The current state of knowledge on the interaction of *Escherichia coli* within vegetative filter strips as a sustainable best management practice to reduce fecal pathogen loading into surface waters

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Abstract Agro-pastoral operations have the potential to threaten public health with loading of diverse pathogens into surface waters through overland flow; increasing awareness of the limitations of fecal indicators has led to development of a number of advancements in detection, source tracking and predictive modeling of public health risk. These tools and techniques are beginning to be integrated into management strategies. The objective of this review was to determine the status of current knowledge and challenges of the fate and transport of *Escherichia coli* in overland flow and their interaction within vegetative filter strip (VFS) as one of these implemented best management practices and to critically evaluate its use in that setting as an indicator organism. With few studies directly focusing on VFS removal of *E. coli* from overland flow, we critically evaluated the available data on movement of *E. coli* from fecal source loading to retention and decay or re-release for potential contamination of water ways and pointed out potential limitations in both pathogen-specific removal and its use as an indicator organisms within overland flow and VFS. Critical areas of focus for future studies to reduce gaps in knowledge were identified, and the integration of newer approaches in source tracking, alternative indicators and the use of non-pathogenic surrogates for field testing of existing VFS models was encouraged. With VFS as a growing field of interest as an

economical conservation practice and as an avenue for conservation of resources for small-scale agro-pastoral operations, management strategies to reduce initial fecal load from either applied manure constituents or shedding from free-range animals will continue to test the limits in the applications of models to overland flow and VFS management strategies. Further studies at the microscale in understanding discrepancies between low and high pathogenicity strains of *E. coli* and between *E. coli* and other fecal pathogens in the context of VFS will be critical. However, nuanced studies are needed to understand either biological or environmental differences in the fate and transport of the diverse types of fecal pathogens within these settings

Keywords Pathogenic *Escherichia coli* · Vegetative filter strip · Microbe fate and transport · Overland flow · Indicator organism · Biofilm · Modeling · Genetic diversity

1 Introduction

This review is intended to review our current understanding of the transport, dynamics and biology of *Escherichia coli* within VFSs and critically evaluate its use in that setting as an indicator organism. We did so breaking down understanding from source to sink in the context of VFSs and how advances in each of those areas have altered our understanding. Since early 1990s, the literature is vast with information based on the fate and transport of manure-

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borne pathogenic microorganisms in overland flows and their interaction with vegetated filter strips including *E. coli*. Manure-borne *E. coli* and other fecal pathogens present a serious management challenge for large and small feedlot operations, as well as, for management of range-grazing herds of domesticated species (Bicudo and Goyal 2003; Gerber et al. 2010; Hubbard et al. 2004). There is a critical need to balance cost-effective and sustainable management options to allow for continued production along while adequately protecting human health from risk of food and waterborne disease outbreaks (Bicudo and Goyal 2003; Boxall et al. 2009; Casey et al. 2015; Gerber et al. 2010). The implications of these public health risks in surface waters from animal operations have been well established since the mid-1970s (Hubbard et al. 2004; Tian et al. 2002), and various mitigation strategies (including vegetative filter strips) have been implemented since the 1980s to address removal of various runoff contaminants into public waters (Lim et al. 1998). The utility of various mitigation strategies continues to evolve with improved technologies for detection and increased understanding of fate, transport and ecology of microorganisms within these systems; however, the advances in understanding and technology juxtapose with severe global pressures such as food scarcity and global climate change that necessitate effective, economically sustainable and practical measures to reduce manure-borne fecal contamination loading into waterways (Boxall et al. 2009; Chiang et al. 2012).

