RESEARCH ARTICLE

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Agricultural intensification heightens food safety risks posed by wild birds

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Abstract

1. Agricultural intensification and simplification are key drivers of recent declines in wild bird populations, heightening the need to better balance conservation with food production. This is hindered, however, by perceptions that birds threaten food safety. While birds are known reservoirs of foodborne pathogens, there remains uncertainty about the links between landscape context, farming practices, and actual crop contamination by birds.

2. Here, we examine relationships between landscape context, farming practices, and pathogen contamination by birds using a barrier-to-spillover approach. First, we censused bird communities using point count surveys. Second, we collected 2,024 faecal samples from captured birds alongside 1,215 faecal samples from brassica fields and food processing areas across 50 farms spanning the USA West Coast. We then estimated the prevalence of three foodborne pathogens across landscape and livestock intensification gradients. Finally, we quantified the number of plants with faeces.

3. *Campylobacter* spp. were detected in 10.2% of faeces from captured birds and 13.1% of faeces from production areas. Non-native birds were 4.1 times more likely to have *Campylobacter* spp. than native birds. *Salmonella* spp. were detected in 0.2% of faeces from production areas and were never detected in captured birds. We detected evidence of Shiga toxigenic *E. coli* in one sample across the >3,200 tested.

4. *Campylobacter* spp. prevalence in faeces from production areas increased with increasing mammalian livestock densities in the landscape but decreased with increasing amounts of natural habitat.

5. We encountered bird faeces on 3.3% of plants examined. Despite the impact on pathogen prevalence, amount of natural habitat in the landscape did not increase the number of plants with bird faeces, although on-farm mammalian livestock density slightly did.

6. *Synthesis and applications*. Food safety and wildlife conservation are often thought to be in conflict. However, our findings suggest that natural habitat around farms may reduce crop contamination rates by birds. This is perhaps because natural habitat can promote native birds that are less likely to harbour foodborne pathogens or because it decreases contact with livestock waste. Our results suggest that preservation of natural habitats around farms could benefit both conservation and food safety, contrary to current standards for 'best practices'.

1 | INTRODUCTION

Wild bird (hereafter, 'bird') populations have experienced precipitous declines in recent decades, even among many once-common species (Rosenberg et al., 2019). Underlying causes are complex, but bird numbers often decrease with increasing intensification and simplification of farming landscapes that result in fewer nesting sites, greater risk of exposure to toxic agrochemicals and fewer insect prey (Chamberlain, Fuller, Bunce, Duckworth, & Shrubb, 2000; Hallmann, Foppen, Turnhout, Kroon, & Jongejans, 2014; Seibold et al., 2019). This heightens the need to develop farming practices that better integrate bird conservation alongside food production. Although birds have the potential to provide valuable ecosystem services, such as consumption of pest insects (Karp et al., 2013), farmers often view them as more of a threat than an ally (Kross, Ingram, Long, & Niles, 2018; Olimpi et al., 2019). This is not only because of crop damage disservices but also because of the threat that birds may pose to food safety (Gardner et al., 2011; Kross et al., 2018; Olimpi et al., 2019).

Indeed, birds are known reservoirs of the leading causes of bacterial gastroenteritis worldwide: *Campylobacter* spp., *E. coli* and *Salmonella* spp. (Carlson, Franklin, Hyatt, Pettit, & Linz, 2011; Hald et al., 2016; Havelaar et al., 2015; Morishita, Aye, Ley, & Harr, 1999; Smith, Snyder, & Owen, 2020); and faecal contamination of produce by birds has been linked to at least one notable outbreak of *Campylobacter* spp. (Gardner et al., 2011). This suggests that conservation efforts to bolster on-farm bird densities could jeopardize food safety. Such fears, in turn, have sometimes triggered widespread natural habitat removal from farmland in an attempt to discourage bird intrusion (Beretti & Stuart, 2008; Olimpi et al., 2019), endangering conservation objectives and valuable ecosystem service provisioning (Karp et al., 2013; Ratto et al., 2018). However, it has been alteration of landscapes that is most likely to have increased the human–wildlife interface, which could subsequently increase the risk of foodborne pathogen spillover (Brearley et al., 2013; Jones et al., 2013). For example, Goldberg, Gillespie, Rwego, Estoff, and

Chapman (2008) found that genetic similarity between human/livestock and non-human primate *E. coli* increased 3-fold when anthropogenic disturbance within forest fragments increased from moderate to high. Thus, removal of natural habitats may worsen, rather than improve, food safety (Karp et al., 2015).

Considerable uncertainty remains about the true risk that birds pose to food safety and how landscape context or farming practices mediate the likelihood of birds causing foodborne illness. The number of people that become infected with foodborne pathogens is a function of contact between people and infectious doses of the pathogens (i.e. force of infection; Hens et al., 2010; Zhang, 2012). The likelihood that foodborne pathogens spillover from birds to humans is impacted by factors that regulate the force of infection that can be thought of as a series of barriers (Figure 1; see Table S1). These factors include pathogen exposure in the environment, reservoir host density and distribution, reservoir competence, and how frequently infected individuals defecate on crops (Plowright et al., 2017; Smith, Snyder, et al., 2020). Foodborne pathogens in the environment (e.g. livestock waste) may be a point of origin for bacteria entering bird communities while physiological and behavioural variation among bird species may affect reservoir competence and the probability of shedding infectious doses of bacteria onto crops (Smith, Snyder, et al., 2020). Furthermore, bird density and behaviour may affect the rate of defecation on crops, thus impacting the per capita exposure for people consuming those crops. Importantly, the broader landscape may influence how these factors align and further shape the risk of infection in people (Lewis, Otero-Abad, Hegglin, Deplazes, & Torgerson, 2014).

