2012. First, we calculated the change in the fraction of samples that tested positive for EHEC and *Salmonella* between early surveys (2007–2008) and late surveys (2011–2013). Next, for each farm, we calculated the change in cropland, riparian areas, and other natural vegetation between 2005 and 2012 at each spatial scale. Given its lower spatial resolution and temporal mismatch with the land cover map, we did not assess changes in grazeable land; instead, we examined the effects of changes in the extent of cropland, riparian, and nonriparian vegetation regardless of whether it was grazed or ungrazed.

Finally, we modeled associations between land cover changes and pathogen prevalence changes between the early and late survey periods using linear mixed models, acknowledging that other factors may contribute to some of the temporal shifts in pathogen prevalence (e.g., adoption of industry-wide reforms; ref. 4). Because seminatural vegetation was often replaced with crops, land cover variables were highly collinear; thus, we constructed separate models to investigate each land cover type, pathogen (EHEC and *Salmonella*), and spatial scale (500, 750, 1,000, 1,250, and 1,500 m). "Nearest town" nested within "county" were included in all models as random effects to account for spatial autocorrelation. For models predicting associations between EHEC and cropland or natural vegetation, we also included an exponential variance structure to account for heteroscedastic residuals (37). Significance was assessed for each model with backward model selection (37).

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Table S1: Model-averaged associations between land covers and generic *E. coli* prevalence in water and EHEC prevalence in leafy greens. Significant land-cover effects are bolded.

		Generic *E. coli* in Water					**EHEC in Leafy Greens**				
Scale (m)	Land Cover	Importance*	β	Std. Err.	Z	*P*	Importance	β	Std. Err.	Z	*P*
500	Intercept		0.16	0.17	0.93	0.35		0.18	0.08	2.05	0.04
	Cropland	0.48	0.27	0.18	1.44	0.15	0.26	-0.07	0.12	0.58	0.56
	Natural	0.26	0.01	1.79	0.00	1.00	0.25	-0.24	0.42	0.56	0.58
	Grazeable land	0.26	0.04	0.35	0.12	0.91	**0.64**	**0.42**	**0.19**	**2.19**	**0.03**
	Riparian	0.36	-0.87	0.89	0.97	0.33	0.23	-0.17	0.61	0.28	0.78
750	Intercept		0.32	0.14	2.11	0.03		0.17	0.09	1.90	0.06
	Cropland	0.16	0.04	0.32	0.10	0.92	0.27	-0.08	0.13	0.64	0.52
	Natural	0.32	-3.61	2.82	1.18	0.24	0.24	-0.20	0.50	0.39	0.70
	Grazeable land	0.17	0.27	0.64	0.40	0.69	**0.82**	**0.42**	**0.15**	**2.67**	**0.01**
	Riparian	0.19	-1.44	2.23	0.60	0.55	0.30	-0.44	0.48	0.88	0.38
1000	Intercept		0.21	0.13	1.56	0.12		0.16	0.09	1.80	0.07
	Cropland	0.38	0.19	0.17	1.13	0.26	0.26	-0.07	0.14	0.48	0.63
	Natural	0.26	0.12	1.37	0.09	0.93	0.26	-0.33	0.48	0.68	0.49
	Grazeable land	0.25	-0.05	0.28	0.19	0.85	**0.91**	**0.42**	**0.14**	**2.98**	**<0.01**
	Riparian	0.32	-0.45	0.60	0.75	0.46	0.29	-0.41	0.47	0.85	0.40
1250	Intercept		0.34	0.13	2.41	0.02		0.14	0.08	1.71	0.09
	Cropland	0.16	0.08	0.32	0.22	0.82	0.25	-0.06	0.15	0.40	0.69
	Natural	0.50	-4.46	2.53	1.63	0.10	0.27	-0.37	0.43	0.83	0.41
	Grazeable land	0.16	0.19	0.50	0.35	0.72	**0.96**	**0.42**	**0.13**	**3.30**	**<0.01**
	Riparian	0.19	-0.79	1.87	0.40	0.69	0.32	-0.51	0.46	1.07	0.28
1500	Intercept		0.23	0.12	1.86	0.06		0.13	0.08	1.59	0.11
	Cropland	0.35	0.17	0.16	1.01	0.31	0.25	-0.08	0.15	0.56	0.57
	Natural	0.27	0.33	1.28	0.25	0.80	0.28	-0.36	0.41	0.87	0.38
	Grazeable land	0.25	-0.04	0.26	0.15	0.88	**0.98**	**0.45**	**0.12**	**3.82**	**<0.01**
	Riparian	0.38	-0.57	0.58	0.98	0.33	0.32	-0.51	0.45	1.09	0.27

*Sum of Akaike weights across all models containing the variable.