Despite all the advances, waterways worldwide continue to receive manure-borne pathogens unabated world over (Guber et al. 2006). As manure application to crops can provide a low-cost fertilizer and subsequently indirectly provides energy to human populations facing food scarcity (Stout et al. 2005), integrative systems can provide feed for grazing animals while allowing for remediation of harmful constituents from direct application of manure to croplands in order to protect human health. These integrated systems need to be understood from both an engineering and ecological perspective to ensure sustainability. This balance becomes all the more apparent and critical for smaller operations with limited resources and within a local community that depends directly on local surface waters and relies on the food security and economic growth contingent upon success of these operations (Randolph et al. 2007). Although VFS may prove costly than other best management practices for reducing pathogen loading into nearby waterways when feedlots and crops lie in distinct regions, the dual utilization of perennial native grasses or livestock feed vegetation brings operational costs to a minimum (Asbornsen et al. 2013; Bond 2010; Lovell and Sullivan 2006).

The objectives of this review were as follows: (1) to synthesize several bodies of knowledge to provide current status and challenges on the fate and transport of *E. coli* in

overland flow and their interaction within vegetative filter strips; (2) to integrate this working knowledge with improved understanding of *E. coli* as a model, indicator, and pathogenic organism in environmental waters; and (3) to identify key areas for future research to improve management of VFS to maximize protection of human health while minimizing both management and monitoring costs, in particular to benefit small-scale farms and local communities.

2 Background

2.1 Limitations of fecal indicators

As enumeration of manure-based pathogens to determine their fate and transport is costly (Pachepsky et al. 2006), it is important to prioritize modeling and understanding of pathogenic organisms. As such, fecal indicator bacteria (FIB) have been mostly utilized in initial investigations on efficacy and mechanisms by which VFSs remove or reduce manure-borne pathogens and prevent loading into valuable waterways (Blaustein et al. 2015a, b; Bond 2010; Doran and Linn 1979; Guber et al. 2007). However, uncertainty around the reliability and consistency of coliforms as prognostic for enumeration and risk of presence of pathogenic bacteria and other fecal-borne health risks (viruses, parasites) are not new (Chao et al. 2004; Guber et al. 2009; Hazen 1988; Rochelle-Newall et al. 2015), and more recent work suggests that the most robust model for monitoring is tiered (Harwood et al. 2005). Additionally, predictive power needs to be delineated for tropical systems, often facing further limited resources that restrict tiered approaches to monitoring (Rochelle-Newall et al. 2015). As such, it is imperative to look for alternative source tracking methods that are effective, rapid, low cost and adequately predictive (Dick et al. 2010).

2.2 *E. coli* as FIB

Escherichia coli has emerged in recent decades as a preferred indicator for fecal contamination in drinking water and surface waters because of the possibility for thermo-tolerant coliforms to represent non-fecal contamination and the development of faster, affordable, easier, sensitive and specific methods for detection of *E. coli* with the major limitation identified as it identifies only recent contaminations due to its lack of environmental stability (Odonkor and Ampofo 2013). With respect to transport dynamics within overland flow, subsurface flow and mechanical filtration, *E. coli* likely provides a reasonable representation for bacterial fecal pollution (Blaustein et al. 2015a, 2016; Martinez et al. 2014; Sinclair et al. 2009). Bacteria sizes range from 0.05 to 10.0 µm, with different shapes such as coccus (spherical or egg-shaped), oval, straight or curved

rods (cylindrical shape), spiral, spiral helix or filaments or often clumped into colonies (Odonkor and Ampofo 2013), and with densities close to that of water ranging from 1.0 to 1.1 g cm⁻³. The facultative anaerobes *Escherichia* are gram-negative straight rods with typically rod-shaped cells, about micrometers (μm) long and 0.5 μm in diameter, with a cell volume of 0.6–0.7 μm. *E. coli* use mixed-acid fermentation in anaerobic conditions, and when combined with their aerobic respiration pathways, they can utilize them a wide variety of redox pairs, making them versatile as an indicator organisms. In general, the species grows optimally at 37 °C; however, pathogenic strains demonstrate delayed growth patterns, growing on MacConkey agar plates at 44.5 °C (Odonkor and Ampofo 2013). *E. coli* grows optimally at 37, and the 44.5 °C incubation step is used as a selective process as *E. coli* can still grow at that temperature, but many environmental bacterial strains cannot. The diversity of *E. coli* strains, origins and pathogenicity necessitates continued evaluation of the context in which *E. coli* is utilized as an indicator organism versus a de facto pathogenic organism of its own right.