While studies have documented the impact of landscape context and farm management on bird communities (i.e. reservoir host distribution and density; Figure 1a,c; Boesing, Nichols, & Metzger, 2017; Šálek, Bažant, & Zmihorski, 2017; Smith et al., 2019), it remains largely unknown if these same factors influence pathogen prevalence or defecation rates on crops (Figure 1b,d). Some evidence suggests that farms embedded within landscapes
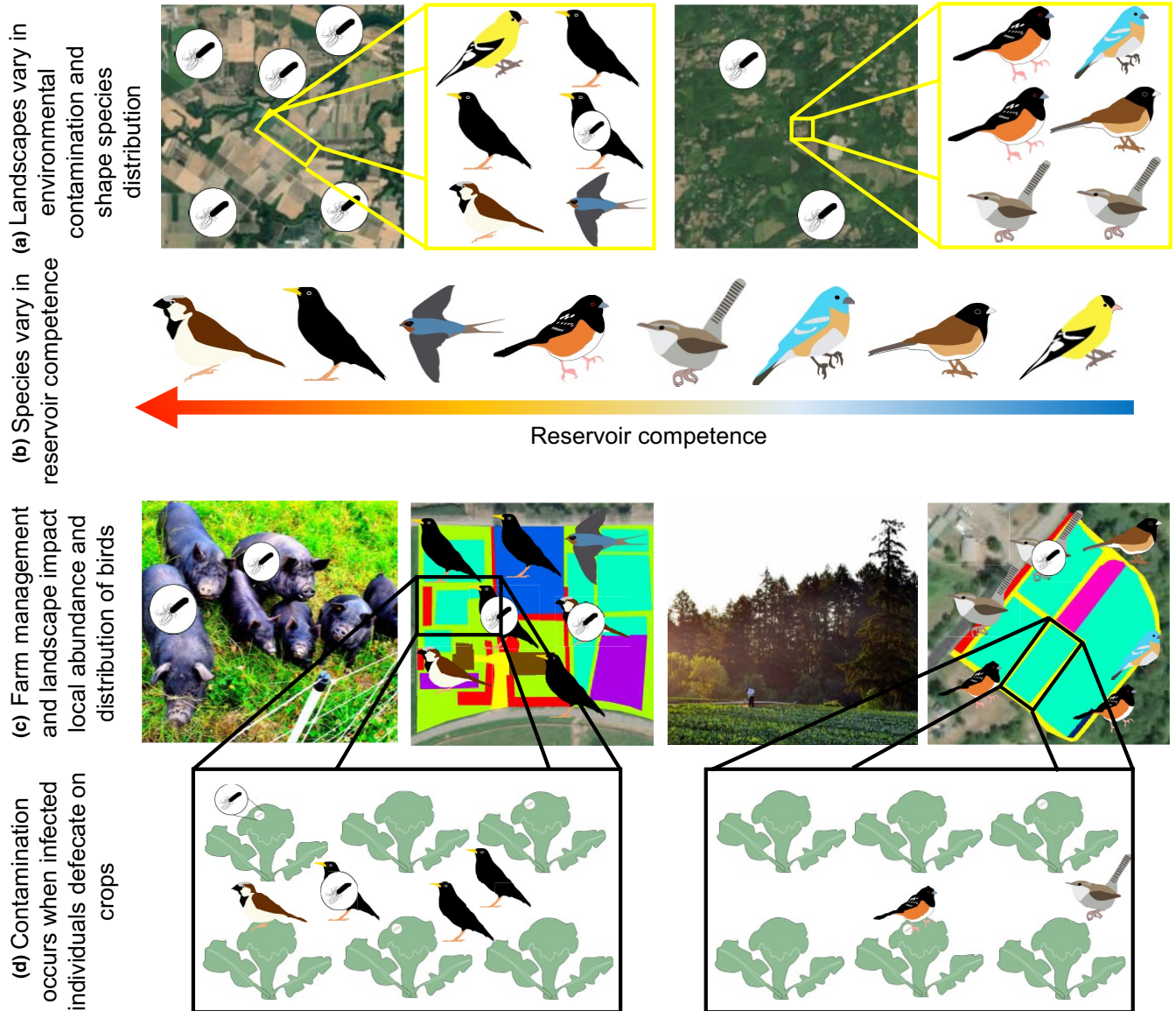
FIGURE 1 Conceptual overview of how landscape context and on-farm crop–livestock integration could impact spillover of foodborne pathogens from birds. (a) Landscape with high % agriculture (left) and high % natural (right) with bird communities found in this study. These landscapes have variable amounts of pathogen in the environment and different bird communities. (b) Bird species vary in reservoir competence from low (blue) to high (red). (c) Farm management can alter abundances of species on-farm and pathogen exposure near crops. Abundances and identities of bird species differ on farms with livestock (left) and without livestock (right). (d) Birds must defecate on crops to cause spillover which may be influenced by farm management and foraging traits. Colour coding in (c): red = hedge, purple = woody crop, yellow = road, lime = grass, brown = structure, blue = livestock, pink = cover crop, navy = flowers, teal = row crop

with large amounts of grazing land have greater foodborne pathogen prevalence in water and on produce compared to those embedded in landscapes with more natural habitat (Benjamin et al., 2013; Karp et al., 2015). Therefore, birds inhabiting farms embedded within landscapes with greater environmental pathogen prevalence, such as those with high contamination of livestock waste, may be more likely to encounter foodborne pathogens (Figure 1a; Hald et al., 2016; Hernandez et al., 2016). At the same time, landscapes with high densities of livestock may attract more competent reservoir host species (Figure 1a,b; Smith, Snyder, et al., 2020). Additionally, on-farm crop–livestock integration could increase the likelihood of spillover by both increasing the overall

bird community competence and by altering contact rates between birds, livestock hosts and produce (Figure 1c,d). Despite these hypothesized relationships, it remains unclear to what degree landscape context and farm management practices mediate the likelihood of bird communities contaminating crops.

Here, we examine the roles of landscape context and on-farm crop–livestock integration in the likelihood of spillover of foodborne pathogens from birds to humans in brassica production. We addressed four overarching questions (see Table S1 for further details): (Q1) does landscape context influence bird community composition in production areas? (Figure 1a), (Q2) does foodborne pathogen prevalence vary by bird species? (Figure 1b), (Q3) does

landscape context and/or on-farm crop–livestock integration influence the number of plants with bird faecal droppings? (Figure 1d) and (Q4) does in-field foodborne pathogen prevalence vary by landscape context and/or with on-farm crop–livestock integration? (Figure 1c,d). To answer these questions, we (Q1) sampled birds via point count surveys in agricultural production areas (Figure 2a; Figure S1); (Q2) estimated *Campylobacter* spp., pathogenic *E. coli* and *Salmonella* spp. prevalence in a diversity of avian host species using mist-netting (Figure 2b) and by amplifying the cytochrome c oxidase subunit I (COI) gene in environmental avian faecal samples; (Q3) conducted a survey of frequency of avian faecal droppings on brassica plants and (Q4) tested environmental avian faecal samples collected from production areas for *Campylobacter* spp., pathogenic *E. coli* and *Salmonella* spp. To assess the impacts of landscape context and on-farm crop–livestock integration on each of these, we quantified the surrounding landscape using remotely sensed

data (Figure S2; see Tables S2 and S3 for metrics examined and hypotheses); calculated on-farm mammalian livestock (cattle, horses, pigs, sheep, goats, donkeys and alpacas) and poultry (chickens, turkeys, geese, ducks and guinea fowl) densities; and used these data to examine the influence of landscape context and on-farm crop–livestock integration on number of plants with faecal droppings and pathogen prevalence.