Table S2: Associations between land-cover change (2005 to 2012) and the temporal change in EHEC and Salmonella prevalence in leafy green vegetables. Models with and without each land cover were compared with likelihood ratio tests. Models with cropland or natural vegetation as predictors, and EHEC as the response, included an exponential correlation structure to account for heteroskedastic residuals. Significant land-use effects are bolded.

Pathogen	Scale (m)	Land Cover	β (slope)	Std. Err.	χ^2	*P*
EHEC	500	**Cropland**	0.602	0.192	**8.46**	**<0.01**
		Riparian	0.429	0.899	0.24	0.62
		Natural	0.001	0.049	0.00	0.99
	750	**Cropland**	0.091	0.047	**3.74**	**0.05**
		Riparian	-0.029	0.244	0.02	0.90
		Natural	-0.091	0.049	3.41	0.06
	1000	Cropland	0.049	0.025	3.67	0.06
		Riparian	-0.026	0.256	0.01	0.92
		Natural	-0.042	0.022	**3.78**	**0.05**
	1250	**Cropland**	0.091	0.047	**3.81**	**0.05**
		Riparian	-0.027	0.314	0.01	0.93
		Natural	-0.099	0.049	**4.00**	**0.05**
	1500	**Cropland**	0.136	0.060	**4.22**	**0.04**
		Riparian	-0.112	0.445	0.07	0.79
		Natural	-0.167	0.076	**4.55**	**0.03**
Salmonella	500	Cropland	0.000	0.000	0.77	0.38
		Riparian	-0.015	0.009	2.89	0.09
		Natural	0.000	0.001	0.50	0.48
	750	Cropland	0.000	0.000	0.85	0.36
		Riparian	-0.004	0.002	3.43	0.06
		Natural	0.000	0.001	0.35	0.56
	1000	Cropland	0.001	0.001	0.90	0.34
		Riparian	**-0.005**	**0.003**	**3.87**	**0.05**
		Natural	0.000	0.001	0.38	0.54
	1250	Cropland	0.001	0.001	0.72	0.40
		Riparian	**-0.007**	**0.003**	**5.75**	**0.02**
		Natural	0.000	0.001	0.25	0.62
	1500	Cropland	0.001	0.001	0.50	0.48
		Riparian	**-0.012**	**0.004**	**7.55**	**0.01**
		Natural	0.000	0.001	0.15	0.70

Table S3: Model-averaged associations between land cover and *Salmonella* prevalence in leafy greens and in rodents.

		***Salmonella* in Leafy Greens**					***Salmonella* in Rodents**				
Scale (m)	Land Cover	Importance	β	Std. Err.	Z	*P*	Importance	β	Std. Err.	Z	*P*
500	Intercept	NA	0.01	0.01	1.48	0.14	NA	0.02	0.04	0.49	0.62
	Cropland	0.24	0.00	0.01	0.37	0.71	0.26	0.08	0.06	1.17	0.24
	Natural	0.32	-0.04	0.04	0.99	0.32	0.15	0.06	0.79	0.07	0.94
	Grazeable land	0.25	0.01	0.02	0.56	0.57	0.15	-0.33	1.10	0.27	0.79
	Riparian	0.23	0.00	0.05	0.04	0.96	0.16	0.22	0.35	0.57	0.57
750	Intercept	NA	0.01	0.01	1.40	0.16	NA	0.02	0.04	0.42	0.68
	Cropland	0.23	0.00	0.01	0.08	0.94	0.24	0.10	0.08	1.18	0.24
	Natural	0.30	-0.04	0.04	0.88	0.38	0.15	0.05	0.74	0.06	0.96
	Grazeable land	0.24	0.01	0.01	0.45	0.65	0.16	-0.30	0.98	0.28	0.78
	Riparian	0.26	-0.03	0.04	0.58	0.56	0.16	0.15	0.23	0.57	0.57
1000	Intercept	NA	0.01	0.01	1.27	0.20	NA	0.04	0.03	1.25	0.21
	Cropland	0.24	0.00	0.01	0.25	0.80	0.14	0.04	0.06	0.51	0.61
	Natural	0.45	-0.05	0.03	1.44	0.15	0.16	0.13	0.77	0.15	0.88
	Grazeable land	0.25	0.01	0.01	0.50	0.62	0.17	-0.45	1.14	0.37	0.71
	Riparian	0.25	-0.02	0.04	0.49	0.62	0.18	0.10	0.13	0.70	0.49
1250	Intercept	NA	0.01	0.01	1.13	0.26	NA	0.02	0.04	0.44	0.66
	Cropland	0.25	0.00	0.01	0.35	0.72	0.25	0.09	0.07	1.15	0.25
	Natural	0.48	-0.05	0.03	1.50	0.13	0.14	-0.02	0.60	0.03	0.98
	Grazeable land	0.27	0.01	0.01	0.68	0.49	0.15	-0.20	0.83	0.21	0.83
	Riparian	0.23	-0.01	0.04	0.30	0.76	0.16	0.19	0.29	0.59	0.56
1500	Intercept	NA	0.01	0.01	1.02	0.31	NA	0.03	0.04	0.79	0.43
	Cropland	0.25	0.00	0.01	0.28	0.78	0.18	0.07	0.07	0.88	0.38
	Natural	0.44	-0.05	0.03	1.38	0.17	0.16	0.08	0.81	0.10	0.92
	Grazeable land	0.33	0.01	0.01	0.98	0.33	0.16	-0.37	1.11	0.31	0.76
	Riparian	0.23	0.00	0.04	0.07	0.95	0.16	0.12	0.18	0.59	0.55

