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Organic farming promotes biotic resistance to foodborne human pathogens

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Abstract

1. Farmland biodiversity benefits pollination, biological control and other key ecosystem services. Food safety has been seen as an exception to this broader pattern, as diverse farmlands attract wildlife that vector foodborne human pathogens. Resulting mitigation efforts thus often seek to deter wildlife by removing natural habitats, while also excluding vertebrate livestock. However, surprising recent evidence suggests that farm simplification actually increases the likelihood that produce will be contaminated with human pathogens.
2. Here, we consider the possibility that intensified agriculture harms faeces-feeding (coprophagous) beetles and bacteria, which could contribute to heightened food-safety risk. In 70 commercial vegetable fields spanning the US west coast, using either organic or conventional farming methods, we surveyed coprophages both above- and below-ground. We also measured removal rates of the faeces of *Sus scrofa*, which vectors foodborne pathogens both as livestock and as feral wildlife.
3. Above-ground, organic farms fostered dung beetle species that removed *S. scrofa* faeces more rapidly than was seen on conventional farms, although this benefit was weakened in simplified landscapes dominated by pasture and an introduced dung beetle. Below-ground, organic farming encouraged significantly higher biodiversity among soil bacteria. Organic farming similarly benefitted dung beetles and bacteria on farms that produced livestock alongside vegetables, or vegetables alone.
4. Complementary laboratory experiments revealed that the dung beetle species and biodiverse bacterial assemblages typical of organic farms were significantly more effective at suppressing human-pathogenic *Escherichia coli* O157:H7, compared to coprophage communities associated with conventional farms. This suggests that farm management practices, coprophage conservation, and human–pathogen suppression might be linked.

5. *Synthesis and applications*. Altogether, our results indicate that insects and microbes can rapidly remove faeces, with the potential to also decrease the persistence of human pathogens. In turn, this suggests that improved food safety may be an important, and perhaps underappreciated, ecosystem service that is enhanced by on-farm biodiversity. We recommend that farm managers and regulators consider the risks and benefits to coprophages when making management decisions regarding food safety.

KEYWORDS
agroecology, coprophage, disease ecology, *E. coli* O157:H7, ecosystem service, farm biodiversity, food safety

1 | INTRODUCTION

Pathogen contamination of fresh produce is a leading human-health threat world-wide (Painter et al., 2013), underlying millions of illnesses and thousands of deaths (Nyachuba, 2010; World Health Organization, 2015). Efforts to minimize this risk target all stages of food production, processing and preparation (Henson & Caswell, 1999; US Food and Drug Administration, 2017). In production fields, food-safety regulations often encourage the removal of hedgerows, ponds and other natural habitats (Beretti & Stuart, 2008). This is done to discourage visits by vertebrate wildlife whose faeces may serve as sources of human pathogens that may contaminate produce (Newell et al., 2010). However, such efforts likely carry ecological and economic costs because removing natural habitats from farms decreases biocontrol agents that prey on herbivorous pests and pollinate crops. Furthermore, habitat disruption can harm conservation of songbirds, amphibians and other sensitive wildlife (Lowell, Langholz, & Stuart, 2010). As such, safe food production and the conservation of beneficial on-farm biodiversity are often considered to be conflicting objectives (Beretti & Stuart, 2008; Karp et al., 2015).

The belief that biodiversity increases food-safety risks (Beretti & Stuart, 2008), however, could undervalue natural biotic resistance to the persistence of human pathogens. Indeed, farms can harbour a diverse community of faeces-feeding beetles and microbes that rapidly remove animal faeces once deposited, and also kill or otherwise antagonize any pathogens they contain. For example, dung beetles (Coleoptera: Scarabaeidae) can rapidly remove livestock faeces from grazeable grassland (Losey & Vaughan, 2006) and, in one case, have been suggested to suppress pathogens in the faeces that they consume (Jones, Tadepalli, Bridges, Wu, & Drummond, 2015). Likewise, soil microbes contribute to degrading faeces (Chu et al., 2007), commonly suppress plant pathogens through some combination of competition and chemical antagonism (Weller, Raaijmakers, Gardener, & Thomashow, 2002), and hinder persistence of human pathogens (Franz et al., 2008). Yet both dung beetles and soil microbial communities are harmed by practices associated with agricultural intensification, such as pesticide applications and the removal of natural habitats (Barbero, Palestrini, & Rolando, 1999; Hutton & Giller, 2003; Staley, Rohr, Senkbeil, & Harwood, 2014). Indeed, a recent study (Karp et al., 2015) found that human–pathogen contamination of fresh produce was more frequently detected in simplified landscapes modified by habitat removal, consistent with declining coprophage communities (although this possible mechanism was not directly examined). Coprophagous arthropod communities are known to be affected by local and landscape-scale disturbances (Beynon, Mann, Slade, & Lewis, 2012; Hutton & Giller, 2003). Additionally, the influence of farm-scale management on biodiversity depends on the availability of species in the landscape to colonize “biodiversity-friendly” farming systems (Tscharntke et al., 2012). If farms naturally resist the persistence of human pathogens through pathways associated with biodiversity-friendly farming practices and the surrounding landscape, regulations (e.g. LGMA, 2014) may need to reconsider the belief that farm simplification only benefits food safety.