2 | MATERIALS AND METHODS

Across 2 years (2016 and 2017), we surveyed 50 farms spanning the USA states of Washington, Oregon and California, always moving in a south to north transect (Figure 2; Data S1). These farms were located within the Fruitful Rim region where the majority of US fruit and vegetable production is concentrated (Aguilar et al., 2015) and included a wide range of landscape contexts (Table S3). Farms were highly diversified and grew a range of crops including cereals (e.g. corn, wheat, barley), vegetables and melons (e.g. brassicas, leafy vegetables), fruits and nuts (e.g. citrus fruits, grapes, berries, walnuts), oilseed crops (e.g. olives, sunflower), roots (e.g. potatoes), spice crops (e.g. chilies, peppers, fennel), beverage crops (e.g. tea), medicinal crops, commercial flowers, and grasses and fodder crops, among others. The average farm size in this study was 27.9 ha ± 7.14 (*SE*; range 0.44–272.2 ha). In all, 39 of the farms were certified organic while the rest used sustainable practices. Livestock were integrated into farming operations on 29 of the farms in a variety of forms, including full crop–livestock field rotations, use of horses to plow and fertilize fields, and permanent housing outside of crop fields, among other management strategies. Twenty-six farms had poultry during at least 1 year of the study, and the average number of poultry on farms across the surveys was 57 birds ± 15.1 (*SE*; range of on-farm average: 1.5–314 birds). In all, 18 farms kept mammalian livestock, and the average number of mammalian livestock on these farms across the surveys was 29 heads ± 8.5 (*SE*; range of on-farm average: 1.5–100 heads). On-farm data collection included point count surveys, mist-netting, examining brassica plants for bird faecal droppings and collecting faeces from production areas. There were some variations in farms surveyed between sample types due to variation in production, farmer cooperation and number of surveys (see details below).
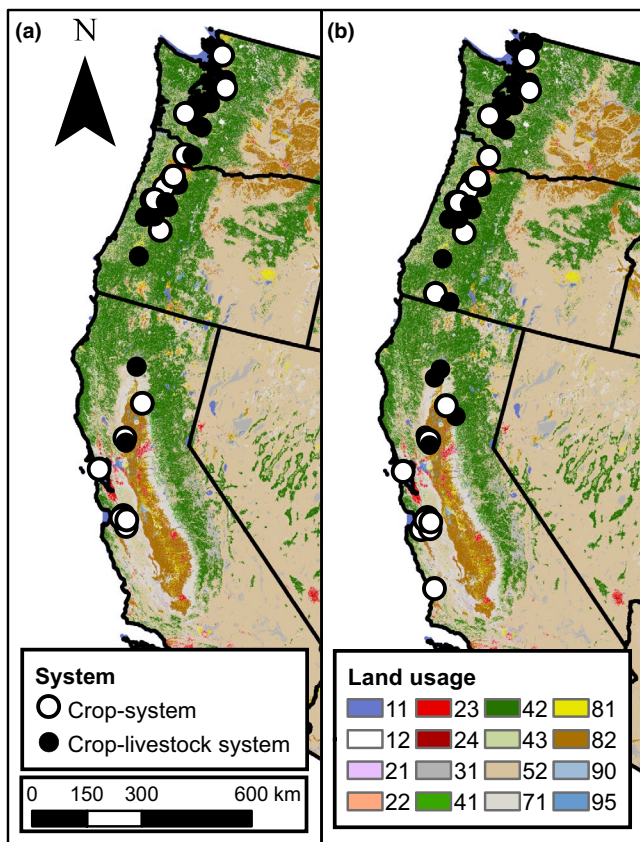

FIGURE 2 Map showing locations of farms included in study. (a) Farms where environmental faecal samples were collected and point counts were conducted and (b) farms where birds were mist-netted. Crop-only farms denoted by open circles and crop–livestock farms denoted by black circles. Land usage from the National Land Cover Database (NLCD) in background. 11 = open water, 12 = perennial ice/snow, 21 = developed/open space, 22 = developed, low intensity, 23 = developed, medium intensity, 31 = barren land, 41 = deciduous forest, 41 = evergreen forest, 43 = mixed forest, 52 = shrub/scrub, 71 = grassland/herbaceous, 81 = pasture/hay, 82 = cultivated crops, 90 = woody wetlands, 95 = emergent herbaceous wetlands

2.1 | Bird surveys

Here, we use a subset of the point count data reported by Smith et al. (2019) corresponding to locations in which we collected environmental faecal samples (see below). Smith et al. (2019) surveyed 232 points across 52 farms, with one additional point surveyed per 4 ha of farmed area. Using these data, we estimated bird community composition at 60 of these point count locations across 37 farms (range = 1–4 points per farm; *M* = 1.6 points) corresponding

to where we collected environmental faecal samples in this study (see Figure S1 for a schematic). Point counts were conducted twice per year between 30 April and 08 August 2016 and 2017. For each survey, we moved in a south–north transect, which we repeated immediately upon conclusion of the first survey. The average number of days between surveys at the same point was 47 days. Points had a fixed radius of 100 m (Smith, Dänhardt, Lindström, & Rundlöf, 2010) and were placed at least 200 m apart (range = 200–1,301 m; M = 348 m). If individuals were observed at multiple points, they were only counted once. Point counts were conducted between sunrise and 5 hr after sunrise, only in the absence of heavy rain. If structures interfered with visual detectability of birds, the observer (always OMS) moved within survey points to see around structures (Šálek et al., 2017). We recorded all individuals seen or heard within points in a 10-min period, denoted the primary habitat type individuals were in (e.g. row crops, orchard, livestock, hedge), and marked if individuals were observed foraging in or above broccoli and kale plots. Individuals flying over sites were excluded from analyses, but aerial foragers (swallows, swifts) were included with a note 'aerial foraging' and included in analyses (Šálek et al., 2017). We used the survey point as the unit of replication due to the variable number of points surveyed per farm, corresponding to where faeces were collected. We additionally conducted point count surveys at three points across two feedlots in California twice per year in 2016 and 2017 following the same protocol to generate a list of birds that interact with high-intensity cattle production.