Table S4: Tested leafy green vegetable species and cultivars.

Sci. Name	Common Name	Cultivars	Samples (all sites)	Samples (Cen. Coast)
Eruca sativa	Arugula	Arugula, Wild Arugula	28626	12895
Beta vulgaris	Chard, Beets	Full Size Green Chard, Full Size Red Chard, Gold Chard, Green Beet Tops, Green Chard, Orange Chard, Pink Chard, Pink Lipstick Chard, Rainbow Chard, Red Beet Tops, Red Chard, Red Cloud, Yellow Chard	42191	19613
Brassica rapa	Chinese cabbage	Baby Pak Choi, Mizuna, Red Mizuna, Red Pak Choi	23391	12833
Coriandrum sativum	Cilantro	Cilantro	8492	4857
*N*A	Combo Mix	Combo Mix	60	14
Anethum graveolens	Dill	Dill	1535	907
Cichorium endivia	Endive	Frisee, Whole Frisee Heads	10182	5503
Brassica oleracea	Kale, Cabbage, Collard Greens	Black Cabbage Kale, Blue Baby Kale, Collard Greens, Dino Kale, Full Size Green Kale, Full Size Red Kale, Green Baby Kale, Green Kale, Lacinato Kale, Premier Kale, Purple Kale, Raw Organic Red Cabbage, Red Baby Kale, Red Cabbage, Red Kale, Red Russian Kale, Texsel Baby Kale	8335	4470
Lactuca sativa	Lettuce	Girondac, Green Oak, Green Romaine, Heirloom Green Bibb, Heirloom Green Butter, Heirloom Green Oak, Heirloom Green Romaine, Heirloom Lollo Rosa, Heirloom Mix, Heirloom Red Bibb, Heirloom Red Butter Heirloom Red Leaf, Heirloom Red Oak, Heirloom Red Romaine, Iceberg, Lollo Rosa, Malawi, Mercury, Processing Romaine, Red Leaf, Red Oak, Red Romaine, Red Thunder, REDWOOD, Tango, Washed Leaf Romaine	221643	111985
Valerianella locusta	Mache	Mache	2223	1240
Brassica juncea	Mustard greens	Full Size Green Mustard, Green Mustard	19	2
Petroselinu m crispum	Parsely	Parsely	1510	980
NA	R&D Samples	R&D Samples	34	0
Cichorium intybus	Radicchio	Proc. Radicchio	8509	3414
Spinacia oleracea	Spinach	Baby Spinach, Spinach, Teen Spinach	124587	58483
Brassica narinosa	Tatsoi	Tatsoi	380	110

Table S5: Mapped vegetation classes and descriptions.