Here, we test a suite of hypothesized relationships between land management (farming practices and landscape context), coprophage community dynamics (dung beetle community mass and soil bacterial biodiversity), and ecosystem services pertaining to food safety (faeces removal and suppression of potential foodborne pathogens). We conducted a broad survey of beetle and soil microbial communities in 70 commercial broccoli (*Brassica oleracea*) fields spanning the US West Coast from northern Washington State to southern California (Figure 1). This region encompasses well over a third of fresh produce production in North America (CDFA, 2017) and has been the source of several notable outbreaks of foodborne illnesses linked to contamination by wildlife faeces (Jay et al., 2007; Laidler et al., 2013). We focused on broccoli fields because this crop is grown across the broad geographic/climate gradient and is often eaten fresh, making it vulnerable to foodborne pathogens. The farms that we visited were managed using one of three farming systems: conventional vegetable, organic assorted vegetable and organic assorted vegetable alongside livestock production (hereafter called an “integrated system”). Organic farming often encourages biodiverse fauna (Tuck et al., 2014), including both wildlife that might enhance food-safety risk

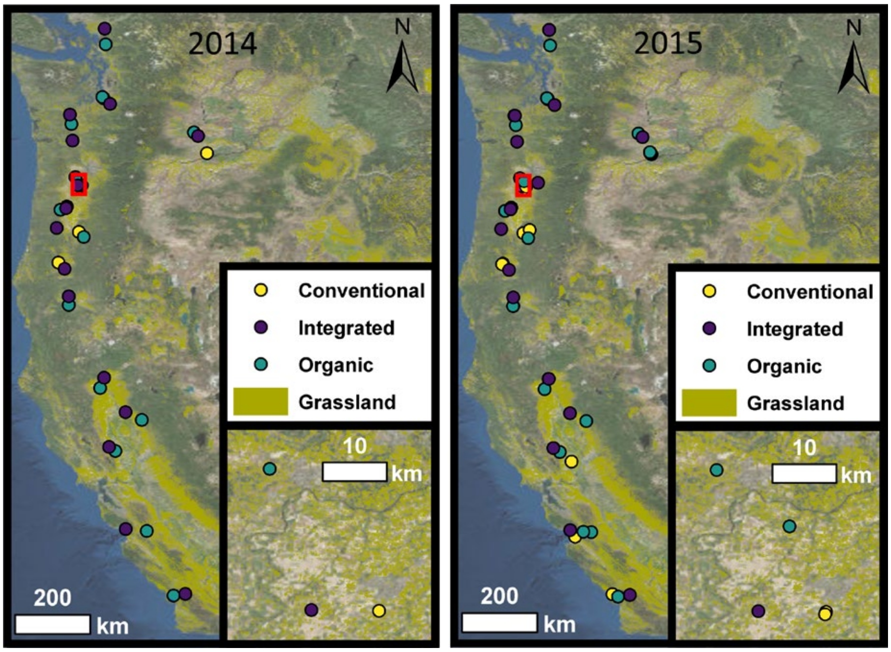

FIGURE 1 Map of study sites. This study included 70 fields over the 2-year field study, with six and nine conventional fields (yellow dots), 13 and 13 organic fields (green dots) and 15 and 14 integrated crop/livestock fields (purple dots) in 2014 and 2015, respectively

(Bengtsson, Ahnström, & Weibull, 2005) and coprophages that might reduce it (Hutton & Giller, 2003). Integrated livestock farms use cows, chickens or other livestock to facilitate weed and pest control, provide natural fertilizer, and diversify markets through meat production (Russelle, Entz, & Franzluebbers, 2007). Faeces produced by these livestock might create food-safety risks (Newell et al., 2010); for instance, cattle are known to serve as a primary reservoir for *Escherichia coli* 157:H7 (Tauxe et al., 1997). However, they might also support particularly robust coprophage communities (Bertone et al., 2005).

Our work included several complementary components. First, in each field, we placed sentinel pig (*Sus scofra domesticus*) faeces onto the soil within broccoli rows as a means to measure ambient faeces-removal rates. We used sentinel pig faeces in these consumption assays because these animals both are often reared on integrated livestock farms and are common reservoirs for human pathogens as feral wildlife (e.g. Jay et al., 2007). Concurrent with these assays, we surveyed dung beetle communities using faeces-baited traps and quantified soil bacterial diversity by sequencing soil-extracted DNA. We then used structural equation modelling (Lefcheck, 2016; Shipley, 2009) to examine links among farming practices, surrounding landscape context, faeces removal, and dung beetle and soil bacterial communities. This approach allowed us to statistically test for direct and indirect correlations among these factors using data collected from working farms. Finally, we experimentally examined the ability of different dung beetle species, and of soils collected from the fields we surveyed, to suppress *E. coli* O157:H7 in a biosafety facility where we could safely work with human pathogens. Altogether then, we sought to test hypothesized links between real-world farm environments, resident coprophage communities and the suppression of human-pathogenic bacteria. Together, this field survey and laboratory experiments suggest that ecological degradation harms coprophage and soil microbial communities and thus natural biotic resistance to the persistence of human pathogens.