2.2 | Faecal sample collection directly from birds

We collected fresh faecal samples from live mist-netted birds to assess prevalence by species (Data S2). We tested 2,042 faeces for pathogens from a total of 2,024 birds from 47 farms captured between 27 April and 18 September 2016 and 03 May–29 August 2017 (Figure 2b). In 2016, birds were sampled from 23 crop-only farms and 20 crop–livestock farms in California (n = 11), Oregon (n = 17) and Washington (n = 15). In 2017, birds were collected from 17 crop-only farms and 24 crop–livestock farms in California (n = 13), Oregon (n = 16) and Washington (n = 12). We visited farms in a south–north transect and generally visited each site twice per year, but variation occurred due to weather and grower schedules. We placed 4–8 mist-nets around farms in locations selected to maximize capture rates and moved nets if capture rates were low and high activity was noted in another location (Figure S1). We placed 46% of all nets in but near the edge of semi-natural habitats (e.g. forest edge, hedges), 26% in but near the edge of agricultural areas (e.g. brassicas, orchard, vineyard, livestock), 13% in the interior (>5 m from edge) of semi-natural habitat (max 97 m from farmed areas), 12% in the interior (>5 m from edge) of agricultural areas, and placed the remaining nets in developed areas around the farms. Our eight polyester mist-nets included three that were 30 mm mesh, 2.6 m high and 12 m long (best for warblers, small sparrows, wrens, etc.); three that were 38 mm mesh, 2.6 m high and 12 m long (best for sparrow to jay-sized birds); and two that were 38 mm mesh, 2.6 m high and 18 m long (Avinet). We occasionally placed nets immediately adjacent to each other to create longer nets along habitats with high bird abundances. We used a combination of passive and targeted mist-netting (i.e. call playbacks for territorial species such as members of the Passerellidae and Troglodytidae), with targeted mist-netting primarily used on days with low capture rates in 2016 and on most days in 2017. Upon capture, birds were placed in cloth bags that were washed after use, given unique leg bands, and released. Faeces were placed in 200 proof ethanol in cryotubes and stored in a liquid nitrogen storage tank until shipment to Washington State University on dry ice. Samples were stored at −80°C until DNA extraction.

To extract bacterial DNA from avian faeces, we used QIAamp® DNA stool mini kits (Qiagen) following the manufacturer's stool pathogen detection protocol with the adjustments described in Supplementary Methods to increase DNA yields. Extracted DNA was stored at −20°C until testing. We tested samples for bacteria using PCR (see Table S4 for primer sequences). We tested for *Salmonella* spp. following conventional PCR described in Park et al. (2011). We tested for *E. coli* virulence genes using multiplex PCR assays for *stx1*, *stx2*, *eaeA*, *hlyA* and *saa* following Paton and Paton (1998, 2002). To consider samples positive for Shiga Toxigenic *E. coli*, we required either a positive *stx1* or *stx2* gene (Shiga toxin producing genes) and *eaeA* (intimin attaching and effacing protein gene). We tested for *Campylobacter* spp. using the multiplex PCR developed by Wang et al. (2002), which tests for *Campylobacter jejuni*, *Campylobacter coli*, *Campylobacter fetus* subsp. *fetus* and the *Campylobacter* 23S rRNA gene. We used ExTaq DNA polymerase (Takara Bio USA) for all PCRs. We obtained positive controls of *E. coli* O157, *Salmonella* Typhimurium DT104, *C. jejuni* 81-16, *C. coli* M275, *C. fetus* subsp. *fetus* RM10986 and *C. upsaliensis* 3195 from the Washington State University College of Veterinary Medicine.

2.3 | Prevalence of faecal droppings on plants

To assess prevalence of avian faecal droppings on brassica plants, we examined plants on 41 farms in 2016 and 2017 (Data S3). We did not collect faecal samples found on these plants. We conducted two surveys per farm per year, provided farms had brassica plantings at the time of the survey (109 total sampling events). We gave preference to broccoli and kale due to their structural similarities that impact bird foraging and differ from other brassicas (e.g. stems and leaves on broccoli and kale allow for perching vs. the single head on cabbage does not). Broccoli and kale were also the most consistently grown brassicas on farms across the study. We surveyed other brassica crops if these were not in production or fewer than 10 were available at the time of the survey. Our final surveys included broccoli (n = 72), kale (n = 31), cauliflower (n = 3), chard (n = 1) and multiple brassicas (n = 2). We chose a transect in the middle of a brassica field that was more than five rows from the edge of the field whenever possible. A total of 10 plants were chosen at 5 m intervals. In fields <50 m in length, plants were chosen at evenly spaced

intervals at least 1 m apart. We visually examined leaves for faecal droppings and recorded the number on each plant. To determine the catchment area and bird foraging suitability of plants, we measured the diameter, height (distance from soil to highest point on the plant) and number of leaves. These three metrics were highly correlated (Pearson's $R^2 \geq 0.47$, $p < 0.001$), so we used plant height for analyses since it had the largest correlation with both variables (Pearson's $R^2 = 0.56$ and 0.72 for number of leaves and width, respectively).

