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Terrestrial landscape impacts the biogeographic pattern of soil *Escherichia coli* via altering the strength of environmental selection and dispersal

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Running Head: Effects of landscape on the distribution of *E. coli*

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ABSTRACT High-quality habitats for wildlife (e.g., forest) provide essential ecosystem services while increasing species diversity and habitat connectivity. Unfortunately, presence of such habitats adjacent to produce fields may increase risk for contamination of fruits and vegetables by enteric bacteria, including *Escherichia coli*. *E. coli* survives in extra-host environments (e.g., soil) and could disperse across landscapes by wildlife. Understanding how terrestrial landscapes impact the distribution of soil *E. coli* is of importance in assessing the contamination risk of agricultural products. Here, we compared the distribution of *E. coli* isolated from soils from two watersheds with different landscape patterns in central New York, USA, and examined the influences of two ecological forces - environmental selection and dispersal - on the distribution of *E. coli*. Results showed that for the watershed with widespread produce fields, sparse forests, and limited interaction between the two land types, *E. coli* composition was significantly different between produce field and forest; this distribution was shaped by relatively strong environmental selection likely triggered by soil phosphorus and antimony. For the watershed with more forested areas and stronger interaction between produce field and forest, *E. coli* composition between these two land types was relatively homogeneous; this distribution was a consequence of weak selective pressure potentially from soil moisture and wildlife-driven dispersal by small flocking insectivore/granivores and large nuisance wildlife, which were identified as potential vehicles by competing models. Collectively, our results suggest that terrestrial landscape could drive the biogeographic pattern of enteric bacteria by adjusting the balance between environmental selection and dispersal.

IMPORTANCE Understanding the ecology of enteric bacteria in extra-host environments is important to allow for development and implementation of strategies to minimize pre-harvest contamination with enteric pathogens. Our findings suggest that watershed landscape is an important factor influencing the ecological drivers and transmission pattern of *E. coli*. For watersheds with widespread produce fields, *E.*

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coli appears to experience local adaptation, likely due to exposure to environmental stresses possibly associated with agricultural activities. In contrast, for watersheds with high forest coverage we found evidence for wildlife-driven dispersal of *E. coli*, which might facilitate more frequent genetic exchange in this environment. Agricultural areas in such watersheds may have a higher risk of produce contamination due to less environmental constrains and higher potential of transmission of enteric bacteria between locations. The significance of our research lies in exploring ecological principles underlying the biogeographic pattern of enteric bacteria at the regional level, which can inform agricultural, environmental and public health policies that aim to reduce the risk of food contamination by enteric bacteria.

KEYWORDS enteric bacteria, landscape, environmental selection, dispersal, wildlife

INTRODUCTION

Forests and other riparian buffers can provide ecological benefits (e.g., reducing soil erosion and leaching of chemical and fecal waste into ground water sources, providing habitat and connective pathways for wildlife) as well as aesthetic benefits (1–3). While high quality habitats (e.g., forest) offer conservation services, they may also bring unintended consequences and may increase the risk of pre-harvest contamination of produce crops. For one, extra-host environments, such as soil in high quality habitats, can be critical reservoirs for enteric bacteria, leading to potential transmission of enteric bacteria to adjacent agricultural regions (4). Direct fecal deposition onto produce by wildlife is another source of enteric bacteria in agricultural regions (5). By providing wildlife movement pathways, high quality habitats may facilitate the wildlife-driven dispersal of enteric bacteria through riparian buffers to adjacent agricultural regions, possibly resulting in contamination of food crops (6–9). Subsequent persistence and regrowth of the pathogenic enteric bacteria introduced in fresh produce would then lead

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to a food safety risk (10). Since the survival of enteric bacteria and movement of wildlife vary by land use types (11, 12), it is reasonable to hypothesize that watershed landscape impacts the distribution of enteric bacteria.

Environmental selection and dispersal are two fundamental ecological forces that drive the distribution of bacteria (13–16). The essential roles of environmental selection via abiotic (e.g., pH, salinity) and biotic selective pressures on bacteria have been well documented in many local and even global habitats (17–20). Environmental selection could facilitate the genetic divergence of some ecophysiological traits owing to their contribution to fitness benefits for adaptation of bacteria to diverse habitats, such as those with different land cover types (21, 22). With the influence of environmental selection, a high level of bacterial diversity can be maintained among locations in a wide range of environments (15, 23, 24). The role of dispersal in driving the distribution of bacteria at local as well as regional scales is evident since dispersal provides a mechanism for bacteria to colonize new habitats (25, 26). Its importance on the distribution varies among microbial taxa due to diversity in the capacity of bacteria to disperse via wind, water, and wildlife. For example, bacteria with a highly successful dispersal capacity (e.g., *Polaromonas*) tend to exhibit a more global distribution (27), while bacteria with a poor dispersal capacity (e.g., *Rhizobiaceae*, *Bradyrhizobiaceae*, *Xanthomonadaceae*) tend to have a more specialized distribution (15). Importantly, wildlife presence and movement is fundamentally affected by the physical elements and features of land (15). Thus, wildlife-driven dispersal of bacteria. can be quantitatively predicted by landscape ecological methods based on the relationship of wildlife behaviors and landscape characteristics (e.g., patchiness, land-use interspersion, patch connectivity, patch diversity, and land-use interactions) (8, 28–30). Based on these principles, investigating environmental selection and dispersal of enteric bacteria from and within habitats with distinct landscape patterns has the power to elucidate the role of terrestrial landscapes in impacting the

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distribution of enteric bacteria and assess the associated risk of preharvest contamination of food by pathogenic enteric bacteria.

As a commensal and pathogenic enteric bacterium widespread in diverse habitats, *Escherichia coli* primarily resides in the intestines of warm-blooded animals, and survives in extra-host environments such as water, soil, sediments as well (31, 32). Soil is a habitat of particular interest for *E. coli*, since the high chemical and physical heterogeneity of soil across different environments could pose environmental selection of varying strengths on *E. coli* (22, 23, 32). Observations that the prevalence of *E. coli* varies by land cover types (e.g., deciduous forest, cropland, pasture) (22), also suggests that different land uses could stimulate different types and intensities of selective pressures that act on *E. coli*. The key edaphic variables influencing the growth of *E. coli* in soil are commonly recognized as pH and moisture (23, 33), while some other soil properties such as organic matter and texture could also play a role (10). In addition, wildlife, such as avian species and ruminant animals, could act as dispersal vehicles of *E. coli* (34, 35). *E. coli* can also be transmitted between wildlife hosts through contact and can be deposited in new locations (e.g., produce fields) by defecation, which often happens when wildlife forages for food (36). Given the intensive interaction with both extra-host and host habitats, *E. coli* may be an useful model for the mechanistic understanding how terrestrial landscape affects the distribution of enteric bacteria overland. Such an understanding is particularly important for land with agricultural environments present, as it could be used to develop better strategies for minimizing pathogen introduction into preharvest environments, particularly those used to grow produce and fruits.

We hypothesize that the importance of environmental selection and dispersal for the distribution of *E. coli* is dependent on landscape; *E. coli* in watersheds with higher coverage of agricultural environments is strongly driven by environmental selection associated with agricultural activity, while *E. coli* in regions with higher coverage of natural environment is largely influenced by wildlife-driven

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dispersal. To test our hypothesis, we characterized 938 commensal *E. coli* isolates obtained from soil samples collected from two watersheds - Flint Creek and Hoosic River, both located in the central New York region, using a hierarchical multi-locus sequence typing (MLST) scheme. These two watersheds represent an interesting comparison between one with widespread produce fields and limited interaction between produce fields and forest (Flint Creek; 69% produce field, 12% forest by area; $adjacency_{produce|forest}$ = 23%; Fig. 1a) and one with heavily forested areas and strong interaction between produce fields and forest (Hoosic River; 28% produce field, 38% forest by area; $adjacency_{produce|forest}$ = 36%; Fig. 1b). Next, we quantitatively assessed the importance of environmental selection via abiotic pressure from soil and dispersal limitation for *E. coli* in these two watersheds. Last, we developed dispersal models for four wildlife vehicle candidates (large nuisance wildlife species, small mammals, small flocking insectivore/granivores, and migratory bird flocks) to understand the role of wildlife-driven dispersal for *E. coli*.

RESULTS

Distribution of *E. coli.* Soil samples from Flint Creek (predominated by produce fields) showed considerably lower prevalence of *E. coli* than soil samples from Hoosic River (predominated by forests); 35% and 72% of soil samples, respectively, were positive for *E. coli* in these two watersheds. These samples yielded 289 and 649 *E. coli* isolates, respectively. Based on initial 2-gene MLST (*mdh* and *uidA*), a total of 138 isolates from Flint Creek and 277 isolates from Hoosic River were selected for characterization by full 7-gene MLST (*aspC*, *clpX*, *icd*, *lysP*, *fadD*, in addition to *mdh* and *uidA*). The 7-gene MLST generated 122 unique multilocus sequence types (ST) for Flint Creek and 181 unique ST for Hoosic River (Table S1, Table S2). Analysis by goeBURST identified 96 and 108 *E. coli* clonal groups for Flint Creek and Hoosic River, respectively, based on ST at single locus variant level (Fig. S1, Fig.

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S2). While *E. coli* clonal group richness did not differ significantly between forest sites and produce field sites for both watersheds, for Flint Creek, forest sites had slightly higher mean richness of *E. coli* clonal groups than produce field sites, while for Hoosic River the pattern was opposite (Fig. S3).