2 | MATERIALS AND METHODS

2.1 | Field survey

Field data were collected during 2 years across 43 individual vegetable farms in California, Oregon and Washington, USA, which included 70 farm fields (34 fields in 2014, 36 fields in 2015) as follows: 6 and 9 "conventional" fields, 13 and 13 "organic" fields and 15 and 14 "integrated" fields in 2014 and 2015, respectively (Figure 1). Broccoli was chosen as the standardizing crop for two reasons: (a) its long growing season across our entire study region, and (b) its susceptibility to faeces-borne contamination due to proximity to the ground and the likelihood of human consumption without cooking. In both 2014 and 2015, sampling started in the southern part of the study range (California) in mid-March and continued northward with the growing season, ending in Washington in early August. "Conventional" farms relied on synthetic inputs. "Organic" farms were either certified organic (USDA, 2017) or uncertified but still relied on natural means of fertilization and pest suppression without using synthetic agrochemicals. "Integrated" farms followed organic principles for vegetable production, with or without being certified, and also raised livestock and/or poultry as part of their production system.

At each farm, we quantified arthropod biodiversity, aboveground faeces removal, and characterized soil physical/chemical properties and bacterial communities. Dung beetles were captured using baited pitfall traps partly filled with soapy water (Seventh Generation Inc., Burlington, VT, USA) and baited with 20 g of frozen organic pig (*S.s. domesticus*) faeces wrapped in nylon tulle (modified from Larsen & Forsyth, 2005). Pig faeces were used to bait traps because pigs are known to vector harmful *E. coli* strains (Jay et al., 2007). Additionally, domesticated pigs (*S.s. domesticus*) are common livestock and feral pigs (*Sus scrofa*) are common wildlife on western mixed-vegetable farms (see SI Materials and Methods for dung beetle trapping specifics).

Immediately following pitfall trapping, pig faeces removal was quantified (see SI Materials and Methods for faeces-removal specifics). Faeces loss due to feeding was quantified by dry mass removal (oven-dried at 70°C until a constant weight was attained as per Slade, Mann, & Lewis, 2011). Removal rates were pooled by site location.

2.2 | Determining the percentage of grazeable grassland in the landscape

We used the Cropland Data Layer (CDL) provided by the United States Department of Agriculture (https://www.nass.usda.gov/Research_and_Science/Cropland/SARS1a.php) to quantify the extent of grassland surrounding focal farms. All of the following CDL land-use types were considered grazeable in our analyses: "Fallow/Idle Cropland," "Wetlands," "Grassland/Pasture," "Herbaceous Wetlands," and "Pasture/Grass." We calculated the fraction of grassland in twenty 100-m concentric rings (up to 2 km) surrounding each study site (see SI Materials and Methods for details about determining the percentage of grazeable grassland in the landscape).

2.3 | Soil property characterization

A composite core sample was taken from each field site (n = 6 cores/farm field) from the location of each pitfall trap; each core was 11 cm width and 15 cm depth. After collecting a composite soil sample from each farm field, homogenized samples were immediately shipped for chemical and physical analyses to Soiltest Farm Consultants (Moses Lake, WA, USA). See SI Materials and Methods for soil property characterization specifics. For soil property results, see Data S2.

2.4 | Soil community characterization

For DNA extraction, 0.25 g soil from each sample was used following the protocols of the PowerSoil DNA Isolation Kit (Mo Bio Laboratories, Carlsbad, CA). DNA concentration was quantified using Qubit assay (Invitrogen, Carlsbad, CA). Thirty-four samples from 2014, 36 from 2015 and 16 samples from 2016 (collected for the "Soil Community Microcosm" experiment described below) were sent to Beijing Genomic Institute for library preparation and sequencing. See SI Materials and Methods for soil community characterization specifics.

2.5 | Dung beetle microcosm experiment

To examine the relationship between beetle species and pathogen suppression, we designed a laboratory microcosm study. Microcosms were composed of 1 L "deli dishes" filled with 100 g of air dry soil and 20 g of pig manure inoculated (then homogenized) with a cocktail of nalidixic acid-resistant *E. coli* O157 strains (E12053, E12057, E12061 and E12063, see Shringi et al., 2012, for specifics regarding SBI genotype, year and origin of each strain). Strains were passaged on Columbia Blood Agar to recover from storage at −80°C. Strains were then inoculated to Brain Heart Infusion broth and incubated at 37°C for 24 hr before being homogenized with pig manure. Initial inoculation rate of each microcosm was approximately 10^{-6} when plated at time zero. Treatment groups consisted of a single dung beetle species and there were four replicates of each treatment group. Beetle species used in the experiment [*Onthophagus taurus*, *Onthophagus nuchicornis* and *Aphodius (Labbarus) pseudolividus*] were the most common in the aforementioned field study and co-occurred in time and space at our field sites. Field-collected beetles (6 individuals) were placed into each microcosm to feed on faeces. After 7 days at room temperature, dung beetles were removed from microcosms and the environment was analysed for *E. coli* counts. Given that dung removal rates cannot be measured using dry mass removal (oven drying would kill *E. coli*), dung removal was "scored" (from 1 to 5) as described previously (Figure S3). See SI Materials and Methods for dung beetle microcosm experiment details.