2.4 | Faecal sample collection from brassica fields and food wash/packing areas

We collected environmental faecal samples from brassica fields and food wash/packing areas from 7 June to 8 August 2016 (Figure 2a; Figure S1; Data S4). Samples were collected from 18 crop-only farms and 19 crop–livestock farms in California ($n = 8$), Oregon ($n = 12$) and Washington ($n = 16$) and collected in a south–north transect. We collected faeces from all types of scat encountered including from birds ($n = 1,215$), domestic ducks ($n = 2$), rodents ($n = 7$), rabbits ($n = 3$), a lizard ($n = 1$) and dogs ($n = 2$). Due to the low encounter rate of non-avian faeces, we do not present results in main text and refer the reader to Table S5 for these data. We collected up to 30 faecal deposits from birds per brassica field ($n = 862$) and per food wash/packing area ($n = 349$) on each farm and all faeces encountered from other animals ($n = 15$). We collected faeces from throughout all brassica patches in production at the time of the survey and throughout food wash/packing areas until we collected our quota of samples or searched the entire area. We again gave preference to collection on broccoli and kale plants but collected faeces from cauliflower or brussels sprouts if broccoli and kale were not in production. We gave preference to samples found on leaves ($n = 86$) but also collected samples under plants ($n = 765$) since droppings on leaves were rare. Food wash/packing areas included open structures with a roof ($n = 23$), closable barns ($n = 13$), exposed tables ($n = 5$), farm stands ($n = 4$) and moving carts ($n = 3$), while two farms had no structures and used the lawn. Upon collection, faeces were placed in 200 proof ethanol in cryotubes, stored and tested for bacteria as described above for mist-net faecal samples. Additionally, we followed the protocol described in Joo and Park (2012) to identify bird species that defecated the samples collected from fields and food wash/packing areas using the COI gene and Sanger sequencing, except that we did not include the plasmid insertion and cloning steps.

2.5 | Landscape classification

We used the bird community weighted average home range size (2.1 km in this study) as our landscape scale (Jackson & Fahrig, 2015). We used home ranges listed in Birds of North America Online (Rodewald, 2015). To calculate the weighted home range size, we used species relative abundances from our point count surveys as the weight (Jackson & Fahrig, 2015). We used the National Land Cover

Database (NLCD) to calculate per cent natural/semi-natural habitat ('natural'), per cent urban/developed, per cent water, natural habitat configurational heterogeneity (spatial arrangement of cover types, e.g. fragmentation) and natural habitat compositional heterogeneity (number and proportions of different cover types) using Program R and FRAGSTATS 4.1 (see Tables S2 and S3 for hypotheses and metric descriptions/calculations, respectively; McGarigal & Marks, 1994; R Core Team, 2018). We used Shannon's habitat diversity index (SHDI) and contagion as our metrics of compositional and configurational heterogeneity, respectively. We initially collected data on five and three metrics representing configurational and compositional heterogeneity, respectively (Table S3), and narrowed these down to one metric each to avoid spurious results. To do so, we first examined pairwise correlations (Figures S3 and S4) and the spread of values across farms then ran each of our model sets with the variables not included to determine robustness of results, which were qualitatively similar. We gathered data on landscape livestock density using the Gridded Livestock of the World Database (Gilbert et al., 2018). We recorded the abundance of each livestock species present on farms and farm size to calculate an on-farm livestock density for mammalian livestock and poultry (see Data S1 and Table S3 for summaries). We assessed multi-collinearity among final landscape and farm variables using Pearson's correlation coefficients. Some landscape and farm variables were correlated (Figure S5). Therefore, our evaluation of the effects of landscape and farm metrics on *Campylobacter* spp. prevalence and number of plants with faecal droppings cannot be completely isolated from the effects of collinear variables, such as per cent natural habitat in the landscape and mammalian livestock density.

2.6 | Statistical analysis

To examine how bird species composition varies across the landscape gradient, we calculated the average species abundance observed in each point count location described above. If farms included more than one survey point, we averaged the average point abundances. We then used non-metric multi-dimensional scaling (NMDS) to describe the variation in species composition across a gradient of natural habitat and mammalian livestock density in the landscape. The NMDS was performed in the VEGAN package of program R v 3.4.3 (Oksanen et al., 2019; R Core Team 2018) using a Bray–Curtis dissimilarity matrix.

We summarized prevalence across samples for *Salmonella* spp., *E. coli* genes and *Campylobacter* spp. for mist-net and environmental faecal samples. We summarized prevalence by species for mist-net samples and for species we could identify through COI gene testing for the environmental samples. *Campylobacter* spp. prevalence was similar in avian faecal samples collected in brassica fields and structures ($\chi^2 = 0.59$, $p = 0.44$) and those that appeared dry versus wet ($\chi^2 = 0.52$, $p = 0.47$). Therefore, we pooled all environmental faecal samples for analyses.

To determine the importance of land usage and farm management on the number of plants with avian faecal droppings, we used generalized

linear mixed models via the GLMMTMB package in R (Magnusson et al., 2016) and AIC$_c$ model selection in the BBLME package in R (Bolker, 2017). We used a binomial distribution and logit link function, with the number of plants with a faecal dropping as the response variable. We used survey nested within farm as random effects to account for multiple visits to the same farms. We ran a series of nested models, each of which included one of the seven final landscape variables and their interactions with on-farm mammalian livestock or poultry density. We assessed multicollinearity for all candidate models in the PERFORMANCE package in R and removed models with variance inflation factors above 5 from further consideration (Ludecke, Makowski, & Waggoner, 2020). We ranked models based on AIC$_c$ and identified those that were most well-supported based on a criteria of ΔAIC$_c$ < 2.0 (Burnham & Anderson, 2002). To examine the impacts of landscape context and farm management on *Campylobacter* spp. prevalence, we repeated analyses described above using the number of samples in which we detected *Campylobacter* spp. as the response variable, which we assumed followed a binomial distribution with a logit link function. Because we only collected environmental faecal samples once per farm for 1 year, we did not include a random effect for farm. See Table S6 for a full summary of models run.

3 | RESULTS

3.1 | Shift in composition of avian reservoir hosts across landscape gradients

The NMDS ordination examining bird community composition sampled via point counts resulted in a three-axis solution (stress = 0.14; non-metric fit R^2 = 97.9%; linear fit R^2 = 84.4%). Non-native species such as European starlings *Sturnus vulgaris* and house sparrows *Passer domesticus* and native species such as blackbirds (family Icteridae) and swallows (family Hirundinidae) were associated with less natural landscapes and landscapes with greater mammalian livestock densities. Conversely, native species such as warblers (family Parulidae) and flycatchers (family Tyrannidae) were more common in more natural landscapes (Figures S6 and S7; see Table S7 for species and number of individuals observed).