E. coli in the two watersheds displayed distinct distribution patterns. For Flint Creek, principal coordinates analysis (PCoA) based on the similarity of *E. coli* clonal groups clustered sampling sites by land-use; PERMANOVA showed that this clustering is significant ($p < 0.05$; Fig. 2a, Table S3). By contrast, the sampling sites were not significantly clustered by land-use in PCoA for *E. coli* clonal groups from Hoosic River (PERMANOVA $p = 0.63$; Fig. 2b, Table S3), indicating a more homogeneous composition of *E. coli* between produce field and forest in this watershed.

Key soil variables shaping the distribution of *E. coli.* Moisture, pH, sodium, phosphorus, barium, manganese, and antimony were included in the canonical correspondence analysis (CCA), after screening for high levels of covariation (Table S4). CCA revealed different key soil variables driving the distribution of *E. coli* clonal groups in the two watersheds. Phosphorus and antimony were identified as the key soil variables ($p < 0.1$) shaping the distribution of *E. coli* clonal groups in Flint Creek, with each explaining about 10% of the biological variation (Table 1). For Flint Creek, mean phosphorus and antimony content were higher for soil samples from produce field sites as compared to samples from forest sites; the difference was significant for phosphorus content, but not for antimony content (Fig. S4a; Fig. S4b). Moisture was identified as the key soil variable ($p < 0.1$) shaping the distribution of *E. coli* clonal groups in Hoosic River, explaining 8.7% of the biological variation (Table 1); mean moisture of soil samples from forest sites was slightly higher than mean moisture of samples from produce sites (Fig. S4c). Overall, 20.3% of variation of *E. coli* clonal group dissimilarity between sites was explained by soil variables in Flint Creek, which suggests a more important role of environmental selection for *E. coli* from Flint Creek compared to Hoosic River (8.7% biological variation explained).

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Dispersal limitation of *E. coli*. To infer dispersal limitation. we assessed the relationship between biologic dissimilarity of *E. coli* and geographic distance. Mantel tests showed a weakly significant correlation between the dissimilarity of *E. coli* clonal groups and geographic distance in Flint Creek (r = 0.16, p = 0.08). By contrast, no significant correlation was observed between the dissimilarity of *E. coli* clonal groups and geographic distance in the Hoosic River watershed (r = -0.02, p = 0.56). Linear regression analysis further showed that the dissimilarity of *E. coli* clonal groups in Flint Creek had a very weak linear relationship with geographic distance (Fig. 3a, R^2 = 0.027, slope = 2.7 $\times 10^{-3}$), while there was no evidence of linear relationship between the dissimilarity of *E. coli* clonal groups and geographic distance in Hoosic River (Fig. 3b, R^2 = 0.0005, slope = -2 $\times 10^{-4}$). These results indicate that the dispersal of *E. coli* in Flint Creek was slightly limited, while *E. coli* in the Hoosic River watershed was likely not constrained by dispersal limitation.

Wildlife-driven dispersal of *E. coli*. Four common classes of wildlife vehicles (large nuisance wildlife species, small mammals, small flocking insectivore/granivores, and migratory bird flocks) were selected for identifying potential dispersal vehicles of *E. coli* (characteristics of these dispersal vehicles are detailed in Table 2). By adjusting distances among sampled sites to account for movement preferences of these four types of wildlife vehicles (i.e., cost-distance or landscape resistance modeling), we sought to assess whether dispersal associated with wildlife behavior explains the *E. coli* distribution better than distance alone. As shown in Table 3, the predicted dispersal model was developed based on the most-likely cost model and attraction model selected for each wildlife vehicle according to their characteristics. The predicted dispersal model for small mammals was defined to have a biological riparian corridor effect, no proximity effect, absolute dispersal barriers effect, and no attraction coefficient. The predicted dispersal model for large nuisance wildlife species was defined to have a biological riparian corridor effect, strong proximity effect, porous dispersal barriers effect, and habitat

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quality coefficient. The predicted dispersal model for migratory bird flocks was defined to have a biological riparian corridor effect, weak proximity effect, no dispersal barriers effect, and area independent coefficient. The predicted dispersal model for small flocking insectivore/granivores was defined to have a biological riparian corridor effect, weak proximity effect, absolute dispersal barriers effect, and area independent coefficient. Definition of these effects can be found in Table 2.

Mantel tests showed that none of these dispersal models significantly predicted the composition of *E. coli* clonal groups in Flint Creek ($p > 0.05$), while two wildlife-driven dispersal models – dispersal via large nuisance wildlife species and via small flocking insectivore/granivores – were found to be significantly correlated with the composition of *E. coli* clonal groups in Hoosic River ($r = 0.21$, $p < 0.05$; $r = 0.25$, $p < 0.05$, respectively) (Fig. 4). Small flocking insectivore/granivores and large nuisance wildlife species thus were identified as potential vehicles colonized by *E. coli* in the Hoosic River site. These results indicate that wildlife-driven dispersal played a more important role in shaping the distribution of *E. coli* in Hoosic River than that in Flint Creek. The observation that cost-distance models correlated with the distribution of *E. coli* genotypes in Hoosic River better than geographic distance alone is consistent with some dispersal among sites by the action of wildlife.

DISCUSSION

E. coli has widely been used as an indicator of fecal contamination (37) and potential presence of other pathogenic enteric bacteria in water (38). *E. coli* comprises a wide spectrum of phenotypes including harmless commensal as well as distinct pathogenic variants with the capacity to either cause intestinal or extraintestinal infections in humans and many animals (39). The fecal-oral transmission route of *E. coli* often involves transient presence in extra-host habitats (e.g., surface water, soil, plant surfaces), including produce fields (23). Therefore, understanding the ecology of *E. coli* in extra-host

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habitats will not only provide an improved understanding of *E. coli* interaction with environment, but will also benefit public health by providing knowledge that can be used to minimizing introduction of *E. coli* and possibly other enteric pathogens into preharvest environments.

Environmental stressors such as availability of nutrients and water, presence of toxic molecules, and large alterations in temperature and moisture can impose fitness cost on *E. coli* and other microbes (40). Fragmented landscapes with smaller forest and grassland patches expose surface soil to sunlight and greatly increase daily variation in soil conditions. Reduced forest and grassland cover could also hinder the movement of organisms, bringing negative demographic and genetic consequences (41). Thus, in order to disperse to and survive new habitats, *E. coli* needs to overcome those barriers by maintaining variable survival strategies such as evolving adaptive traits relying on dispersal to rescue local populations. In this scenario, landscape structure imposes constrains on environmental selection and dispersal, which is particularly essential for the transmission of *E. coli* among different extra-host habitats.

To quantitively probe the importance of environmental selection and dispersal in driving the distribution and composition of *E. coli* in soil under the impact of landscape, we compared the biogeographic pattern of *E. coli* isolated from two watersheds with distinct landscape patterns (i.e., Flint Creek, one area with widespread produce fields and limited interaction between produce fields and forest, and Hoosic River, one heavily forested area with strong interaction between produce fields and forest). Our data specifically suggest that in the watershed with widespread produce fields and sparse forest coverage, strong environmental selection caused by soil phosphorus and antimony and slightly limited dispersal may result in potential local adaptation in *E. coli*. In contrast, in watershed with heavily forested areas, weak environmental selection and dispersal facilitated by small flocking insectivore/granivores and large nuisance wildlife may enhance the likelihood of genetic exchange

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among *E. coli* populations, resulting a relative homogeneous composition between forest and produce field. This higher level of homogeneity is consistent with greater interaction between produce fields and forests in the Hoosic River watershed ($adjacency_{produce|forest}$ = 36%) compared to Flint Creek ($adjacency_{produce|forest}$ = 23%).

Agricultural practice involving input of phosphorous and antimony in soil may enhance the selective pressure on *E. coli*. Agricultural activities normally involve cultivation and soil amendments, which could dramatically change soil organic matter and nutrient pools in comparison to undisturbed systems (e.g., forest) (42). Consequently, long-term organic and chemical amendments could dramatically impact the abundance, diversity, and composition of bacterial communities in soil of agricultural land (43). This is because such alteration of soil properties could trigger selective pressures on bacteria, sorting the individuals or traits that better cope with modified soil condition, which has been termed "local adaptation" (23). For example, copper-amendment in agricultural soil has been found to significantly increase the frequency of copper-resistant Gram-negative bacteria (44). Based on the results of our study reported here, agricultural practices may have caused selective pressure on soil *E. coli*, partially resulting in the distinct *E. coli* composition between produce fields sites and forest sites. Consistent with our findings, Dusek et al. (22) observed different population structure of *E. coli* between cropland and forest, with much lower prevalence of *E. coli* in cropland than forest. The diverse lifestyles and phenotypes of *E. coli* strains were thought to be caused by population expansion paired with differential niche adaptation under specific selective pressures in the last 5 million years (39). Our findings suggest agriculture-stimulated selective pressure contributing to the diversification of *E. coli*.