Vegetation Class	Analysis Class	Description
California Forest & Woodland	Other natural	Dry upland trees; for example, Coast live oak (*Quercus agrifolia*), Blue oak (*Q. douglasii*), Interior live oak (*Q. wislizenii*), Valley oak (*Q. lobata*), and California buckeye (*Aesculus californica*)
Riparian Forest & Woodland	Riparian	Wetland native trees; for example, Red willow (*Salix laevigata*), Black willow (*S. gooddingii*), Shining willow (*S. lucida*), Fremont cottonwood (*Populus fremontii*), Box elder (*Acer negundo*), Big leaf maple (*Acer macrophyllum*), California sycamore (*Platanus racemosa*), and White alder (*Alnus rhombifolia*)
Exotic Trees	NA	Non-native dry upland trees; for example, Conifers, Eucalyptus, Pepper, and Tamarisk.
Southwestern North American Riparian Scrub	Riparian	Wetland thickets; for example, Fremont cottonwood (*Populus fremontii*), *Salix* spp. (Shining willow [*S. lucida*], Arroyo willow [*S. lasiolepis*], Narrowleaf willow [*S. exigua*], Black willow [*S. gooddingii*], and/or Red willow [*S. laevigata*]), Mule-fat (*Baccharis salicifolia*), Scale broom (*Lepidospartum squamatum*), and Coyote brush (*Baccharis pilularis*).
Upland Scrub	Other natural	Chaparral, California Coastal Scrub, and Pacific Coast Scrub; for example, Chamise (*Adenostoma fasciculatum*), Scrub oak (*Quercus berberidifolia*), Toyon (*Heteromeles arbutifolia*), Buckthorn (*Rhamnus* spp.), Manzanita (*Arctostaphylos* spp.), Coyote brush (*Baccharis pilularis*), California sagebrush (*Artemisia californica*), California buckwheat (*Eriogonum californica*) and Dune scrub species among others
Mediterranean Grasslands & Forbs	Other natural	Dry upland herbaceous plants; for example, Brome (*Bromus* spp.), Oats (*Avena* spp.), and Barley (*Hordeum* spp.), Mustards (*Brassica* spp.), and other invasive exotic species including Pepperweed (*Lepidium latifolium*), Poison hemlock (*Conium maculatum*), and Iceplant (*Carpobrotus edulis*).
Meadow and Marsh	Other natural	Wetland herbaceous plants; for example, include Bulrush (*Schoenoplectus* sp.), Cattails (*Typha latifolia*), sedges (*Carex* sp.), Rushes (*Juncus* spp.), Spike-rush (*Eleocharis* sp.), Alkali heath (*Frankenia* sp.), Pickleweed (*Salicornia* sp.), Saltgrass (*Distichlis spicata*), *Jaumea* sp., Gumweed (*Grindelia* sp.), and Giant Cane (*Arundo donax*).
Naturally Occurring Unvegetated	Bare ground	Areas with little or no vegetation cover of natural origin; for example, sparsely vegetated stream or river flats, upland rock outcrops, and escarpments.
Human Caused Unvegetated	Bare ground	Areas with little or no vegetation cover of human origin; for example, agricultural "staging areas," bare-ground field buffers, and cleared areas associated with buildings.
Active and Recently Active Agriculture	Cropland	Vegetable, row, or field crops in nurseries, fields, or greenhouses. Fallow land that was active within 5 years is also included.
Pasturelands	NA	Fields that are improved and are associated with a homestead or animal ranch.
Orchards/Vineyards	Cropland	Citrus orchards, fruit and nut orchards, and vineyards.
Dairy or Confined Feedlot Operations	NA	Dairies, pens, or feedlots associated with bovine animals.
Poultry or other small animal confined feedlot operations	NA	Facilities for chickens, turkeys, pigs, goats, and other small animals.
Urban/Built-Up	NA	Impervious surfaces including buildings, roads, or other permanent structures.
Water	NA	Permanently, seasonally, temporarily, and intermittently flooded water features, such as lakes, ponds, basins, reservoirs, large ditches, major canals, and rivers