2.6 | Soil community microcosm

To examine the relationship between soil bacterial diversity and pathogen suppression, we designed a second laboratory microcosm study. Soils were collected from 16 farms (in 2016) and the bacterial community characterized as described for the field study. Microcosms were again composed of 1 L "deli dishes," filled with 100 g of soil from one of the 16 farms (collected <3 days prior), and 20 g of pig manure inoculated (homogenized) with *E. coli* O157 as previously described. Faeces was homogenized with soil and left for 7 days. Each farm soil treatment group had four replicates, and *E. coli* was enumerated as in the above-described beetle experiment.

2.7 | Statistical analyses

2.7.1 | Detecting the effects of farm management and grassland composition on dung beetle and soil bacterial communities

Preliminary assessment of the data indicated potential direct and indirect effects of local and landscape drivers on dung beetle diversity and subsequently on faeces removal. We used two generalized multilevel path models (Shipley, 2009), based on linear mixed effects models, which offer a flexible way to take into account different error distributions, nonlinear relationships, and interactions specific to different variables within the overall structure of the path model (Lefcheck, 2016; Shipley, 2009). The first model tested the relative influence of local (farm management practices) and landscape (% grassland within 250 m) processes on the dung beetle community and ultimately on faeces removal. The second path model tested the influence of farm management practices on soil properties and ultimately on the soil bacterial community. These models tested the direct pathways between variables, while tests of independence claims allowed us to assess overall model fit (Shipley, 2009). See SI Materials and Methods for model specifics. To calculate the percent of variation explained by each mixed effect model, we calculated both the marginal R^2 (R^2 based solely on fixed effects) and conditional R^2 (incorporating the random effects) (Nakagawa & Schielzeth, 2013). These analyses were performed in R (3.2.3), using the “lme4,” “MuMIn,” “nlme,” “multcomp” and “piecewiseSEM” packages (Bartoń, 2016; Bates, Mächler, Bolker, & Walker, 2014; Hothorn, Bretz, & Westfall, 2008; Lefcheck, 2016; Pinheiro, Bates, DebRoy, & Sarkar, 2016; R Core Team, 2013). For data visualization, the “ggplot2,” “scatterplot3d,” “viridis” and “visreg” packages (Breheny & Burchett, 2016; Garnier, 2018; Ligges & Mächler, 2003; Wickham, 2009) were used.

2.7.2 | Dung beetle and soil community microcosm experiments

Dung beetle species treatment effects on *E. coli* suppression were assessed using analysis of variance with pairwise comparisons of treatment means performed using a post hoc Tukey HSD. Bacterial diversity effects on *E. coli* suppression were assessed using a general linear model. In both models, *E. coli* detected were log-transformed to satisfy model assumptions (e.g. normality, heteroscedasticity). All analyses were performed in R (3.2.3) (R Core Team, 2013); the “ggplot2” package (Wickham, 2009) was used for data visualization.

3 | RESULTS

3.1 | Relationships between farm management, biodiversity and pathogens

Generalized multilevel path models (Shipley, 2009) were used to test (a) the relative influence of farm management practices and the landscape availability of grazeable grassland on dung beetle community composition and faeces removal, and (b) the effect of farm management practices on soil properties and the soil bacterial community. Above-ground, models revealed strong direct and indirect effects of local and landscape drivers on dung beetle communities and faeces removal (Figure 2a, Table S1). Below-ground, local farm management significantly influenced the bacterial community (Figure 2b, Table S1). Both above- and below-ground path models provided good fits for the data ($\chi^2 = -9.64$, $df = 6$, $p > 0.999$ and $\chi^2 = -0.29$, $df = 2$, $p > 0.999$, respectively).

3.2 | Dung beetles

Dung beetle species richness ranged from one to eight species, with the most common species being *O. taurus*, *O. nuchicornis* and a