Based on the key soil variables shaping the distribution of *E. coli* in watershed with widespread produce fields we identified, agriculture-stimulated selective pressure on *E. coli* likely came from phosphorus and antimony, though physical soil parameters may have also played a role. Phosphorus is

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one of the soil variables well documented to dramatically change after the conversion of undisturbed systems to agriculture (42, 45). The input of phosphorus in fertilizer and manure to agricultural systems have been reported to often exceed the output in harvested crops (46). Consistently, in this study, phosphorus concentration of soil from produce field sites was significantly higher than that from forest sites. Phosphorus is a critical nutrient for the growth of bacteria and is part of many biomolecules in bacterial cells (e.g., DNA, phospholipids, polyphosphates, and ATP). Phosphorus availability could act as an important selective force driving divergence among bacteria populations. For example, Coleman et al. (21) identified a number of genes encoding functions related to phosphorus acquisition and metabolism (e.g., alkaline phosphatase, a pathway for phosphonate utilization, upregulation during phosphorus-starvation conditions) as significantly enriched in *Prochlorococcus* populations in locations with lower phosphate concentrations in North Atlantic and North Pacific subtropical gyres. Our finding suggests that excessive phosphorus in produce field may also yield selective pressure on *E. coli*, contributing to diversification. However, it is not clear what specific traits the excessive phosphorus may be selecting on *E. coli*. Future studies using comparative population genomics are needed to better understand the adaption of *E. coli* to excessive phosphorus conditions.

Another potential environmental factor acting on soil *E. coli* in watershed with widespread produce fields identified in this study is antimony. Antimony is a toxic metalloid present widely at trace concentrations in natural soil (47, 48). Its concentration could be elevated or even reach contamination threshold in agricultural lands due to human activities (49). For example, application of lead arsenate pesticides in produce field can increase antimony concentration, since antimony is present as a contaminant in the antimony- and arsenic-containing ores used for pesticide manufacturing (50). In some areas, past mining activities, such as exploitation of ore minerals which are frequently present with antimony, arsenic and lead, could be responsible for increased levels of antimony in agricultural fields

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(51, 52). For the areas studied here, though there is no evidence of past mining activity, average antimony concentration was found to be higher for soil from produce fields than forests. A previous study has shown that increased antimony could prevent the growth of *E. coli*, *Bacillus subtilis* and *Streptococcus aureus*, and may affect nitrogen cycle in soil by changing urease activity under neutral pH (53). Microbes including *E. coli* have developed various strategies (e.g., efflux system) to cope with the toxicity of antimony (54, 55). Plasmids contain an operon conferring resistances to antimony as well as arsenate and arsenite salts have been observed in *E. coli* as early as 1980s (56). With the importance of antimony in shaping *E. coli* in watershed with widespread produce fields, *E. coli* in this region might have developed molecular strategies to address antimony stress. However, further functional experiments on the response of relevant soil *E. coli* to antimony would be needed to test this hypothesis. Importantly, our findings suggest that *E. coli* populations found in different watersheds and environments may differ in their adaptive traits, which may impact our ability to control these organisms throughout the food chain.

***E. coli* in a watershed with high forest coverage may experience weak selective pressure from moisture and proximity effect of forest.** In this study, environmental selection tended to be weaker on *E. coli* in watershed with higher forest coverage. This might be because, compared to produce fields, plant cover and shading in forest could moderate perturbations in soil moisture, nutrients and temperature, thus providing a more favorable and stable condition with fewer environmental stressors for *E. coli* (4, 22). As previously proposed (4), soil in undisturbed temperate forest could act as potential habitat for long-period persistent, even resident *E. coli* populations rather than acting as a transient habitat. Albeit *E. coli* may be exposed to fewer or less intense stressors in undisturbed environments, as compared to disturbed ones, some factors such as temperature, moisture and nutrients have been shown to be correlated with *E. coli* density in forest (57, 58). In our study reported here, only moisture was

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identified as potential selective stressor for *E. coli* in the watershed with high forest coverage. This is consistent with previous studies that reported *E. coli* to be sensitive to soil desiccation and its relative density to fluctuate with moisture (4, 59). While further investigation is required to explain how moisture impacts *E. coli* composition in watersheds with higher forest coverage, we expect *E. coli* in these areas to be exposed to less environmental stress, providing potentially more favorable growth conditions for *E. coli* as compared to watersheds with lower forest coverage does. Due to lack of niche differentiation caused by environmental selection, we observed more homogeneous *E. coli* compositions between forest and produce field in watershed with higher forest coverage. We also observed that *E. coli* was much more prevalent in the watershed with higher forest coverage (72%) as compared to the watershed with lower forest coverage (35%), consistent with previous findings by Dusek et al. (22).

The higher prevalence of *E. coli* in the watershed with higher forest coverage might be caused by proximity effect, which proposes that the likelihood of *E. coli* isolation from surrounding sites such as produce field increases with the proximity to forests (22). Such a proximity effect is formed by the spread of *E. coli* out of forests into surrounding areas, given that forest is a vital sink for *E. coli* (4). In addition, the large adjacency between forest and produce fields in the watershed with higher forest coverage, which indicates strong direct interactions between the two land covers, may enhance the proximity effect. Consistent with our findings, Dusek et al. (22) reported that *E. coli* was more prevalent in a landscape with greater forest coverage; this study specifically showed that *E. coli* was most prevalent in soils sampled in close proximity (0 to 38 m) of forests, but was up to 90% less prevalent when forest cover in the 250m radius was less than 7%. In addition to *E. coli*, such proximity effects of forest have also been reported for *Listeria monocytogenes* and other *Listeria* species. Weller et al. (60) found that with a 100m increase in the distance of a sampling site from forests, the likelihood of *L. monocytogenes* and other *Listeria* species isolation in croplands decreased by 14% and 16%,

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313 respectively.

314 **Watershed landscape could constrain or facilitate the dispersal of soil *E. coli* by influencing**
315 **the movement of wildlife host.** Wildlife, which is thought to be an important vehicle for transmission
316 of foodborne pathogens between hosts and locations (36), could enable bacteria to overcome landscape
317 barriers and make the dispersal of bacteria more active. Several studies have specifically indicated that
318 wildlife is a major source of *E. coli* in surface waters and may contribute to the contamination of *E. coli*
319 in rural watersheds and produce fields by defecation (11, 36, 61, 62). Landscape connectivity (i.e., the
320 degree to which a landscape facilitates or prevents movement of organisms among resource patches) and
321 particular landscape elements such as the structure of habitat (e.g., riparian corridor, terrestrial land,
322 waterbody) have also previously been shown to influence dispersal of pathogens (63, 64) and the
323 movement of wildlife (41). Wildlife-dependent dispersal of *E. coli* would thus be indirectly impacted by
324 landscape. Our results showed that the dispersal of soil *E. coli* in the watershed with widespread produce
325 fields was slightly limited, while the dispersal of soil *E. coli* in the watershed with high forest coverage
326 was facilitated by wildlife, demonstrating the influence of different watershed landscapes on the
327 dispersal of *E. coli*. These influences may consequently shape the spatial patterns of disease persistence
328 and incidence associated with pathogenic *E. coli* (65). Consistent with our findings, Mechai et al. (66)
329 showed evidence of the impact of landscape connectivity on the dispersal patterns of *Borrelia*
330 *burgdorferi*, particularly rodent-associated strains, which is relevant to the spread of Lyme disease risk
331 across locations.

332 Based on above notions, our observation here that the dispersal of soil *E. coli* in the watershed
333 with widespread produce fields was limited could be explained by a combination of different
334 environmental selection in soil and poor connectivity of agricultural areas, which impedes the movement
335 of wildlife that disperses *E. coli* (41). By contrast, the dispersal of soil *E. coli* in the watershed with high

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forest coverage tended to be facilitated by wildlife, largely because forest exhibits better connectivity and may provide passage and support to the movement of wildlife vehicles of *E. coli*. Besides wildlife, it is also possible that the dispersal of *E. coli* was directly influenced by the landscape elements of the two watersheds. Forest and most produce fields in Hoosic River, which is heavily forested, were both located in a floodplain. By contrast, forest in Flint Creek was in a floodplain but produce fields were not. Since during periods of high discharge, a floodplain normally experiences flooding, such events could facilitate the transmission of *E. coli* between forest and produce field particularly in the Hoosic River wateshed.

Small flocking insectivore/granivores and large nuisance wildlife were identified as the potential vehicles for *E. coli* in watershed with high forest coverage in this study. Small flocking insectivore/granivores (e.g., European starling) tend to have low movement cost in all land-use types except for open water and heavy urban development areas (67). Large nuisance wildlife (e.g., white tailed deer or feral swine) tend to have low movement cost in forests, scrublands, grasslands, wooded wetlands and cultivated croplands, while they can have high movement cost to cross roads (68). Both classes of wildlife have been previously reported to serve as dispersal vehicles of *E. coli* and have been considered public health concerns in terms of agricultural contamination. For example, European starlings, which are considered an invasive species in the United States and a nuisance pest to agriculture, were proposed to be a potential suitable reservoir and vector of *E. coli* O157:H7, and can carry and disseminate this human pathogen to cattle (34). In addition, deer feces were reported to contaminate fresh strawberries, being responsible for an outbreak of *E. coli* O157:H7 infections in Oregon (35). Forest is a relative stable environment with less disturbance of anthropologic activities, thus serving as an ideal living habitat for animals including small flocking insectivore/granivores and large nuisance wildlife (69). Forest could provide easy transport pathways for small flocking

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359 insectivore/granivores and large nuisance wildlife to move around, facilitating the dispersal of colonized
360 *E. coli* among locations.