2.3 Diversity of fecal pathogens and sources contaminating surface waters

Fecal loading can pose a wide array of pathogens of concern to human health, including bacteria, protozoa, viruses and helminthes (Gerba and Smith 2004; Savichtcheva and Okabe 2006; Tran et al. 2015). The main sources of contamination include animal feedlots, impervious surfaces, and overland flow from agricultural land, failing septic systems, birds/wildlife, domestic pets and raw sewage (Pachepsky et al. 2006). Source tracking methods have emerged as one means by which to determine key contributors to surface waters in order to refine monitoring and evaluate potential interventions (Dick et al. 2010; Savichtcheva and Okabe 2006; Tran et al. 2015). Indeed, though fecal indicators may provide a warning for potential risk in surface waters, the diverse potential sources, physical properties, environmental hardness and life cycles of all these pathogens make it difficult to find a single adequate indicator (Lalancette et al. 2014). Further, complicating detection and risk assessment is the diversity of pathogenicity of strains of any of these organisms.

Despite some limitations, *E. coli* continues to advance as a versatile organism for water quality monitoring. Considerable advances for the application of *E. coli* as an index or model organism have been made in recent years (Odonkor and Ampofo 2013). Both diagnostics specific to disease-causing strains of *E. coli* (Ahmed et al. 2007; Bonetta et al. 2011; Ram et al. 2011; Shelton et al. 2006) and rapid detection methods for specific bacterial microorganisms have shown good correlation with

standardized indicator methods for *E. coli* and, at times, coliforms that depend upon organism replication, taking minimally 18–24 h (Liu et al. 2009; Noble and Weisberg 2005; Savichtcheva and Okabe 2006; Shih et al. 2015). These newer diagnostics hold promise in that results are delivered within hours. Both environmental detection data and outbreak incidents with protozoa and viruses have indicated traditional coliforms and FIB may not be adequate predictors for presence of these organisms (Karanis et al. 2007; Lalancette et al. 2014; Savichtcheva and Okabe 2006). Thus, application of these indicators in any new environment or evaluation of an intervention strategy in environmental management must be critically evaluated.

2.4 Role of VGFs in contaminant removal

VGFs have emerged as a low-cost, remarkably effective BMP in the abatement of the loading of agricultural contaminants from overland flow to transport into surface waters (Hickey and Doran 2004; Zhang et al. 2010). Understanding of mechanism of removal with respect to the sediment trapping (Liu et al. 2008) of nutrients (Mayer et al. 2007; Roberts et al. 2012), land-applied herbicides, fertilizers (Liu et al. 2008; Sabbagh et al. 2009) or other toxicants (Allaire et al. 2015), and finally animal- or human-derived fecal pathogens (Table 1) (Tyrrel and Quinton 2003) continues to evolve as the implementation and subsequently utility of the BMP advances. Removal can result from physical infiltration, deposition and sorption of compounds (Fig. 1) (Allaire et al. 2015), as well as direct uptake by vegetation and microbial degradation of compounds or pathogens through biofilm formation. While the VGFs slow the speed of overland flows, the efficacy can vary significantly and is less well described for underground movement. Slope (Kouznetsov et al. 2007), surface area, width, soil (Rahmana et al. 2014), rainfall (Blaustein et al. 2016), topography and hydrology can all influence the variability. Recent work has emphasized the role of preferential flow, particularly during saturation, heavy rainfall and formation of surface gullies and eddies phenomena and in particular for the environmental fate of hydrophilic compounds (Allaire et al. 2015) and colloids or colloidal bound contaminants or microorganisms (Mohanty et al. 2016).