3.2 | Pathogen prevalence in faeces from birds sampled by mist-netting

We sampled 2,024 individuals representing 76 species through mist-netting across a subset of 47 farms (18 birds were recaptured; see Table S8 for prevalence by species and Table S9 for recapture data; see Figure S8 for relative abundances of captures). We detected no *Salmonella* spp. (*n* = 2,024, Figure S9). Seven PCRs failed in our *E. coli* gene panel, giving us data for 2017 birds. One individual (white-crowned sparrow *Zonotrichia leucophrys*) tested positive for Shiga Toxigenic *E. coli*. We detected *Campylobacter* spp. in 207/2,024 (10.2%) faecal samples [35/76 (46%) of bird species had positive samples]. Non-native species had higher *Campylobacter* spp. prevalence
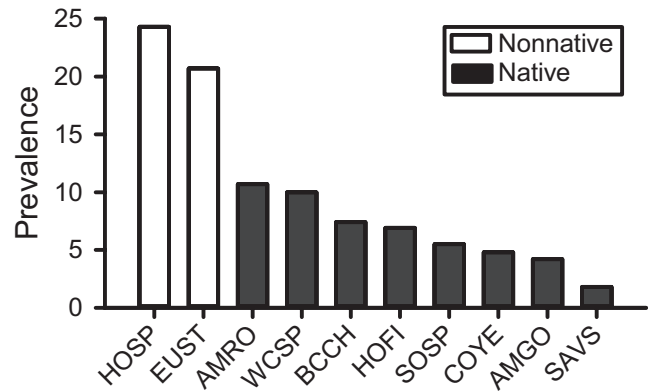

FIGURE 3 *Campylobacter* prevalence for the 10 most-captured species. White, non-native; black, native; HOSP, house sparrow; EUST, European starling; AMRO, American robin; WCSP, white-crowned sparrow; BCCH, black-capped chickadee; HOFI, house finch; SOSP, song sparrow; COYE, common yellowthroat; AMGO, American goldfinch; SAVS, savannah sparrow

than native species [Figure 3; odds ratio = 4.1; β = 1.42 ± 0.58 (*SE*), p = 0.015]. Post hoc analyses found that *Campylobacter* spp. prevalence in species observed in feedlots (Table S10) was higher than species not observed in feedlots [odds ratio = 2.8; β = 1.0 ± 0.35 (*SE*), p = 0.004].

3.3 | Bird species in brassica fields

We observed 104 bird species in point count survey locations (Figure S8, Tables S7 and S11). European starlings, barn swallows *Hirundo rustica* and American robins *Turdus migratorius* were the most abundant across farms and occurred across the most farms. We observed 20 species foraging in/above broccoli and kale fields during our surveys. Barn swallows, violet-green swallows *Tachycineta thalassina* and Vaux's swifts *Chaetura vauxi* were the most common. Some species were only observed in hedges or other semi-natural margins, such as willow flycatcher *Empidonax traillii* and orange-crowned warbler *Leiothlypis celata*. We were able to determine a bird species identity in 463/1,215 (38.1%) of the environmental faecal samples using our COI gene identification and identified 35 species (Table S12). White-crowned sparrows, song sparrows (*Melospiza melodia*) and house sparrows were the most frequently identified species through COI testing. *Campylobacter* spp. prevalence was similar between samples in which we were able to identify species [57/463 (12.3%)] compared to those that we could not [103/752 (13.7%); χ^2 = 0.48, p = 0.49].

3.4 | Prevalence of faecal droppings on plants

Avian faeces were found on 36/1,086 (3.3%) brassica plants examined from 2016 to 2017 across 41 farm locations. We found that the interaction between chicken density in the landscape and on-farm

mammalian livestock density was the best predictor of finding avian faecal droppings on brassica plants, when accounting for variation in plant height (Figure S10a; Table S13). Farms with mammalian livestock that were embedded in landscapes with lower chicken densities and farms without mammalian livestock embedded in landscapes with high chicken densities had the highest probability of plants with faecal droppings. Conversely, farms with mammalian livestock that were embedded in landscapes with high chicken densities had the lowest probabilities. The second-best model included plant height and on-farm mammalian livestock density ($\Delta AIC_c = 1.4$; Figure S10b). Plant height [$\beta = 0.052 \pm 0.022$ (SE), $p = 0.017$] and on-farm mammalian livestock density [$\beta = 0.55 \pm 0.25$ (SE), $p = 0.021$] were both positively correlated with finding faecal droppings on plants. All other models had ΔAIC_c values >2 compared to the top-ranked model.

3.5 | Pathogen prevalence in environmental bird faeces from production areas

We tested 1,215 avian faecal samples for foodborne pathogens that were collected from brassica fields and food wash/packing stations across a subset of 37 farms. We detected *Salmonella* spp. in 3/1,215 (0.2%) faecal samples (Figure S9; Table S14). We did not detect *saa* (Shiga Toxigenic *E. coli* autoagglutinating adhesion gene), *stx1* or *stx2* genes. We detected *eaeA* in 11/1,215 (0.9%) and *hlyA* (cytolytic pore-forming toxin produced by enterohemorrhagic *E. coli*) in 5/1,215 (0.4%) faecal samples. We detected *Campylobacter* spp. in 160/1,215 (13.1%) avian faecal samples. We detected *C. coli* in 6.0%, *C. jejuni* in 6.7%, both *C. coli* and *C. jejuni* in 3.2%, and *C. fetus* subsp. *fetus* in 4.4% of samples.