361 **Conclusion.** By comparing the biogeographic patterns of *E. coli* isolated from two watershed
362 with distinct landscape characteristics in New York state, we showed that terrestrial landscape could
363 impact the distribution of *E. coli* by adjusting the importance of environmental selection and dispersal.
364 Environmental stress, which may contribute to local adaptation, tends to be strong on *E. coli* in
365 watershed with widespread produce fields. Wildlife-driven dispersal, which could facilitate genetic
366 exchange, was observed as the major force in shaping *E. coli* in watershed with high forest coverage. As
367 such, our findings not only highlight the critical role of landscape in driving the biogeographic pattern of
368 *E. coli* in perspective of ecology, but also open the possibility that the evolutionary forces (e.g., positive
369 selection, genetic drift, gene flow) driving its diversification vary by watershed landscape as well. In
370 addition, our study suggests that due to the less intense environmental stress, frequent wildlife-facilitated
371 dispersal, and the proximity effect of forest on *E. coli*, produce fields in watershed with high forest
372 coverage may have higher risk in *E. coli* contamination. This information can be proactively applied to
373 inform spatial modeling of food contamination risk associated with produce fields in watershed, which
374 can be used to modify pre-harvest product sampling strategies and produce harvest methods to account
375 for the spatial structure in contamination risk in a produce field. Such methodology development could
376 improve the prediction of produce contamination risk based on the potential influence of landscape on
377 transmission of *E. coli* to produce field, benefit the development of trade-off risk assessments of food
378 contamination, and eventually help to decrease human exposure to pathogenic enteric bacteria.

379

380 **MATERIALS AND METHODS**

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Study sites and soil collection. Two watersheds with different landscape patterns, Flint Creek and Hoosic River, located in the central New York region, were selected for this study based on topography and land-cover composition. Flint Creek is an area with widespread vegetable and livestock production that is sparsely forested (69% produce field, 12% forest by area), whereas the Hoosic River watershed is a heavily forested area with interspersed produce production (28% produce field, 38% forest by area). Soil sampling was carried out between September 4 and October 10, 2012 on 7 farms comprising 16 produce field sites and in 11 forest sites (Fig. 1). For produce fields, two parallel 200 m transects were laid in each field, perpendicular to the forest boundary. Along each transect, five soil samples (at approximately 5 cm-depth) were collected at 50 m intervals using sterile scoops (Fisher Scientific, Hampton, NH) and sterile Whirl-Pak bags (Nasco, Fort Atkinson, WI). Latex gloves and disposable plastic boot covers (Nasco, Fort Atkinson, WI) were worn for sample collection. Gloves and boot covers were changed between each site, and gloves were disinfected with 70% ethanol prior to sample collection. A total of 278 soil samples were collected with 142 and 136 samples collected from the Flint Creek and the Hoosic River watershed, respectively. All samples were transported to the Food Safety Lab at Cornell University in an icebox. Samples were stored at 4 ± 2°C in dark and processed within 24 h of collection.

Isolation of *E. coli*. *E. coli* were isolated from soil samples as previously described (23). Briefly, 8 g sieved soil was diluted 1:10 in EC medium with 4-methylumbelliferyl-β,D-glucuronide broth (EC-MUG). To maximize genetic diversity among recovered *E. coli* isolates, the suspension was subdivided among four 96-well microtiter plates for a total of 384 subsamples of approximately 180 uL each. Microtiter plates were incubated at 37°C. Bacteria from fluorescent wells were isolated on EC-MUG agar plates and were further tested with a standard biochemical assay for glutamate decarboxylase and

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beta-glucuronidase activity. Isolates that were positive for these two tests were presumptively identified as *E. coli*, which were confirmed by subsequent gene sequencing as detailed below.

DNA extraction, MLST genotyping and clonal groups. Genomic DNA was extracted from *E. coli* by alkaline lysis of biomass in 50 mM NaOH at 95°C. Two genes (*mdh* and *uidA*) were sequenced first from all isolates. Then, only the unique two-gene sequence types from each sample were subjected to additional sequencing in five additional genes (*aspC*, *clpX*, *icd*, *lysP*, *fadD*) by Sanger sequencing, performed by the Cornell University Life Sciences Core Laboratories Center. Evaluation of sequence read quality and assembly of forward and reverse reads were performed using Perl scripts, which iterated runs of phred and CAP3, respectively. Sequences with a probability of error of > 0.005 (Q score < 23) in terms of read quality were edited manually, where possible, or discarded. Assembled sequences of each MLST locus were aligned and trimmed to standard base positions matching the *E. coli* K-12 sequence type from the STEC Center website (http://www.shigatox.net) (23). Alignments of assembled sequences for isolates from Flint Creek and Hoosic River are available on GitHub (https://github.com/pbergholz/Dispersal-cost-modeling).

The clonal groups of *E. coli* strains for Flint Creek and Hoosic River were determined based on MLST sequence types using the goeBURST analysis program (70) at single locus variant level.

Remotely sensed data and soil property data. GPS coordinates of sites were imported into the Geographical Resources Analysis Support System (GRASS) geographic information system (GIS) environment. Map layers for land cover (National Land Cover Database [NLCD], 2006) and the digital elevation model (DEM; Shuttle Radar Topography Mission, 1-arc-second data set) were acquired from the U.S. Geological Survey (USGS) Earth Explorer geographical data bank (http://earthexplorer.usgs.gov/). Map layers for soil characteristics were acquired from the U.S. Department of Agriculture Soil Survey Geographic (SSURGO) database

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(http://soils.usda.gov/survey/geography/ssurgo/). Road and hydrologic line graphs were obtained from the Cornell University Geospatial Information Repository (CUGIR; http://cugir.mannlib.cornell.edu/).

Percent landcover and adjacency were estimated by using FRAGSTATS v. 3.3 to analyze landcover within a 2 km buffer surrounding the Flint Creek and Hoosic River, respectively (71). Percent adjacency was calculated as the proportion pixels in the NLCD map that were adjacent forest and field, compared to the total of non-self adjacencies in 2 km buffer surrounding the waterway. For example, $adjacency_{produce|forest}$ = 10% would indicate that 10% of the edges of produce fields abutted forest in a given area.

Organic matter, moisture, pH, aluminium, arsenic, boron, barium, calcium, cadmium, cobalt, chromium, copper, iron, potassium, magnesium, manganese, molybdenum, sodium, nickel, phosphorus, lead, sulphur, strontium, and zinc content of soil samples were measured at Cornell Nutrient Analysis Lab.

Distribution of clonal groups, dispersal limitation, and key soil variables. The Mann-Whitney test was used to determine if number of clonal groups differed significantly between soil samples from produce field sites and forest sites for Flint Creek and Hoosic River. Principal coordinate analysis (PCoA), as implemented in CANOCO for Windows Version 5.0, was employed to visualize the distribution of *E. coli* clonal groups among sites, based on Bray-Curtis distance. Permutational multivariate analysis of variance (PERMANOVA) (72) was employed using the adonis function in R version 3.6.0's vegan package to test whether the centroids and dispersion of sample groups as defined by land-use (produce field or forest) are equivalent for all groups based on Bray-Curtis distance of *E. coli* clonal groups in Flint Creek and Hoosic River. PERMANOVA test statistics (F) and p-values were obtained by 999 permutations.

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Biological dissimilarity of *E. coli* clonal groups was calculated in Bray-Curtis distance, while geographic distance was calculated in Euclidean distance based on latitude and longitude coordinates. Mantel tests were performed in R version 3.6.0 to assess the relationship between the biological dissimilarity of *E. coli* and geographic distance. Linear regression analysis of biological dissimilarity of *E. coli* and geographic distance was performed in R version 3.6.0. Dispersal limitation was inferred from R^2 of the linear regression. A value of R^2 closer to 1 suggests stronger dispersal limitation.

After screening for high levels of covariation, soil variables ($r < 0.7$ and $p < 0.05$ in Pearson's correlation analysis) were selected for canonical correspondence analysis (CCA). CCA was conducted in CANOCO for Windows Version 5.0 to quantify the effects of selected soil variables on variation of the biological dissimilarity of *E. coli*. Key soil variables were determined when $p < 0.1$. The Mann-Whitney test was performed to determine if phosphorous, antimony and moisture differed significantly between soil samples from produce field sites and forest sites.

Dispersal model formulation and selection. To predict the dispersal of *E. coli* across watershed landscapes, multiple dispersal models were developed to describe landscape effects by integrating remotely sensed and field-collected data into resistance surfaces for wildlife vehicles. Four common classes of wildlife vehicles including (i) large nuisance wildlife species, (ii) small mammals, (iii) small flocking insectivore/granivores, and (iv) migratory bird flocks were selected in this study.

Predicted dispersal among sites was calculated according to the equation below:

$$D_{i,j} = \frac{L_i \times A_j}{C_{i,j}}$$

Where $D_{i,j}$ is the dispersal rate among sites *i* and *j*, L_i is the *E. coli* load from the source site (i.e., starting point), A_j is the attraction (gravity) coefficient of the sink site (i.e., stopping point) to vehicle and $C_{i,j}$ is the least-cost distance between sites *i* and *j*. *E. coli* load L_i expresses the expected mobility of *E. coli* from these areas as a function of expected prevalence. Expected prevalence was inferred from

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471 random forest analysis of *E. coli* prevalence based on sampling excursions. One load map was generated
472 per watershed. The attraction (gravity) coefficient A_j describes the tendency of a dispersal vehicle to
473 move towards an area on the landscape and expected residence-time of dispersal vehicle after they arrive
474 at a location. Attraction was primarily a function of percent favored land-cover for each of the vehicles
475 and interspersion of land-cover types. The least-cost distance $C_{i,j}$ describes the movement preferences of
476 a dispersal vehicle in terms of a friction surface (borrowed from circuit theory) that predicts resistance of
477 the landscape to movement of dispersal vehicles. The cost surfaces were a function of baseline
478 resistance (dependent on the dispersal vehicle), riparian corridor effect (i.e., the tendency of wildlife to
479 prefer movement through riparian forests), dispersal barrier effect (i.e., the strength of barriers to
480 movement, such as major road- and water-ways), and proximity effect (i.e., the strength and type of
481 edge interactions among forests, produce fields, pasturage, and urban areas). The least-cost distance was
482 measured as the distance along the path that accrued the least cumulative cost between pairs of
483 movement start and stop sites. The characteristics of the dispersal vehicles, *E. coli* load model (L_i),
484 attraction model (coefficient A_j), cost model (i.e., riparian corridor effect, dispersal barrier effect and
485 proximity effect) were shown in Table 2, which were summarized on the basis of published literature
486 (73–84). Based on these characteristics, the most-likely attraction model and cost model were selected
487 for each class of vehicle, generating the predicted dispersal models (Table 3).