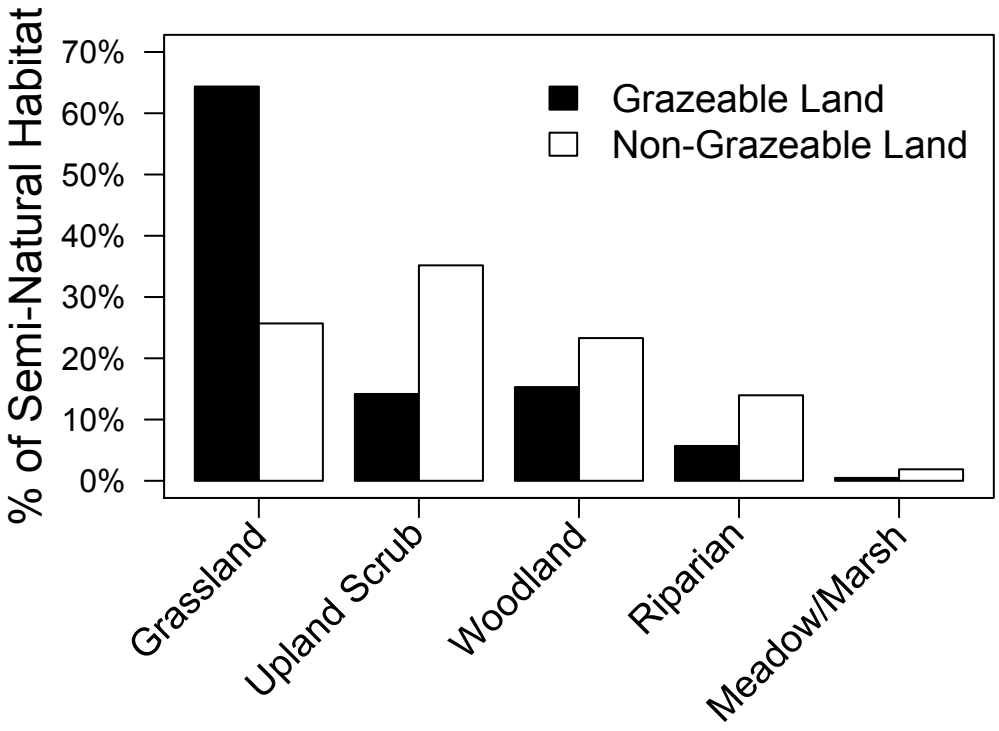

Fig. S1: Composition of natural vegetation classes in grazeable and non-grazeable land. Land-cover fractions were derived from the 2012 hand-classified land-use/land-cover dataset; grazeable land was delineated from the 2010 California Department of Conservation's Farmland Mapping and Monitoring Program map of land suitable for livestock grazing.

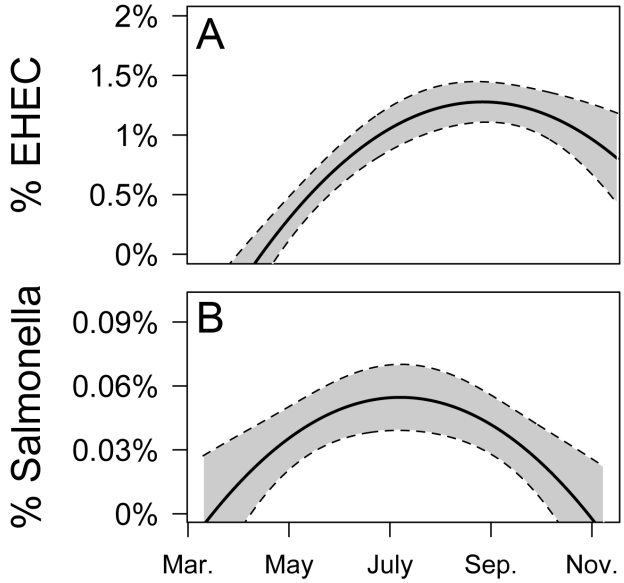

Fig. S2: Seasonal changes in EHEC and *Salmonella* prevalence in Central Coast leafy green vegetables. (Panel A) EHEC prevalence in Central Coast produce peaked in the late summer (N= 222 days/248820 tests, Julian Date $P< 0.001$, Julian Date^2 $P< 0.001$). (Panel B) Similarly, *Salmonella* prevalence was most frequently encountered in the summer (N= 222 days/248820 tests, Julian Date $P< 0.001$, Julian Date^2 $P< 0.001$). Solid lines are model predicted seasonal effects on pathogen prevalence; dotted lines are prediction intervals.