3.6 | Impact of landscape context and farm management on pathogen prevalence in environmental faecal samples

Because *Salmonella* spp. and *E. coli* virulence genes were rarely detected, we did not assess local or landscape factors impacting their prevalence. Per cent natural habitat in the landscape was the best predictor of *Campylobacter* spp. prevalence (Figure 4a; Table S15). Per cent natural habitat was inversely correlated with *Campylobacter* spp. prevalence [$\beta = -0.011 \pm 0.004$ (SE), $p = 0.006$]. For every 1% decrease in natural habitat, the odds of recovering *Campylobacter* spp. increased by 1.1%. Mammalian livestock density in the landscape was the second-best predictor ($\Delta AIC_c = 1.0$, Table S15) and was positively correlated with prevalence [$\beta = 0.033 \pm 0.012$ (SE), $p = 0.006$]. For every 1 unit increase in mammalian livestock density (livestock/km^2), the odds of recovering *Campylobacter* spp. increased by 3.3%. The model containing per cent natural habitat in the landscape and on-farm poultry density was the third-most supported ($\Delta AIC_c = 1.2$, Table S15), but the top model containing only per cent natural
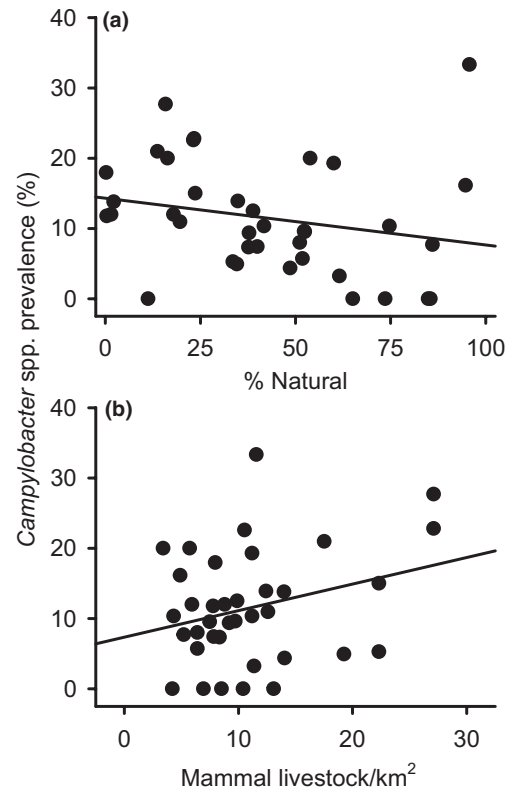

FIGURE 4 *Campylobacter* prevalence in environmental faecal samples versus (a) % natural habitat and (b) mammalian livestock density (livestock/km^2) in the landscape. Points represent prevalence across samples per farm
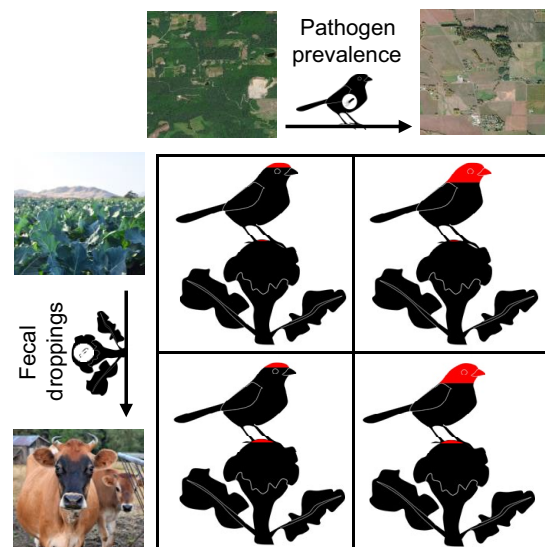

FIGURE 5 Diagram depicting likelihood of food pathogens contaminating brassicas from wild birds along two axes: pathogen prevalence and number of plants with wild bird droppings. *X*-axis shows predicted prevalence (depicted by song sparrow silhouette) from the most natural landscape to the least natural landscape. *Y*-axis shows predicted number of plants with faecal droppings (depicted with broccoli silhouette) from crop-only farms to those with integration of mammalian livestock. Red region shows predicted prevalence and number of faecal droppings calculated as bird and plant height, respectively × probability

habitat in the landscape was fully nested within this model, and on-farm poultry density was not significant [$\beta = -0.0082 \pm 0.0082$ (*SE*), $p = 0.32$], suggesting it was not an important predictor. All other models had ΔAIC_c values >2 compared to the top-ranked model containing only per cent natural habitat in the landscape. Finally, we calculated the probability of a brassica plant having an avian faecal dropping with *Campylobacter* spp. by multiplying the percentage of plants with faecal droppings (3.3%) by the average *Campylobacter* spp. prevalence in our environmental faecal samples (13.1%; Figure 5). Thus, the probability of a brassica plant in our study having a faecal dropping with *Campylobacter* spp. is estimated to be 0.4%.

4 | DISCUSSION

Disentangling the relationships between landscape context, farming practices and spillover of foodborne pathogens from wildlife is important for balancing food safety, bird conservation and ecosystem service provisioning in agroecosystems. Our central goal was to determine how the risk of spillover of foodborne pathogens from birds is affected by landscape context and farming practices. *Campylobacter* spp. prevalence in bird faeces from production areas declined with increasing amounts of natural habitat surrounding farms (Figure 4a; Table S15), contrary to frequent assumptions (Beretti & Stuart, 2008; Karp et al., 2015; Olimpi et al., 2019). Conversely, intensified mammalian livestock production in the landscape increased *Campylobacter* spp. prevalence in bird faeces collected from production areas (Figure 4b).

Per cent natural habitat in a landscape was recently shown to decrease environmental *E. coli* levels (Karp et al., 2015), and birds foraging in more natural landscapes may be less likely to encounter pathogens than those foraging in more simplified or intensified landscapes (Hernandez et al., 2016). Several studies have found increased prevalence of foodborne pathogens in environments in close proximity to livestock production (Benjamin et al., 2013; Karp et al., 2015; Park et al., 2013), and a recent meta-analysis (Rossler et al., 2019) found greater *C. jejuni* prevalence in cattle in intensified production systems relative to cattle in more extensified systems. Moreover, birds foraging closer to livestock have been found to have higher *Campylobacter* spp. prevalence than those foraging further away, likely from greater environmental exposure (Hald et al., 2016). Accordingly, intensification of mammalian livestock production around farms might expose birds to more pathogens, thereby increasing food safety risks (Rossler et al., 2019).

Interestingly, we found no evidence for increased pathogen prevalence in bird faeces on farms that integrated livestock. The extensified, small-scale livestock production on farms in our study might have decreased environmental runoff alongside decreased pathogen prevalence in the livestock compared to their counterparts in more intensified systems (Gerber, Chilonda, Franceschini, & Menzi, 2005; Rossler et al., 2019). Conversely, the large daily movements of many

bird species, such as European starlings and native blackbirds (Gaulker, Homan, George, & Bleier, 2012; Heisterberg, Knittle, Bray, Mott, & Besser, 1984), may increase the importance of landscape-scale live-stock intensification relative to on-farm livestock integration for pathogen prevalence dynamics because highly mobile organisms can acquire and disseminate pathogens across large distances. On-farm livestock integration may, therefore, primarily influence food safety risks through greater attraction of birds to farms, which could increase the number of plants with faeces (Smith et al., 2019). Despite our finding that farms with on-farm mammalian livestock had slightly increased numbers of plants with faeces, only 3.3% of plants examined had faecal droppings, and we estimated only 0.4% of plants would have an avian faecal dropping with *Campylobacter* spp.