488 For each of the predicted dispersal models for the four classes of wildlife vehicles, an association
489 matrix $D_{i,j}$ containing predicted dispersal rates along least cost paths among all pairs of sites was
490 generated. This was accomplished by using a set of scripts developed in the GRASS GIS ver. 6.4.3
491 programming environment; Perl scripts were used to automate calculations in the GIS; scripts are
492 available on GitHub (https://github.com/pbergholz/Dispersal-cost-modeling). Mantel tests were
493 employed to estimate the correlation between predicted dispersal models and biological dissimilarity of

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494 *E. coli* clonal groups among sampled sites in each watershed using R version 3.6.0. Statistical
495 significance of model fits was estimated by 9,999 permutations. The wildlife vehicle for which the
496 predicted model had the highest significant correlation coefficient was deemed to represent the dominant
497 dispersal vehicle for *E. coli*.

498

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502

503 **REFERENCES**

504 1. Berges SA, Moore LAS, Isenhart TM, Schultz RC. 2010. Bird species diversity in riparian buffers,
505 row crop fields, and grazed pastures within agriculturally dominated watersheds. Agrofor Syst
506 79:97–110.
507 2. Borin M, Passoni M, Thiene M, Tempesta T. 2010. Multiple functions of buffer strips in farming
508 areas. Eur J Agron 32:103–111.
509 3. Finder RA, Roseberry JL, Woolf A. 1999. Site and landscape conditions at white-tailed
510 deer/vehicle collision locations in Illinois. Landsc Urban Plan 44:77–85.
511 4. Byappanahalli MN, Whitman RL, Shively DA, Sadowsky MJ, Ishii S. 2006. Population structure,
512 persistence, and seasonality of autochthonous *Escherichia coli* in temperate, coastal forest soil
513 from a Great Lakes watershed. Environ Microbiol 8:504–513.
514 5. Mostaghimi S, Benham B, Wolfe ML. BSLC: A tool for bacterial source characterization for
515 watershed management. Appl Eng Agric.
516 6. Kouznetsov MY, Roodsari R, Pachepsky YA, Shelton DR, Sadeghi AM, Shirmohammadi A,

bioRxiv preprint doi: https://doi.org/10.1101/2020.06.30.181495; this version posted July 1, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Starr JL. 2007. Modeling manure-borne bromide and fecal coliform transport with runoff and infiltration at a hillslope. J Environ Manage 84:336–346.

7. Lowe WH, McPeek MA. 2014. Is dispersal neutral? Trends Ecol Evol. Elsevier Ltd.

8. Oliver DM, Heathwaite AL, Fish RD, Chadwick DR, Hodgson CJ, Winter M, Butler AJ. 2009. Scale appropriate modelling of diffuse microbial pollution from agriculture. Prog Phys Geogr Earth Environ 33:358–377.

9. Walsh CJ, Kunapo J. 2009. The importance of upland flow paths in determining urban effects on stream ecosystems. J North Am Benthol Soc 28:977–990.

10. Wang H, Zhang T, Wei G, Wu L, Wu J, Xu J. 2014. Survival of *Escherichia coli* O157:H7 in soils under different land use types. Environ Sci Pollut Res 21:518–524.

11. Harmel RD, Karthikeyan R, Gentry T, Srinivasan R. Effects of agricultural management, land use, and watershed scale on *E. coli* concentrations in runoff and streamflow. Trans ASABE 53:1833–1841.

12. Foster DR, Motzkin G, Bernardos D, Cardoza J. 2002. Wildlife dynamics in the changing New England landscape. J Biogeogr 29:1337–1357.

13. Gibbons SM. 2017. Metapopulation theory provides new insight into microbial biogeography. Environ Microbiol 19:849–850.

14. Nemergut DR, Costello EK, Hamady M, Lozupone C, Jiang L, Schmidt SK, Fierer N, Townsend AR, Cleveland CC, Stanish L, Knight R. 2011. Global patterns in the biogeography of bacterial taxa. Environ Microbiol 13:135–144.

15. Nemergut DR, Schmidt SK, Fukami T, O'Neill SP, Bilinski TM, Stanish LF, Knelman JE, Darcy JL, Lynch RC, Wickey P, Ferrenberg S. 2013. Patterns and processes of microbial community assembly. Microbiol Mol Biol Rev 77:342–356.

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16. Liao J, Cao X, Wang J, Zhao L, Sun J, Jiang D, Huang Y. 2017. Similar community assembly mechanisms underlie similar biogeography of rare and abundant bacteria in lakes on Yungui Plateau, China. Limnol Oceanogr 62:723–735.

17. Yashiro E, Pinto-Figueroa E, Buri A, Spangenberg JE, Adatte T, Niculita-Hirzel H, Guisan A, van der Meer JR. 2016. Local environmental factors drive divergent grassland soil bacterial communities in the western Swiss Alps. Appl Environ Microbiol 82:6303–6316.

18. Lozupone CA, Knight R. 2007. Global patterns in bacterial diversity. Proc Natl Acad Sci U S A 104:11436–11440.

19. Semenov A V., Franz E, Van Overbeek L, Termorshuizen AJ, Van Bruggen AHC. 2008. Estimating the stability of *Escherichia coli* O157:H7 survival in manure-amended soils with different management histories. Environ Microbiol 10:1450–1459.

20. Liao J, Wang J, Huang Y. 2015. Bacterial community features are shaped by geographic location, physicochemical properties, and oil contamination of soil in main oil fields of China. Microb Ecol 70:380–389.

21. Coleman ML, Chisholm SW. 2010. Ecosystem-specific selection pressures revealed through comparative population genomics. Proc Natl Acad Sci U S A 107:18634–18639.

22. Dusek N, Hewitt AJ, Schmidt KN, Bergholz PW. 2018. Landscape-scale factors affecting the prevalence of *Escherichia coli* in surface soil include land cover type, edge interactions, and soil pH. Appl Environ Microbiol 84:e02714-17.

23. Bergholz PW, Noar JD, Buckley DH. 2011. Environmental patterns are imposed on the population structure of *Escherichia coli* after fecal deposition. Appl Environ Microbiol 77:211–219.

24. Fierer N, Jackson RB. 2006. The diversity and biogeography of soil bacterial communities. Proc

bioRxiv preprint doi: https://doi.org/10.1101/2020.06.30.181495; this version posted July 1, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

563 Natl Acad Sci U S A 103:626–631.

564 25. Forbes AE, Chase JM. 2002. The role of habitat connectivity and landscape geometry in

565 experimental zooplankton metacommunities. Oikos 96:433–440.

566 26. Berga M, Östman Ö, Lindström ES, Langenheder S. 2015. Combined effects of zooplankton

567 grazing and dispersal on the diversity and assembly mechanisms of bacterial metacommunities.

568 Environ Microbiol 17:2275–2287.

569 27. Darcy JL, Lynch RC, King AJ, Robeson MS, Schmidt SK. 2011. Global distribution of

570 *Polaromonas* phylotypes - Evidence for a highly successful dispersal capacity. PLoS One

571 6:e23742.

572 28. Biek R, Real LA. 2010. The landscape genetics of infectious disease emergence and spread. Mol

573 Ecol 19:3515–3531.

574 29. Cushman SA, McKelvey KS, Hayden J, Schwartz MK. 2006. Gene flow in complex landscapes:

575 testing multiple hypotheses with causal modeling. Am Nat 168:486–99.

576 30. Storfer A, Murphy MA, Evans JS, Goldberg CS, Robinson S, Spear SF, Dezzani R, Delmelle E,

577 Vierling L, Waits LP. 2007. Putting the “landscape” in landscape genetics. Heredity (Edinb).

578 Nature Publishing Group.

579 31. Jang J, Hur HG, Sadowsky MJ, Byappanahalli MN, Yan T, Ishii S. 2017. Environmental

580 *Escherichia coli*: ecology and public health implications—a review. J Appl Microbiol. Blackwell

581 Publishing Ltd.

582 32. Nandakafle G, Seale T, Flint T, Nepal M, Venter SN, Brözel VS. 2017. Distribution of diverse

583 Escherichia coli between cattle and pasture. Microbes Environ 32:226–233.

584 33. Chandler DS, Craven JA. 1980. Relationship of soil moisture to survival of *Escherichia coli* and

585 *Salmonella typhimurium* in soils. Aust J Agric Res 31:547–555.