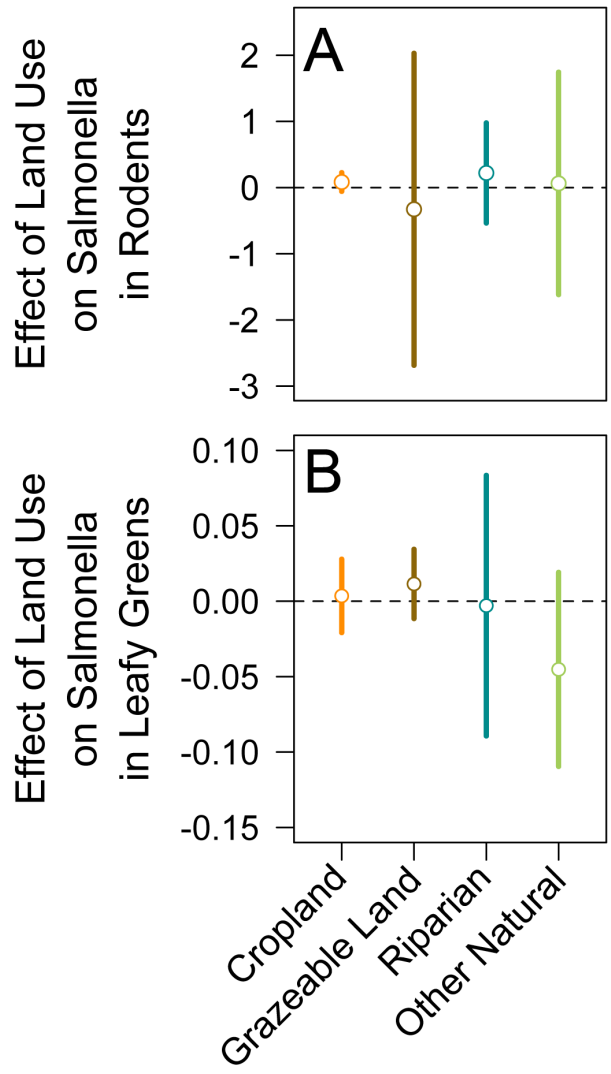

Fig. S3: *Salmonella* prevalence did not significantly increase at sites with more surrounding riparian or other natural vegetation. Model-averaged linear mixed models show no associations between grazeable land, cropland, riparian vegetation, or other natural habitat and *Salmonella* prevalence in rodents (Panel A) or leafy greens (Panel B). Points and lines are model-averaged estimates and confidence intervals of vegetation effects on Salmonella occurrence.

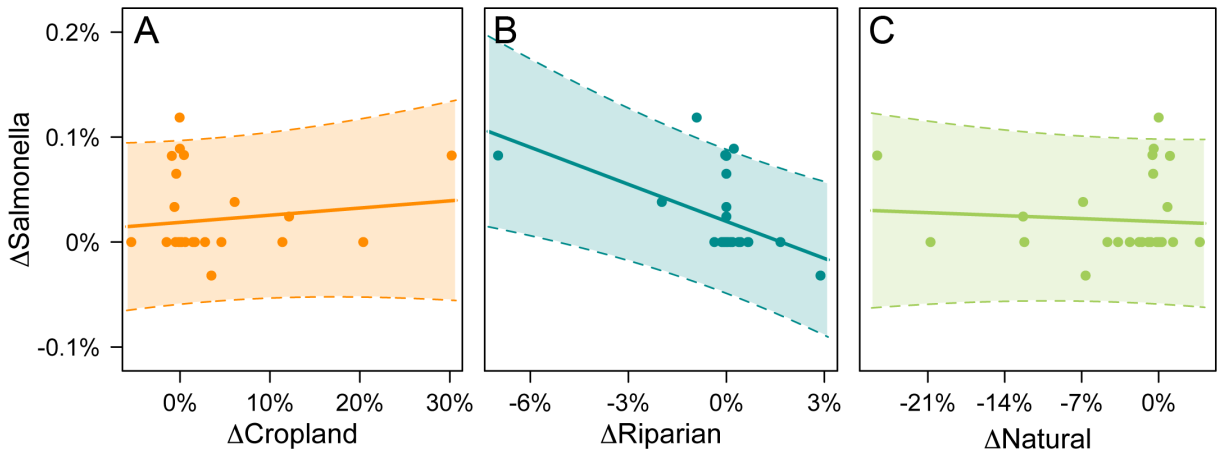

Fig. S4: Riparian vegetation removal increases *Salmonella* prevalence in leafy green vegetables. *Salmonella* prevalence in leafy greens did not change on farms that experienced an increase in cropland (Panel A; likelihood ratio test— N= 28 farms, χ^2= 0.50, *P*= 0.48) or a decline in non-riparian natural vegetation (Panel C; N= 28, χ^2= 0.15, *P*= 0.70). In contrast, *Salmonella* prevalence increased on farms that experienced riparian vegetation removal (Panel B; note negative values on x-axis, N= 28, χ^2= 7.55, *P*= 0.01). Solid lines depict predicted land-use effects on EHEC from linear mixed models, dotted lines are prediction intervals, and points are farms.