Three distinctive layers act in contaminant filtration and removal: surface vegetation, root zone and subsoil horizon (Stocker et al. 2015; Olilo et al. 2016). Overland flow occurs when inflow rate exceeds the infiltration VFS's infiltration capacity due to saturation and soil hydraulics (soil type and infiltration capacity, plot width and slope, topography, microclimate, and vegetation characteristics). Once the overland flow infiltrates into subsoil, it becomes lateral subsurface flow or interflow return capillary flow.

Table 1 Some seminal pollutant removal efficiency for vegetated filter strips

Filter type	Microorganism source	Slope (%)	Plot length (m)	Soil type	Pollutant	Removal efficiency (%)	References
Kentucky Blue grass (<i>Poa pratensis</i> L.)	Friesian lactating dairy manure (<i>Bos taurus</i>)	2, 4	2.7	Silt loam	Fecal coliform	60.9, 69.7	Stout et al. (2005)
Residual dry matter of rye grass (<i>Lolium multiflorum</i> Lam.), wild oats (<i>Avena fatua</i> L.), soft chess (Bromus hordeaceus, L.), redstem filaree [<i>Erodium cicutarium</i> (L.) L'Her]	Cattle manure	5, 20, 35	3	Fine loam	Fecal coliform, <i>E. coli</i>	94.8–99.995	Tate et al. (2006)
Pensilvania grasses	Bovine manure	20	6	Sandy loam and silt loam	<i>E. coli</i>	Above 90	Pachepsky et al. (2006)
Annual grasses e.g., forbs, perennial grasses of California coastal rangelands	Dairy cattle manure	2, 13, 15, 30	5.6–61	Silt loam	Fecal coliform bacteria	75, 24–80, 75–99	Lewis et al. (2010)
Fescue grass	Feedlot	2	30, 150	Silt loam	Fecal coliform, <i>E. coli</i> , fecal streptococci bacteria	100, 79.1–100, 69.2–99.8	Douglas-Mankin (2011)
Fescue grass	Swine manure, bovine manure	5	6.5	Loamy, clay loam, loam	<i>Escherichia coli</i> , <i>Salmonella</i>	5–30	Cardoso et al. (2012)

Fig. 1 Conceptual model of *E. coli* sources, transformations and transport processes in an agro-pastoral land-use system

Steep slope and microtopography can increase overland flow velocity, transport capacity and uniformity, thus reducing overall removal capacity. Since VFS can directly influence both these parameters through alterations in land use and topography, strategic implementation of VFS can influence the fate and pathway of dissolved nutrients, chemicals, and fecal pathogens through direct mediation of infiltration capacity and interflow in the vadose zone (root zone of VFS plants) and subsoil. Furthermore, the width of VFSs regulates the strip's removal capacity by influencing contaminant lag time during adsorption and degradation processes in the vadose and subsoil zones.

3 Pathogen movement in overland flow

3.1 From manure to surface waters: variability in release

In evaluation of VFS as a remediation for overland flow to prevent surface water contamination by fecal pathogens and the role of *E. coli* as an indicator organism in that process, it is imperative to understand the diverse life cycle and size of manure-borne pathogens, variability of pathogen release from manure and potential variability of pathogen virulence (Blaustein et al. 2015a; Doran and Linn 1979; Gerba and Smith 2004; Noble and Weisberg 2005; Odonkor and Ampofo 2013). In the delineation of predictive models, this integration of microorganism biology with understanding of

hydraulics and local agricultural engineering is absolutely critical in the face of climate change, which will test the limits of any applied model (Chiang et al. 2012).