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586 34. Kauffman MD, LeJeune J. 2011. European Starlings (*Sturnus vulgaris*) challenged with
587 *Escherichia coli* O157 can carry and transmit the human pathogen to cattle. Lett Appl Microbiol
588 53:596–601.
589 35. Laidler MR, Tourdjman M, Buser GL, Hostetler T, Repp KK, Leman R, Samadpour M, Keene
590 WE. 2013. *Escherichia coli* O157:H7 infections associated with consumption of locally grown
591 strawberries contaminated by deer. Clin Infect Dis 57:1129–1134.
592 36. Avery SM, Moore A, Hutchison ML. 2004. Fate of *Escherichia coli* originating from livestock
593 faeces deposited directly onto pasture. Lett Appl Microbiol 38:355–359.
594 37. Byappanahalli M, Fowler M, Shively D, Whitman R. 2003. Ubiquity and persistence of
595 *Escherichia coli* in a Midwestern Coastal Stream. Appl Environ Microbiol 69:4549–4555.
596 38. Bolster CH, Haznedaroglu BZ, Walker SL. 2009. Diversity in cell properties and transport
597 behavior among 12 different environmental *Escherichia coli* isolates. J Environ Qual 38:465–472.
598 39. Leimbach A, Hacker J, Dobrindt U. 2013. *E. coli* as an all-rounder: The thin line between
599 commensalism and pathogenicity. Curr Top Microbiol Immunol 358:3–32.
600 40. Ramos JL, Gallegos MT, Marqués S, Ramos-González MI, Espinosa-Urgel M, Segura A. 2001.
601 Responses of gram-negative bacteria to certain environmental stressors. Curr Opin Microbiol
602 4:166–171.
603 41. Shepard DB, Kuhns AR, Dreslik MJ, Phillips CA. 2008. Roads as barriers to animal movement in
604 fragmented landscapes. Anim Conserv 11:288–296.
605 42. Compton JE, Boone RD. 2000. Long-term impacts of agriculture on soil carbon and nitrogen in
606 New England forests. Ecology 81:2314–2330.
607 43. Chaudhry V, Rehman A, Mishra A, Chauhan PS, Nautiyal CS. 2012. Changes in bacterial
608 community structure of agricultural land due to long-term organic and chemical amendments.

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609 Microb Ecol 64:450–460.

610 44. Berg J, Tom-Petersen A, Nybroe O. 2005. Copper amendment of agricultural soil selects for
611 bacterial antibiotic resistance in the field. Lett Appl Microbiol 40:146–151.

612 45. Cambardella CA, Elliott ET. 1994. Carbon and nitrogen dynamics of soil organic matter fractions
613 from cultivated grassland soils. Soil Sci Soc Am J 58:123–130.

614 46. Sharpley AN. 1995. Soil phosphorus dynamics: agronomic and environmental impacts. Ecol Eng
615 5:261–279.

616 47. Li J, Wang Q, Oremland RS, Kulp TR, Rensing C, Wang G. 2016. Microbial antimony
617 biogeochemistry: Enzymes, regulation, and related metabolic pathways. Appl Environ Microbiol
618 82:5482–5495.

619 48. Steely S, Amarasiriwardena D, Xing B. 2007. An investigation of inorganic antimony species and
620 antimony associated with soil humic acid molar mass fractions in contaminated soils. Environ
621 Pollut 148:590–598.

622 49. Tóth G, Hermann T, Da Silva MR, Montanarella L. 2016. Heavy metals in agricultural soils of
623 the European Union with implications for food safety. Environ Int 88:299–309.

624 50. Wagner SE, Peryea FJ, Filby RA. 2003. Antimony impurity in lead arsenate insecticide enhances
625 the antimony content of old prchard soils. J Environ Qual 32:736–738.

626 51. Álvarez-Ayuso E, Otones V, Murciego A, García-Sánchez A, Regina IS. 2012. Antimony, arsenic
627 and lead distribution in soils and plants of an agricultural area impacted by former mining
628 activities. Sci Total Environ 439:35–43.

629 52. Hammel W, Debus R, Steubing L. 2000. Mobility of antimony in soil and its availability to plants.
630 Chemosphere 41:1791–1798.

631 53. An YJ, Kim M. 2009. Effect of antimony on the microbial growth and the activities of soil

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enzymes. Chemosphere 74:654–659.

54. Filella M, Belzile N, Lett MC. 2007. Antimony in the environment: A review focused on natural waters. III. Microbiota relevant interactions. Earth-Science Rev 80:195–217.

55. Carlin A, Shi W, Dey S, Rosen BP. 1995. The ars operon of *Escherichia coli* confers arsenical and antimonial resistance. J Bacteriol 177:981–986.

56. Silver S, Budd K, Leahy KM, Shaw W V, Hammond D, Novick RP, Willsky GR, Malamy MH, Rosenberg H. 1981. Inducible plasmid-determined resistance to arsenate, arsenite, and antimony (III) in *Escherichia coli* and *Staphylococcus aureus*. J Bacteriol 146:983–96.

57. Carrillo M, Estrada E, Hazen TC. 1985. Survival and enumeration of the fecal indicators Bifidobacterium adolescentis and *Escherichia coli* in a tropical rain forest watershed. Appl Environ Microbiol 50:468–476.

58. Tate RL. 1978. Cultural and environmental factors affecting the longevity of *Escherichia coli* in Histosols. Appl Environ Microbiol 35:925–9.

59. Zhang Q, Yan T. 2012. Correlation of intracellular trehalose concentration with desiccation resistance of soil *Escherichia coli* populations. Appl Environ Microbiol 78:7407–7413.

60. Weller D, Shiwakoti S, Bergholz P, Grohn Y, Wiedmann M, Strawn LK. 2016. Validation of a previously developed geospatial model that predicts the prevalence of *Listeria monocytogenes* in New York State produce fields. Appl Environ Microbiol 82:797–807.

61. Casarez EA, Pillai SD, Mott JB, Vargas M, Dean KE, Di Giovanni GD. 2007. Direct comparison of four bacterial source tracking methods and use of composite data sets. J Appl Microbiol 103:350–364.

62. Parajuli PB, Mankin KR, Barnes PL. 2009. Source specific fecal bacteria modeling using soil and water assessment tool model. Bioresour Technol 100:953–963.

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655 63. Tischendorf L, Fahrig L. 2000. On the usage and measurement of landscape connectivity. Oikos
656 90:7–19.
657 64. Plantegenest M, Le May C, Fabre F. 2007. Landscape epidemiology of plant diseases. J R Soc
658 Interface 4:963–972.
659 65. Thrall PH, Burdon JJ. 1997. Host-pathogen dynamics in a metapopulation context: The ecological
660 and evolutionary consequences of being spatial. J Ecol 85:743.
661 66. Mechai S, Margos G, Feil EJ, Lindsay LR, Michel P, Kotchi SO, Ogden NH. 2018. Evidence for
662 an effect of landscape connectivity on *Borrelia burgdorferi sensu stricto* dispersion in a zone of
663 range expansion. Ticks Tick Borne Dis 9:1407–1415.
664 67. Shepard ELC, Wilson RP, Rees WG, Grundy E, Lambertucci SA, Vosper SB. 2013. Energy
665 landscapes shape animal movement ecology. Am Nat 182:298–312.
666 68. Putman RJ. 1997. Deer and road traffic accidents: Options for management. J Environ Manage
667 51:43–57.
668 69. Robinson SK, Yahner RH. 1997. Eastern deciduous forests: Ecology and wildlife conservation. J
669 Wildl Manage 61:1445.
670 70. Francisco AP, Bugalho M, Ramirez M, Carriço JA. 2009. Global optimal eBURST analysis of
671 multilocus typing data using a graphic matroid approach. BMC Bioinformatics 10:152.
672 71. FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps.
673 72. Anderson MJ, Walsh DCI. 2013. PERMANOVA, ANOSIM, and the Mantel test in the face of
674 heterogeneous dispersions: What null hypothesis are you testing? Ecol Monogr 83:557–574.
675 73. Bruun M, Smith HG. 2003. Landscape composition affects habitat use and foraging flight
676 distances in breeding European starlings. Biol Conserv 114:179–187.
677 74. Minderman J, Reid JM, Hughes M, Denny MJH, Hogg S, Evans PGH, Whittingham MJ. 2010.

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678 Novel environment exploration and home range size in starlings *Sturnus vulgaris*. Behav Ecol
679 21:1321–1329.
680 75. Getz LL, Mcguire B. 2008. Factors influencing movement distances and home ranges of the
681 short-tailed shrew (*Blarina brevicauda*). Northeast Nat 15:293–302.
682 76. Wang M, Grimm V. 2007. Home range dynamics and population regulation: An individual-based
683 model of the common shrew *Sorex araneus*. Ecol Modell 205:397–409.
684 77. Morales JM, Moorcroft PR, Matthiopoulos J, Frair JL, Kie JG, Powell RA, Merrill EH, Haydon
685 DT. 2010. Building the bridge between animal movement and population dynamics. Philos Trans
686 R Soc B Biol Sci 365:2289–2301.
687 78. Brandl MT. 2006. Fitness of human enteric pathogens on plants and implications for food safety.
688 Annu Rev Phytopathol 44:367–392.
689 79. Blanchong JA, Samuel MD, Scribner KT, Weckworth B V, Langenberg JA, Filcek KB. 2008.
690 Landscape genetics and the spatial distribution of chronic wasting disease. Biol Lett 4:130–133.
691 80. Somarelli JA, Makarewicz JC, Sia R, Simon R. 2007. Wildlife identified as major source of
692 Escherichia coli in agriculturally dominated watersheds by BOX A1R-derived genetic
693 fingerprints. J Environ Manage 82:60–65.
694 81. Lam TTY, Ip HS, Ghedin E, Wentworth DE, Halpin RA, Stockwell TB, Spiro DJ, Dusek RJ,
695 Bortner JB, Hoskins J, Bales BD, Yparraguirre DR, Holmes EC. 2012. Migratory flyway and
696 geographical distance are barriers to the gene flow of influenza virus among North American
697 birds. Ecol Lett 15:24–33.
698 82. Kreakie BJ, Fan Y, Keitt TH. 2012. Enhanced migratory waterfowl distribution modeling by
699 inclusion of depth to water table data. PLoS One 7:e30142.
700 83. Carlson JC, Engeman RM, Hyatt DR, Gilliland RL, DeLiberto TJ, Clark L, Bodenchuk MJ, Linz

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GM. 2011. Efficacy of European starling control to reduce *Salmonella enterica* contamination in a concentrated animal feeding operation in the Texas panhandle. BMC Vet Res 7.