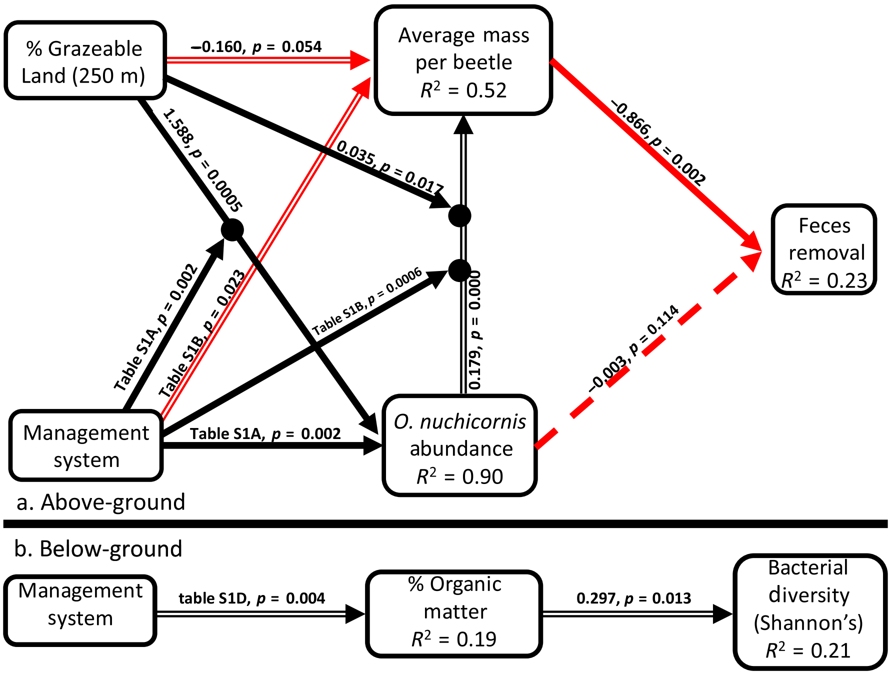

FIGURE 2 Effects of above- and below-ground, local and landscape drivers on the coprophage community and pathogen suppression predictors. Arrows represent the flow of causality between external drivers, intermediate drivers, and final field predictors for pathogen suppression (as indicated by “Faeces Removal” and “Bacterial Diversity”). Black arrows indicate positive effects, red arrows indicate negative effects, solid arrows indicate linear relationships, hollow arrows indicate nonlinear (log-transformed) relationships and hollow red arrows indicate negative nonlinear (log-transformed) relationships. Solid circles indicate an interaction effect whereby the driver makes the relationship more positive. Dotted arrow represents nonsignificant ($p > 0.05$) relationships that were part of our initial hypothesized pathway of effects. Path coefficients are unstandardized partial regression coefficients. Both the above-ground (a) and below-ground (b) models provided the best fit to our data and were well supported ($\chi^2 = -9.64$, $df = 6$, $p > 0.999$ and $\chi^2 = -0.29$, $df = 2$, $p > 0.999$, respectively). See Table S1 for full model results

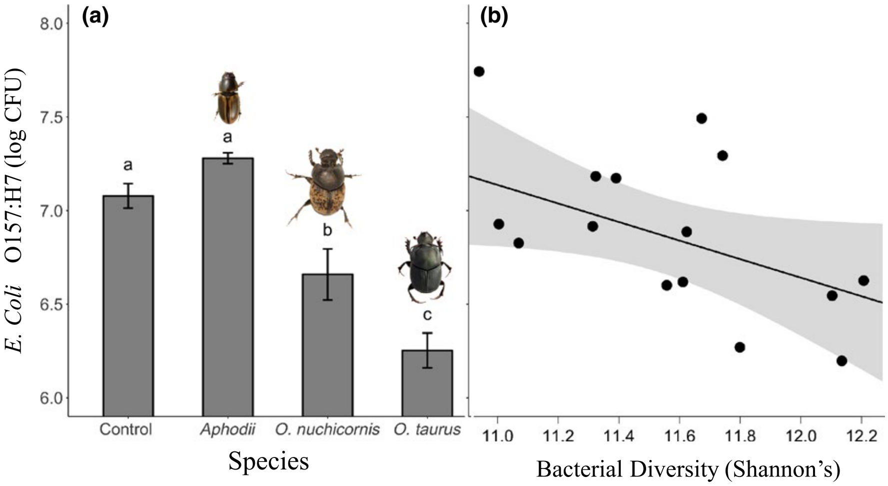

FIGURE 3 Suppression of pathogenic *Escherichia coli* O157:H7 in response to coprophage feeding and bacterial diversity. (a) Levels of *E. coli* O157:H7 suppression differed significantly among beetle species ($F_{3,12}$ = 25.68, $p < 0.0001$). Lowercase letters indicate significant differences based on a Tukey's HSD post hoc test; data are means ± *SE*, of log-transformed colony forming units (CFU). (b) A negative relationship was found between soil bacterial diversity (Shannon's Index) and the persistence of pathogenic *E. coli* O157:H7 (R^2 = 0.194, p = 0.0494)

variety of *Aphodius* spp. (primarily *A. pseudolividus*) (Data S1). Floate, Watson, Weiss, and Olfert (2017) report models predicting the distribution of *O. taurus* and *O. nuchicornis* along the west coast; our collections nearly mirror these geographic predictions. Despite dung beetles being diverse in samples across the west coast, we found that introduction of the exotic dung beetle *O. nuchicornis* appeared to be restructuring dung beetle communities (Floate et al., 2017); where *O. nuchicornis* was established from northern Washington State to central Oregon, this single species dominated dung beetle assemblages (north of approx. 42°N, see Figure S1).