The increased pathogen prevalence in bird faeces collected from farms surrounded by intensified mammalian livestock production and little natural habitat may reflect a shift in the bird community towards competent reservoirs, including non-native species (Figure 3; Figures S6 and S7; Smith et al., 2019; Smith, Snyder, et al., 2020). *Campylobacter* spp. were 4.1 times more likely to be detected in non-native species compared to native species in our study. This could be driven by several factors including association with more simplified or intensified landscapes with higher environmental pathogen prevalence (Karp et al., 2015), behaviours that increase contact with animal waste (e.g. foraging in feedlot grain bins), large daily movements, fast life-history strategies and gregariousness (e.g. greater contact with conspecific faeces; Barron, Gervasi, Pruitt, & Martin, 2015; Carlson et al., 2011; Gaulker et al., 2012; Heisterberg et al., 1984; Ostfeld et al., 2014; Rodewald, 2015; Smith et al., 2019; Smith, Snyder, et al., 2020). Our analysis including both native and non-native species observed foraging in feedlots suggested other feedlot foraging species may also be competent hosts. For example, native brown-headed cowbirds *Molothrus ater* had a *Campylobacter* spp. prevalence of 46.3% (*n* = 54) and exhibit similar behaviours to non-natives including frequently foraging among cattle, having large daily movements between feedlots and breeding sites and congregating in large flocks (Rothstein, Verner, & Steven, 1984).

We tested 76 bird species for *Campylobacter* spp., of which 57 (75%) had no previous reports in the literature (Smith, Snyder, et al., 2020). We detected *Campylobacter* spp. in 35 of the 76 species, of which 29 (82.9%) have not been previously confirmed reservoirs in the literature. We found a lower average *Campylobacter* spp. prevalence in both our environmental faecal samples (13.1%) and mist-net samples (10.2%) than Smith, Snyder, et al. (2020) found in their meta-analysis collating prevalence estimates across species (27%), including their estimate for passerines (28%), which formed the majority of our samples. The estimate reported by Smith, Snyder, et al. (2020) was likely inflated due to the majority of past research focusing on a small number of synanthropic species. For example, Hald et al. (2016) found an overall *Campylobacter* spp. prevalence of 20.0% on livestock farms, with the highest prevalence in thrushes (61.8%) and *Passer* sparrows (21.3%). Sanad, Closs, Kumar, and Lejeune (2013) found a high *Campylobacter* spp. prevalence of 50.4% in European starlings on cattle feedlots. As

another example, Taff et al. (2016) found a high prevalence of *C. jejuni* (53%) in urban American crows. This suggests extrapolation of food safety risks from studies conducted in systems such as intensive feedlots or urban areas (e.g. Colles et al., 2009; Sanad et al., 2013; Taff et al., 2016) are likely to inflate the perceived risk that birds pose to produce safety. Conversely, our data suggest that many native species may be misperceived as non-reservoirs due to lack of data. For example, American robins were previously unconfirmed *Campylobacter* spp. reservoirs (Smith, Snyder, et al., 2020) and had a prevalence of 10.7% in our study. More work is needed to elucidate the reservoir competence of the whole bird community, as well as to identify if particular species play disproportionate roles in transmission (i.e. 'superspreaders' or 'supersponges', Barron et al., 2015). Further, our point count data suggest that some insectivorous species, such as warblers (Parulidae) and flycatchers (Tyrannidae), rarely use crop fields (Table S7). This suggests that farmers interested in promoting pest control services may be able to do so with a low risk of crop contamination by selectively targeting some native insectivores that can control pest source populations in adjacent semi-natural habitat, limiting pest immigration to fields (Tscharntke et al., 2012).

Our results suggest that produce production in more natural landscapes and spatiotemporal separation of produce and livestock production could lower the risk of spillover of foodborne pathogens from birds. Conversely, produce farming in landscapes with high-intensity livestock production likely comes with the greatest risks. Although we found no evidence that on-farm crop–livestock integration increased pathogen prevalence in bird faeces, it may increase the number of plants with faecal droppings (Smith et al., 2019). Therefore, farmers need to think critically about the configuration of crop–livestock rotations and the logistics of on-farm animal integration. Broadening the temporal and physical space between crop and livestock production may reduce risk, and planting crops likely to be cooked before consumption adjacent to livestock production may help lower risk (Karp et al., 2015).

Farmers of fresh produce are increasingly facing conflicting demands to improve environmental sustainability while meeting 'buyer agreements' that require actions such as removal of wildlife habitat. These 'buyer agreements' are assumed to improve food safety but are based on few data, including a few sensationalized outbreaks linked to wildlife (Beretti & Stuart, 2008; Gardner et al., 2011; Karp et al., 2015; Smith, Snyder, et al., 2020). Importantly, our finding that *Campylobacter* spp. prevalence declines when farms are surrounded by more natural habitat suggests that actions taken towards Sustainable Development Goals, such as wildlife conservation, may align with efforts to reduce foodborne pathogen spillover from wildlife (Karp et al., 2015).

AUTHORS' CONTRIBUTIONS
O.M.S., A.E., J.M.T., M.S.J., C.M.K., A.T., J.P.O. and W.E.S. conceived the work and designed the study; O.M.S., A.E., L.A.M., C.S., J.M.T. and A.T. collected the data; O.M.S. and C.E.L., wrote code for analyses and landscape classification, respectively; O.M.S. created figures and analysed data with assistance from T.N.; O.M.S. led the writing of the manuscript; and O.M.S., A.E., J.M.T., M.S.J., A.T., C.M.K., Z.F., C.E.L., K.A.C., T.N., W.E.S. and J.P.O. revised the manuscript. All authors gave final approval for publication.

DATA AVAILABILITY STATEMENT
Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.z8w9ghx8z (Smith, Edworthy, et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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