84. Carlson JC, Franklin AB, Hyatt DR, Pettit SE, Linz GM. 2011. The role of starlings in the spread of *Salmonella* within concentrated animal feeding operations. J Appl Ecol 48:479–486.

FIGURE LEGENDS

FIG 1 Sampling maps of (a) Flint Creek and (b) Hoosic River. Red dots indicate the sampling sites within each watershed. Map layers for land cover (National Land Cover Database [NLCD], 2006) were acquired from the U.S. Geological Survey (USGS) Earth Explorer geographical data bank (http://earthexplorer.usgs.gov/).

FIG 2 PCoA plots of *E. coli* clonal groups of sites in (a) Flint Creek (FC) and (b) Hoosic River (HR). Green dots indicated forest sites; orange dots indicated produce field sites; Green circle indicated cluster of forest sites; orange circle indicated cluster of produce field sites. *p* value of permutational multivariate analysis of variance (PERMANOVA) test is shown; "*" indicates the clustering of sampling sites by land-use is significant at $p < 0.05$. (a) PCo Axis 1 and 2 explained 15.92% and 11.84%, respectively, of the variation of *E. coli* clonal groups for Flint Creek. (b) PCo Axis 1 and 2 explained 16.11% and 13.06%, respectively, of the variation of *E. coli* clonal groups for Hoosic River.

FIG 3 Linear relationship between biological dissimilarity of *E. coli* clonal groups and geographical distance for (a) Flint Creek (FC) and (b) Hoosic River (HR). The biological dissimilarity of *E. coli* clonal groups was calculated as Bray–Curtis distance. Geographical distance was calculated in Euclidean distance. Linear regression line is in grey; shaded area indicates 95% confidence region; R^2 indicates the variability explained by fitted linear regression model and the formula of the linear relationship is shown.

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724 **FIG 4** Mantel test result of wildlife-driven dispersal models and composition of *E. coli* clonal groups for
725 Flint Creek and Hoosic River. M106, M377, M459, and M556 on the x-axis are the identification
726 numbers of the predicted dispersal models for small mammals, large nuisance wildlife, migratory bird
727 flocks, and small flocking insectivore/granivores, respectively. Examples of each wildlife vehicle type
728 are also shown. The description of the predicted dispersal model for each wildlife vehicle is detailed in
729 Table 3. Significant *p* values ($p < 0.05$) are denoted by "*".

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TABLE 1 Effects of selected soil variables on the composition of *E. coli* clonal groups.

Variables	Flint Creek		Hoosic River	
	% biological variation explained[a]	*p-value*[b]	% biological variation explained[a]	*p-value*[b]
Phosphorus	10.3	**0.098**	7.1	0.558
Antimonies	10	**0.02**	7.2	0.616
Manganese	8.3	0.376	7	0.592
pH	7.7	0.554	7.5	0.51
Sodium	8.2	0.434	7.2	0.616
Barium	7.3	0.588	8.3	0.2
Moisture	8.3	0.458	8.7	**0.049**

[a]The percentage of biological variation explained by a given soil variable
[b]Significant values ($p < 0.1$) are in bold.

TABLE 2 Basic dispersal model characteristics

Class	Description
Dispersal vehicles[a]	
LT: Large nuisance wildlife species (e.g. "deer" or "feral swine")	Forests, scrublands, grasslands, wooded wetlands and cultivated croplands impose low movement costs, roads impose increased movement costs based on census category
ST: Small mammals (e.g. "shrews", "voles" and "mice")	Light urban development, grassland and scrublands impose low movement costs, roads impose increased movement costs based on census category
LB: Small flocking insectivore/granivores (e.g., "starlings")	Open water and heavy urban development are higher cost, all other movement costs are low
MB: Migratory bird flocks (e.g. "Canada goose")	Heavy urban development imposes higher cost, all other movement costs are low.
Riparian corridor (movement costs are reduced by half)	
Adjacency	All land parcels that overlap a 100 m zone around the main river/creek
Distance	Land within 100 m of the main river/creek
Biological	Land below the 50 yr flood height for the main river/creek and adjacent wetlands
None	No riparian corridor effect
Dispersal barriers	
Absolute	Major roads and waterways are absolute barriers (movement cost 40,000 per pixel)
Porous	Major roads and waterways are porous barriers (movement cost 200 per pixel)
None	No barrier effect
Proximity effects (specifics vary by vehicle)	
Strong	Nearness to high quality habitat substantially reduces movement cost
Weak	Nearness to high quality habitat somewhat reduces movement cost
None	No benefit of proximity to good cover
Attraction (gravity) coefficients (specifics vary by vehicle)	
Habitat Quality	Proximity, interspersion and area of high quality habitat increase the chances that *E. coli* will be deposited
Reduced Habitat Effect	Effect of high quality habitat is reduced by half
Area Independent	As habitat quality model, but area of high quality habitat does not impact the result
None	Attraction does not influence dispersal
Load (source) coefficient	
E. coli load estimation	Areas close to forest or pasture-class landcover are higher load.

[a]Conceptual models are based on published literature (73-84).

TABLE 3 The predicted dispersal model for each wildlife vehicle

Vehicles	Most-likely cost model[a]			Most-likely attraction model (coefficient)[b]
	Riparian corridor	Proximity effects	Dispersal barriers	
ST (Small mammals)	Biological	None	Absolute	None
LT (Large nuisance wildlife species)	Biological	Strong	Porous	Habitat Quality
MB (Migratory bird flocks)	Biological	Weak	None	Area Independent
LB (Small flocking insectivore/granivores)	Biological	Weak	Absolute	Area Independent

[a]Cost model was developed based on three factors, riparian corridor, proximity effects, and dispersal barriers. Definition of the three factors can be found in Table 2. The most-likely cost model was selected based on the characteristics of each wildlife vehicle (Table 2).
[b]Definition of classes of attraction model can be found in Table S5. The most-likely attraction model was selected based on the characteristics of each wildlife vehicle (Table 2).