Faeces removal varied substantially (from 4.5% to 99.5%) among our geographically diverse broccoli fields, and was impacted by a complex web of interactions among dung beetle community structure, farming practices and landscape context (Figure 2a). We found that the two organic farming systems (with and without livestock) encouraged relatively biodiverse and effective coprophage communities that helped to increase the rates of faeces removal. Specifically, rates of faeces removal decreased as the average size of dung beetles on a farm increased (Figure 2a; Figure S2). This somewhat paradoxical result appeared to be driven by the impact of a single large dung beetle species, the introduced *O. nuchicornis*, which apparently replaces other dung beetles as it colonizes and thereby increases mean dung beetle size (Figure 2a; Figures S1 and S2). Therefore, dominance by *O. nuchicornis* is indirectly correlated with decreasing rates of faeces removal (Figure 2a). While the amount of grazeable land in surrounding landscapes generally correlated positively with densities of *O. nuchicornis*, this effect was reduced on organic and integrated farms, which encouraged relatively high numbers of native dung beetles and relaxed *O. nuchicornis*' dominance (Figure 2a; Figure S2). Therefore, organic farming methods decoupled the relationships that otherwise existed between the amount of grazeable grassland in the surrounding landscape, the dominance of a single introduced dung beetle species, and slower faeces removal.

We exposed pig faeces contaminated with human-pathogenic *E. coli* serotype O157-H7 to feeding by each of the three most common dung beetle species detected in our dung beetle survey, under controlled laboratory conditions (described below). Dung beetles broadly differed in their abilities to remove pathogenic *E. coli* during 7 days of feeding (Figure 3, Table S2). *Aphodius pseudolividus*, a relatively small dung beetle (~4 mm, 0.005 g), did not significantly alter *E. coli* densities, while the widely distributed resident beetle *O. taurus* (6 mm, 0.01 g) reduced pathogenic *E. coli* numbers by >90%. *Onthophagus nuchicornis* (6 mm, 0.01 g) also reduced *E. coli*, but was less effective than *O. taurus* and reduced pathogenic *E. coli* numbers by <50%. Both *O. taurus* and *O. nuchicornis* bury faeces as a part of their breeding behaviour, while *A. pseudolividus* does not (Bertone et al., 2005). In addition to being a smaller species, this difference in *A. pseudolividus*' breeding behaviour may also be responsible for its lower efficiency at suppressing *E. coli* levels. Indeed, *E. coli* reduction tightly correlated with the amount of faeces removed in each treatment group (Figure S3).

3.3 | Soil bacteria

A diversity of soil chemical and physical characteristics informed our SEM efforts (Data S2). However, we found the strongest statistical support for a simple interaction chain with just two factors linked to greater bacterial diversity (Figure 2b): farming system and % organic matter. Both organic vegetable farming systems (vegetables alone or with integrated livestock) fostered a higher percentage of organic matter in the soil (Figures 2b and 4a). In turn, higher organic matter correlated with greater bacterial diversity (Figures 2b and 4b).

In the laboratory, we found that increasing bacterial diversity in soils was correlated with decreased survivorship of the pathogens (Figure 3b). To verify that the effect we were finding was solely an attribute of microbial diversity as opposed to other soil variables (i.e. phosphorus, potassium, calcium, magnesium, sodium, pH, electrical conductivity, ammonium, nitrate and soil texture), we reduced these variables into principal component axes and re-ran the analysis with the first principle component analysis axis included as a covariate. Including this axis in the analysis reduced the relative fit of the model (AIC = 25.149) compared to the original model (AIC = 19.115).

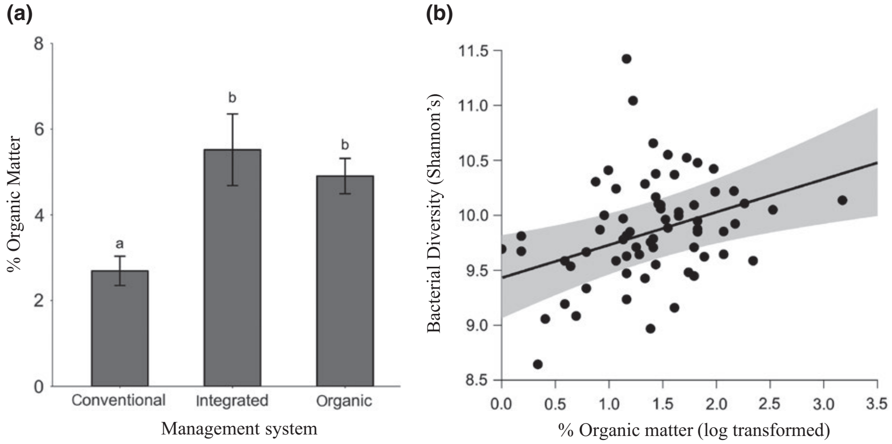

FIGURE 4 Important effects from below-ground SEM. (a) Percent soil organic matter was significantly higher on organic and integrated farms than on conventional farms ($F_{2,64}$ = 6.88, *p* = 0.002). Lowercase letters indicate significant differences based on a Tukey's HSD post hoc test; data are means ± *SE*. (b) A positive relationship was found between % soil organic matter and bacterial diversity (Shannon's Index) (*p* = 0.0037)

4 | DISCUSSION

Both above- and below-ground, we found the potential for biotic resistance to the persistence of human pathogens that contaminate fresh produce (Figures 2–4). On the soil surface, a diverse community of dung beetle species was capable of removing >90% of animal waste over several days of feeding (Figure 2a). Complementary feeding experiments suggested that several of these beetle species also reduced the prevalence of human-pathogenic *E. coli* while feeding (Figure 3a). Many dung beetle species work faeces into the soil as they feed (Bertone et al., 2005) and, in the soil too, we found the potential for biotic resistance. Taxon-rich bacterial communities, typical of many of the organic farms that we sampled, most effectively suppressed persistence of pathogenic *E. coli* (Figure 3b). This set up the potential for complementarity between above- and below-ground coprophages to further strengthen overall suppression of human pathogens across the two habitats. More generally, our results suggest that the current prevailing view that farm simplification benefits food safety (e.g. LGMA, 2014) undervalues natural resistance to human–pathogen survival. Indeed, the ecological protection of food safety may itself be a critical, if perhaps underappreciated, ecosystem service rooted in farm biodiversity.

