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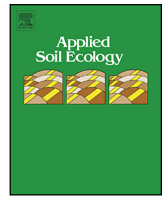

Enteropathogen survival in soil from different land-uses is predominantly regulated by microbial community composition

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ABSTRACT

Microbial enteropathogens can enter the environment via landspreading of animal slurries and manures. Biotic interactions with the soil microbial community can contribute to their subsequent decay. This study aimed to determine the relative impact of biotic, specifically microbial community structure, and physico-chemical properties associated with soils derived from 12 contrasting land-uses on enteropathogen survival. Phenotypic profiles of microbial communities (via phospholipid fatty acid (PLFA) profiling), and total biomass (by fumigation-extraction), in the soils were determined, as well as a range of physicochemical properties. The persistence of *Salmonella* Dublin, *Listeria monocytogenes*, and *Escherichia coli* was measured over 110 days within soil microcosms. Physicochemical and biotic data were used in stepwise regression analysis to determine the predominant factor related to pathogen-specific death rates. Phenotypic structure, associated with a diverse range of constituent PLFAs, was identified as the most significant factor in pathogen decay for *S.* Dublin, *L. monocytogenes*, non-toxigenic *E. coli* O157 but not for environmentally-persistent *E. coli*. This demonstrates the importance of entire community-scale interactions in pathogen suppression, and that such interactions are context-specific.
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1. Introduction

Microbial enteropathogens are released in faecal waste of both animals and humans, and enter the soil environment either directly via faecal shedding, or indirectly via the application of slurry, manure and sewage sludge. In addition, wild animals and birds contribute to enteropathogen load in the environment (Jones, 2001; Jiang et al., 2007; Benskin et al., 2009), and there is evidence to suggest that potentially pathogenic enteric bacteria can exist as naturalised populations within the soil matrix (Texier et al., 2008; Ishii et al., 2006; Brennan et al., 2010). Enteropathogens can pose a serious public health risk, contingent on survivability within the soil environment. Viable pathogens may be transmitted to humans by direct contact with contaminated surfaces and accidental ingestion of faeces or contaminated soil particles (Davis et al., 2005). Pathogens can also be transported via overland or subsurface flow to surface and groundwaters, and infection may arise via ingestion of contaminated water, e.g. Walkerton Outbreak, Ontario in 2000 (Hrudey et al., 2003). It is also possible that pathogens could be present on the crop surface following manure application. In this case, a person may become infected if they consume the contaminated produce, as demonstrated by the 2011 *Escherichia coli* O104 outbreak in Germany, associated with consumption of contaminated beansprouts (Böhmer et al., 2011).

To date, enteropathogen survival in soil has been mostly investigated in relation to prevailing physicochemical conditions. Factors known to affect pathogen survival include moisture, temperature, texture, pH, cation exchange capacity (CEC), UV irradiation, organic matter (OM) and soil nutrient status (summarised by van Elsas et al., 2011). For example, persistence is favoured by cool moist conditions (Cools et al., 2001), where exposure to UV is limited (Hutchison et al., 2004b). Typically, the survival of enteric bacteria is reduced at low pH, and tends to increase when approaching a neutral to alkaline state (Sjogren, 1994). Fine textured soils with well-developed microstructure and high clay content offer habitat, water and nutrients, which can sustain pathogens introduced via manure application (England et al., 1993).

Soil biology also plays an important function in regulating pathogen survival; however research on interactions with the soil community has been comparatively limited. Pertinent biotic interactions include predation (Sørensen et al., 1999), antagonism from indigenous microorganisms (Garbeva et al., 2004) and

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competition for resources (Irikiin et al., 2006). It has been found that bacteria introduced into soil decline more rapidly when other microbes are present. This decline is apparently accelerated when the indigenous microbial community is increasingly diverse. A range of experimental approaches have been used to manipulate microbial diversity with a view to investigating the relationship between diversity and *E. coli* survivability (Vivant et al., 2013; Yao et al., 2013; Ma et al., 2013; Korajkic et al., 2013). All of these studies showed an inverse relationship between community complexity and pathogen survival, attributed to progressively increasing competition for resources and antagonistic interactions associated with greater diversity.

The soil microbial community is typically sensitive to changing environmental conditions (Waldrop and Firestone, 2006), and consequent shifts in community structure could influence the survival behaviour of introduced enteric pathogens. Land-use and management has been implicated in shaping the microbial community by modulating the physicochemical environment (Lauber et al., 2008). It has been shown that intensity of land-use (Jangid et al., 2008), length of time under a particular management (Buckley and Schmidt, 2001), substrate addition (Degens et al., 2000) and the presence of a plant rhizosphere (Garbeva et al., 2004) can contribute to defining microbial community structure. Some work has been carried out to demonstrate the effects of land-use and management on pathogen suppression (van Elsas et al., 2002; Williams et al., 2007; Franz et al., 2008 Yao et al., 2013). However, the pathogen survival response is often variable and difficult to predict within a framework of complex interactions between site-specific factors, including current and historical land-use, the physicochemical environment, predominant management strategies and resultant impact on community composition. In addition, these studies focused solely on a single pathogen, namely *E. coli* O157, despite the fact that survival and behavioural profiles within soil are species, and even strain-specific (Topp et al., 2003). This is because enteropathogens have different physiological properties and life cycles which will influence survivability within the soil matrix (Winfield and Groisman, 2003).