N

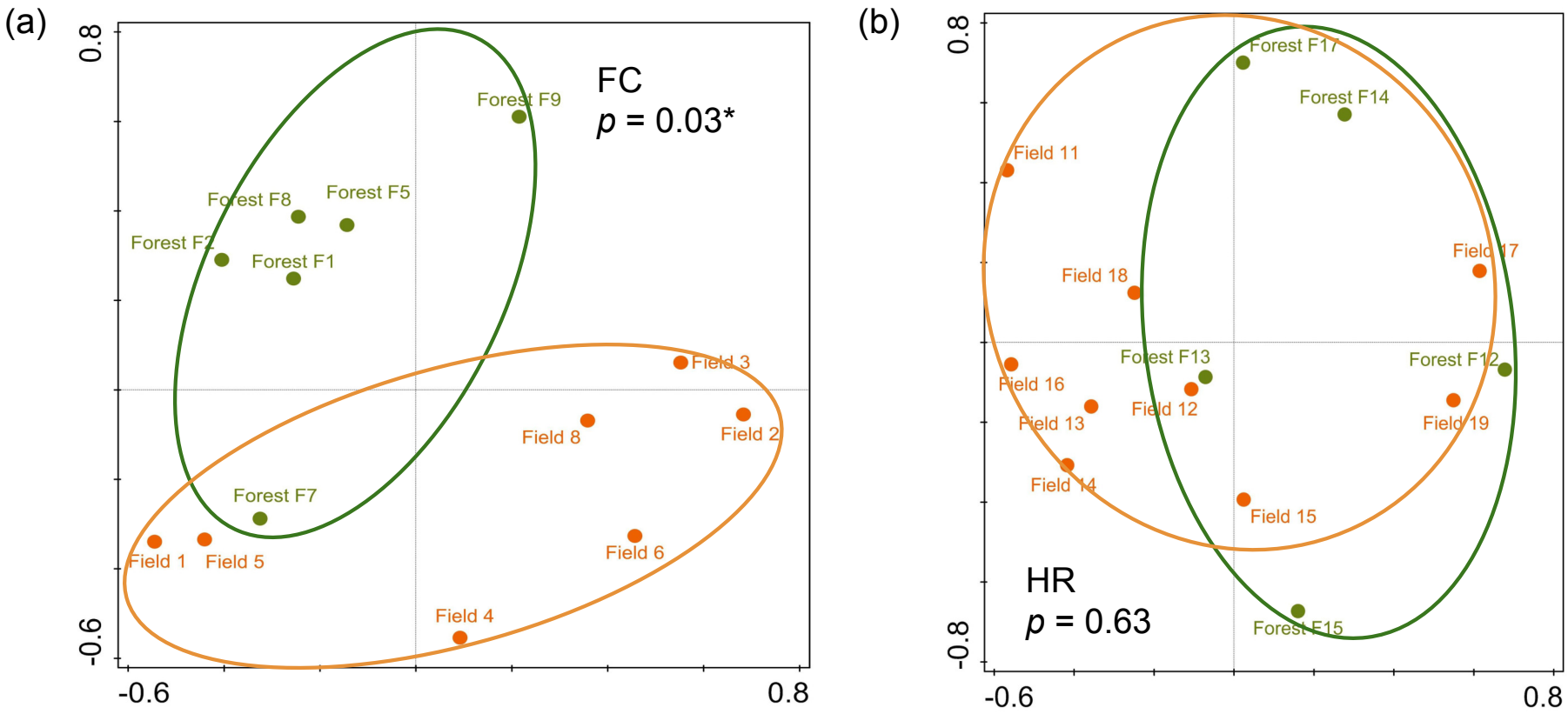
0 0.45 0.9 1.8 2.7 3.6
Miles

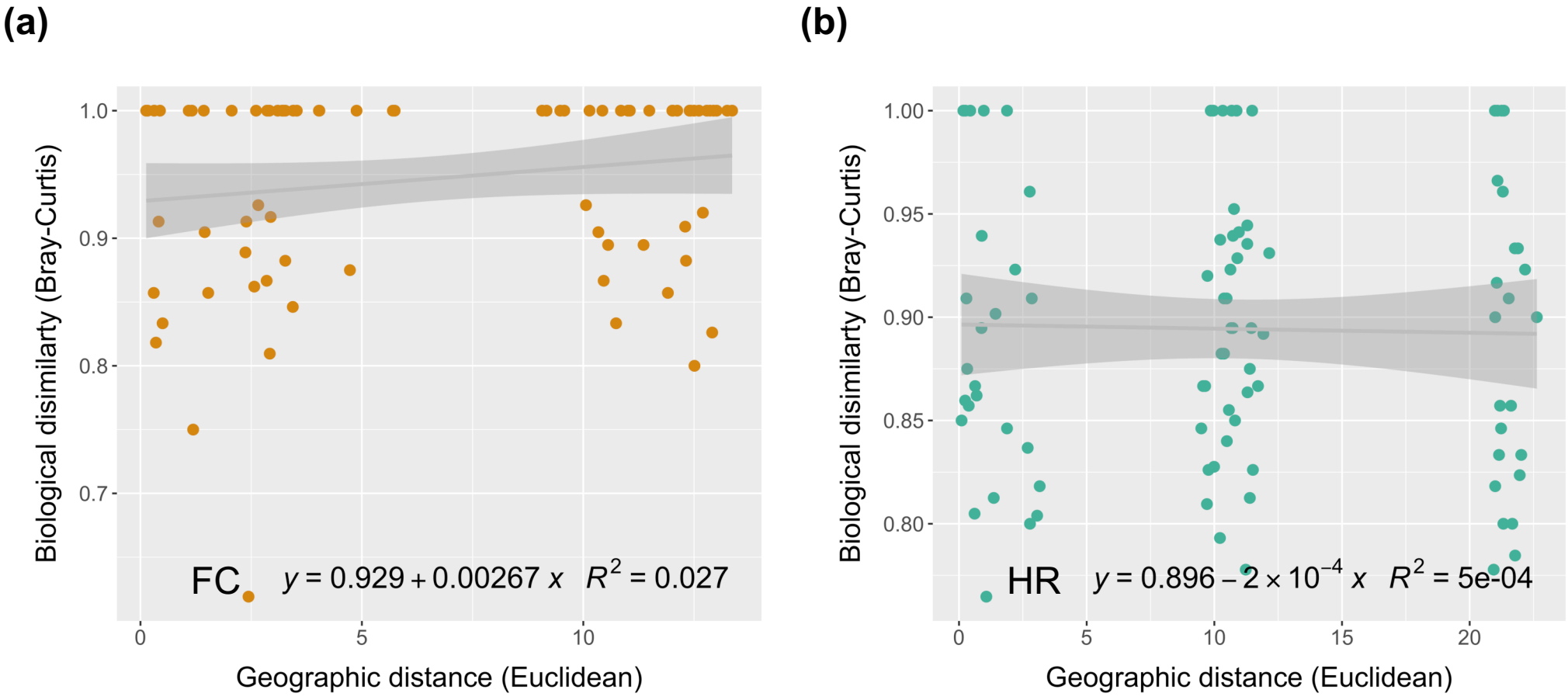
(A) Flint Creek

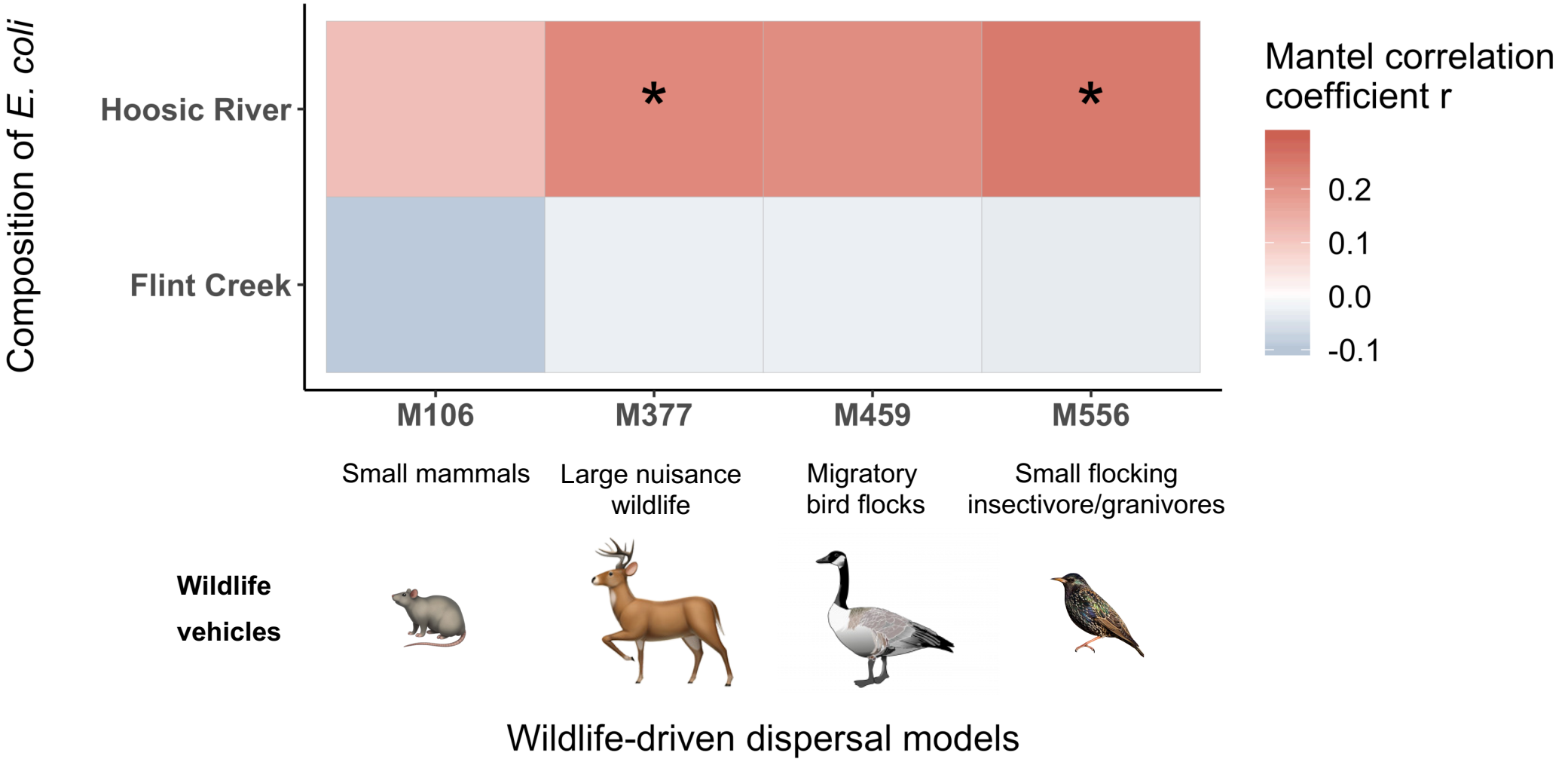
N

0 1 2 4 6 8
Miles

(B) Hoosic River


(a)
FC
p = 0.03*
Forest F9
Forest F8
Forest F5
Forest F2
Forest F1
Field 3
Field 8
Field 2
Forest F7
Field 1
Field 5
Field 6
Field 4
0.8
-0.6
-0.6
0.8
(b)
HR
p = 0.63
Forest F17
Forest F14
Field 11
Field 17
Field 18
Forest F13
Forest F12
Field 16
Field 12
Field 13
Field 19
Field 14
Field 15
Forest F15
0.8
-0.8
-0.6
0.8


(a)
(b)
Biological disimilarty (Bray-Curtis)
Geographic distance (Euclidean)
1.0
0.9
0.8
0.7
0
5
10
FC
$y = 0.929 + 0.00267\,x$
$R^2 = 0.027$
1.00
0.95
0.90
0.85
0.80
15
20
HR
$y = 0.896 - 2 \times 10^{-4}\,x$
$R^2 = 5e\text{-}04$


Composition of E. coli
Hoosic River
Flint Creek
*
*
M106
M377
M459
M556
Small mammals
Large nuisance wildlife
Migratory bird flocks
Small flocking insectivore/granivores
Wildlife vehicles
Mantel correlation coefficient r
0.2
0.1
0.0
-0.1
Wildlife-driven dispersal models