Organic agriculture can bring widespread ecological benefits to farmland relative to conventional practices (Reganold & Wachter, 2016). Organic farmers often use fewer insecticides and promote greater in-field plant and arthropod diversity, which can lead to stronger natural pest control and more effective crop pollination (e.g. Kennedy et al., 2013; Lichtenberg et al., 2017; Snyder, Snyder, Finke, & Straub, 2006). Likewise, cover crops and application of animal manures build soil organic matter, which enhances microbial abundance and diversity (Kremen & Miles, 2012). In turn, organically farmed soils have been shown to exceed their conventional counterparts in the delivery of such ecosystem services as biological pest control, soil formation and the mineralization of plant nutrients (Sandhu, Wratten, & Cullen, 2010). However, some food-safety regulations (Beretti & Stuart, 2008) conflate several biodiversity-friendly practices often deployed by organic farmers with greater risk of produce contamination. For example, organic farms often house particularly robust populations of songbirds and other wildlife (Bengtsson et al., 2005) that could possibly act as a reservoir for human pathogens (Jones et al., 2015), though the degree to which wildlife actually elicit foodborne disease outbreaks remains unclear (Atwill, 2008). Likewise, animal manures on organic farms may harbour human pathogens (Newell et al., 2010). Both risks might be further enhanced on organic farms that intentionally integrate livestock.

Despite these concerns, however, our study suggests that organic farms might also foster beneficial biodiversity with the potential to counterbalance any heightened food-safety risks. This is consistent with other work linking organic farming to greater dung beetle diversity, compared to conventional farming (e.g. Hutton & Giller, 2003). Likewise, we found that organic farming indirectly led to more diverse soil bacterial communities, congruent with previous findings of lower plant pathogen levels in organically managed soils (Drinkwater, Letourneau, Workneh, Van Bruggen, & Shennan, 1995). Organic farming indirectly benefitted soil bacterial diversity by increasing organic matter in the soil (Figure 4), a well-known benefit of organic farming to soil quality (Reganold & Wachter, 2016) and ecosystem health (Delgado-Baquerizo et al., 2016). Critically, the effects of organic production methods on dung beetles and soil bacteria were seen across farms bridging a wide range of soil, landscape and climatic variation. In turn, this suggests that the possible benefits of organic farming for food safety in our study could reflect advantages for organic farming systems more generally (e.g. Lichtenberg et al., 2017).

The delivery of ecosystem services, such as pollination and natural pest control, is known to reflect management within farms and in the surrounding landscape (Lichtenberg et al., 2017; Sandhu et al., 2010). We found that food-safety-related ecosystem services might conform to these broader patterns. For example, dung beetle communities responded to the percentage of grazeable land in farm landscapes, in addition to the local farming system (Figure 2a). Possible causes of this apparent influence of landscapes are unclear, but could result from cattle on grazeable land providing food that particularly benefited the introduced dung beetle *O. nuchicornis* (Floate & Kadiri, 2013). This species was unintentionally introduced to Northeastern North America from Eurasia, was first detected in western North America in 1945, and has since rapidly expanded its distribution across Canada and the Northern United States (Floate et al., 2017). Due to differences in cold-hardiness and diapause requirements for *O. nuchicornis*, the current North American distributions of *O. nuchicornis* and *O. taurus* do not broadly overlap; however, in areas were the species do overlap, there is no evidence of competitive exclusion, and this is unlikely to change (Floate, Watson, Coghlin, & Olfert, 2015; Floate et al., 2017). The dominance of *O. nuchicornis* could result from a number of possible mechanisms. This species may either be out-competing others, or filling an empty niche created by the introduction of cattle from Europe into North America in concert with conversion of habitats with trees to open cattle pastures (Floate, 2011). Indeed, it is well established that roughly half of the arthropod species associated with cattle dung are non-native (Floate & Gill, 1998; Macqueen & Beirne, 1974). Lastly, while we cannot fully separate the geography of the farm from the beetle community present, we realize that these factors are likely linked. In contrast, the structure of the soil bacterial communities appeared to be determined by soil management practices on a particular farm or within a particular field (Reganold, Palmer, Lockhart, & Macgregor, 1993), consistent with field-scale influences on functional soil biodiversity that have been broadly reported elsewhere (Reeve et al., 2010).