It is therefore unclear whether physicochemical or biotic factors play a dominant role in governing pathogen survival, particularly as few studies have considered both in a coherent manner. Therefore, the aim of this study was to investigate pathogen survival in relation to naturally-contrasting community phenotypes derived from different land-uses. We hypothesised that soil biology, specifically the phenotypic microbial community structure, would be more significant in regulating pathogen decay than soil physicochemical composition, and conducted a controlled microcosm-based study to test this in the context of four model pathogenic bacteria. We prescribed the phenotype as the operationally important entity in this context, as it represents the literal manifestation of the microbial community which the introduced bacteria would have encountered.

2. Materials and methods

2.1. Soil collection and initial screening

Thirty-nine sites across Ireland were initially prescribed based on contrasting land-use, soil type and management regime. Sites consisted of a single uniform field, free of livestock, which was divided into 3 sections. Approximately 20 cores were taken from the top 15 cm of soil (A horizon) across the W transect from each section, and were combined to yield a composite sample. Soils from these sites were then homogenised and sieved to 4 mm. Sub-samples of approximately 5–10 g freeze-dried soil were weighed out and analysed for community composition by PLFA, as described by Frostegård et al. (1997). Soils were also tested for pH using an automated Aqualyser pH meter, % OM (Davies, 1973), and were assessed by hand texturing (DEFRA, 2010). These data were used to select a suite of 12 contrasting soil types, comprising mainly cambisols, gleysols and stagnosols (Table 1), for use in a microcosm experiment investigating pathogen death rates. These 12 soils

Table 1
Physicochemical and biomass properties of the 12 soils utilised for pathogen survival analysis experiments.

Soil ID[a]	Site coordinates	Land use category	Specific land use	Total CEC (ME 100 g^{-1})	pH	Organic matter (%)	Olsen P (ppm)	Organic C (%)	C (%)	N (%)	C:N ratio	Clay (%)	Silt (%)	Sand (%)	Moisture (% field capacity)[b]	Biomass C ($\mu g C g^{-1}$ dry soil)	WRB soil classification
A	52.17N, 6.31W	Grass	Grazing	11.7	6.2	6.1	46.7	3.3	3.75	0.36	10.42	13.6	34.1	52.3	46.3	356	Haplic cambisol
B	52.17N, 6.31W	Grass	Grazing	13.2	5.6	6.4	54.7	3.6	3.80	0.36	10.56	12.9	31.6	55.5	48.3	384	Stagnic cambisol
C	52.52N, 6.55W	Wood	Forestry	26.4	7.5	5.2	8.0	4.1	4.55	0.25	17.97	25.2	33.0	41.8	41.1	230	Ferralic cambisol
D	52.51N, 6.54W	Wood	Willow	17.8	7.6	5.4	94.7	3.5	3.79	0.31	12.09	21.0	22.0	57.0	38.8	263	Ferralic cambisol
E	52.21N, 7.19W	Arable	Maize	10.0	6.4	3.0	70.3	1.5	1.89	0.21	8.84	19.4	32.6	48.1	43.0	81	Luvic gleysol
F	52.21N, 7.18W	Arable	Cabbage	10.0	7.0	3.8	47.0	2.0	2.47	0.22	11.04	21.9	35.9	42.1	44.3	113	Leptic cambisol
G	52.10N, 8.14W	Grass	Grazing	14.8	5.5	7.2	138.0	3.9	5.78	0.44	13.24	16.5	32.3	51.2	41.7	381	Haplic cambisol
H	52.21N, 7.18W	Grass	Grazing	11.8	5.7	6.8	54.7	3.9	4.17	0.41	10.17	19.3	45.8	43.9	45.0	485	Haplic cambisol
I	52.30N, 8.12W	Grass	Grazing	22.0	6.4	13.8	240.0	5.9	7.60	0.77	9.83	23.5	41.4	35.1	54.5	695	Haplic cambisoil
J	52.51N, 6.55W	Arable	Till, mustard cover	13.3	6.9	4.2	178.7	3.0	3.04	0.27	11.26	10.7	22.4	66.9	35.6	122	Haplic cambisol
K	52.21N, 7.19W	Grass	Grazing	12.9	5.9	7.8	86.7	4.0	4.55	0.48	9.55	20.3	36.2	43.6	44.7	415	Haplic cambisol
L	52.51N, 6.55W	Arable	Till, sprayed	12.9	6.9	4.2	145.0	2.8	2.84	0.28	10.27	8.8	21.7	69.5	36.0	115	Haplic stagnosol

[a] c.f. Figs. 2–4 and Supplementary material Fig. S1.
[b] Moisture content at which samples were incubated.

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