It was notable that several species of dung beetles, and also diverse communities of soil bacteria, were capable of suppressing human-pathogenic *E. coli* (Figure 3). Our study did not examine specific mechanisms that might underlie this apparent harm to the pathogens, but previous studies suggest some possible directions for future investigation. For dung beetles, it has been suggested that, in addition to the physical damage cause by masticatory and gastrointestinal systems (Miller, Chi-Rodriguez, & Nichols, 1961), some insects' exoskeletons possess antimicrobial properties, perhaps as a means to suppress microbial food competitors also common in faeces (Hwang et al., 2008). It is also likely that when the dung beetles physically disturbed the manure, the subsequent desiccation of the manure caused a less suitable environment for the pathogen (e.g. Kudva, Blanch, & Hovde, 1998). In our study, suppression of *E. coli* was seen for two dung beetle species, congeners in the genus *Onthophagus* (Figure 3a), consistent with previous results for a closely related species (Jones et al., 2015). Suppression of pathogenic *E. coli* largely scaled with beetles' rates of faeces removal (Figure S3a); because the exotic dung beetle *O. nuchicornis* is intermediate in its faeces consumption rate, so too is this species intermediate in its ability to remove pathogenic *E. coli* (Figure 3a). What remains unexplained is why faeces removal was greatest by the two relatively large *Onthophagus* species in microcosms, whereas faeces removal was negatively correlated with mean beetle size in the open field. While more research is needed to resolve this apparent contradiction, an obvious possibility is that the laboratory experiment presented the beetles with physically simple foraging environments where interspecific differences in faeces discovery rates, interspecific interactions, and other aspects of real-world complexity were excluded.

In contrast to the scarce evidence for dung beetles, a great deal is known about bacterial antagonism of human and other pathogens (Franz et al., 2008; Hornby, 1983). In soils, the suppression of plant pathogens can be facilitated by soil physical–chemical characteristics (e.g. texture, structure, pH, Ca) and by soil biota through competition, antibiosis and parasitism (Höper & Alabouvette, 1996). We found that taxon-rich soil microbial communities had increasingly strong suppression of pathogenic *E. coli*, which is consistent with the widespread complementarity between bacterial species seen in many other contexts (Bell, Newman, Silverman, Turner, & Lilley, 2005). However, without further information about the identities and impacts of particular bacterial species and how their densities scale with increasing bacterial diversity, species identity effects (as we observed for dung beetles) cannot be entirely excluded in our study. Controlled experiments, which explicitly manipulate dung beetle and/or bacterial species composition and measure resulting impacts on suppression of human-pathogenic *E. coli* (or other foodborne human pathogens), would be invaluable for further elucidating which mechanisms are at work in these coprophage communities.

Increasingly, food-safety regulations focus on ecological simplification of farms as a means to discourage visits by wildlife, which are feared to vector human pathogens that contaminate produce (LGMA, 2014). The effectiveness of biodiversity reduction in this setting has received relatively little attention, but results published thus far present reason to question the overall effectiveness of many food-safety plans. For example, growers are often encouraged to remove non-crop vegetation around their farms to prevent wildlife from moving onto their farm fields and potentially spreading foodborne pathogens (Baur, Driscoll, Gennet, & Karp, 2016). Karp et al. (2015) found, however, that pathogen prevalence did not increase on farms that were surrounding by more non-crop vegetation. Moreover, vegetation removal was associated with an increase rather than a decrease in pathogenic *E. coli*. These authors suggested that possible mechanisms may be some combination of (a) ineffective bare ground wildlife buffers, (b) increased risk of pathogen persistence due to efficient disease vectors, (c) longer persistence of *E. coli* in agricultural soils than riparian soils, and (d) decreased sequestration of human pathogens from adjacent hillsides due to the removal of beneficial non-crop vegetation. However, the work presented here suggests an additional possibility: that ecological degradation might harm coprophage and soil microbial communities and thus natural biotic resistance to the persistence of human pathogens. In summary, we recommend greater consideration of food safety as an ecosystem service associated with coprophagous arthropods and soil bacteria – two key components of on-farm biodiversity that might be harmed as farms are simplified, or augmented when farms are managed to be more diverse. Indeed, farm-safety schemes that ignore biodiversity's benefits might inadvertently worsen, rather than mitigate, food-safety risks.

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AUTHORS' CONTRIBUTIONS

M.S.J., Z.F., J.P.R., T.E.B. and W.E.S. designed research. M.S.J., Z.F. and D.S.K. performed research. M.S.J., Z.F and D.S.K. collected data. M.S.J., Z.F., D.S.K., J.M.T. and W.E.S. analysed data and results. M.S.J., Z.F., J.P.R., D.S.K., J.M.T. and W.E.S. wrote the paper.

DATA ACCESSIBILITY

The datasets generated during and analysed during the current study are available via the Dryad Digital Repository https://doi.org/10.5061/dryad.5vn554c (Jones et al., 2018) Although field data are made available, geographic location is masked to protect grower privacy. The raw reads are achieved in Sequences Read Archives (SRA) of NCBI with SRA accession SRP126862. Model code for the entire pipeline of the 16S rDNA sequencing analyses is available via Zenodo https://doi.org/10.5281/zenodo.2557792 (Fu, 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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