Reports show that farm animals often carry and release *E. coli* serotype O157:H7 that could cause death in humans at concentrations as low as 50 CFU/100 mL⁻¹ (Dombek et al. 2000). Potentially severe disease-causing *E. coli* bacteria isolated from manure and/or sewer systems include Enteroaggregative *E. coli* (EAEC), Diffusely adherent *E. coli* (DAEC), Enterotoxigenic *E. coli* (ETEC), Enteroinvasive *E. coli* (EIEC), Uropathogenic *E. coli* (UPEC), Meningitis-associated *E. coli* (MNEC), Enterohaemorrhagic *E. coli* (EHEC), Extraintestinal pathotypes (EIEC) and Enteropathogenic *E. coli* (EPEC) (Kaper et al. 2004; Lewis et al. 2010). Although the provisional guidelines for surface water bodies are 100 colony-forming units (cfu)/100 mL of fecal coliforms (US EPA 1994), for swimming, these limits are often exceeded (for instance, US policy response to this is the introduction of total maximum daily loads, TMDL, policy), which refers to loading from a source (for instance, 126 cfu/100 mL for *E. coli*). Waters exceeding limits for drinking are considered impaired (0 CFU/100) (Gallagher et al. 2013).

3.2 Microbe transport in overland flow

Given the variability in release, size and durability of fecal pathogens, it becomes critical to determine the extent which *E. coli* can adequately model transport in overland

flow both by understanding its infiltration, deposition and sorption, as well as uptake or degradation (Fig. 1). Once released into overland flow, microorganisms can be partitioned and transported as single cells, attached to manure particles, or attached to soil particles (Muirhead et al. 2006a; Tyrrel and Quinton 2003). Subsequently, pathogenic *E. coli* and other fecal microorganisms may be trapped in sediment and soil, attached to subsurface solids, detached, or retained in litter, micropores, or soil macropores, of variable shape and size (Abu-Ashour et al. 1998). Pore size and shape influence transport and dynamics in overland flow and VFS, while microenvironmental conditions, such as the availability of nutrients and predation, influence longevity (Abu-Ashour et al. 1998). The role of each in microorganism transport can be critically evaluated through studies of variable scale along the transport pathway, including at the soil core, pedon, hill slope or catchment areas (Pachepsky et al. 2006). Data generated from the fine scale help to determine mechanism of transport and survival; the coarse scale studies help compare relative importance of each, while watershed studies help to apply knowledge to the decision making and management (Pachepsky et al. 2006). Further studies at each level are needed to integrate understanding across manure pathogen categories and types and evaluate fecal indicators in the context of various interventions or management decisions.

Interaction of VFS, infiltration into soil matrix, partitioning, biofilm formation, adsorption/detachment, straining and biological die-off/regrowth have to be combined to design and assess manure management strategies in association with projected overland flow regimes and pathogen loads (Blount 2015; Gallagher et al. 2013; Pachepsky et al. 2006; Quero et al. 2015). While initial studies of manure-borne fecal microorganisms pathogens such as *E. coli*, developed in the 1980s, were typically concerned with pedon and hill slope scales, in recent years, hill slope and watershed scales have led insight into the effects of soil, vegetation, management, and weather on the fate and transport of fecal pathogens (Overcash et al. 1981; Moore et al. 1982, 1983, 1988; Guber et al. 2005a, b, 2006, 2007; Pachepsky et al. 2006; Moreira et al. 2006; Allaire et al. 2015; Rippy 2015). Understanding at both the macro- and microscale can lend insight into how various management strategies can reduce fecal pathogen loading into surface waters and how well fecal indicators function as a predictive means in the implementation of those strategies. Since it is impossible to cover every possible scenario in field studies, it becomes imperative to develop robust predictive models for ground-truthing and field validation.

Despite the identified limitations of *E. coli* as an indicator organism and existing gaps in knowledge of how broadly findings can be extrapolated across strain, species

and organisms, *E. coli* has been a key player in the critical evaluation of best management practices to reduce fecal loading to surface waters, particularly with respect to manure-borne pathogens in the agricultural setting. A number of recent reviews have improved the understanding of different segments of the fate and transport of fecal pathogenic microbes (Jamieson et al. 2002; Ferguson et al. 2003; Tyrrel and Quinton 2003; Kaper et al. 2004; Oliver et al. 2005, 2006, 2007; Unc and Goss 2003; Duchemin and Hogue 2009; Davies et al. 2009; Rippy 2015) in overland flow, and research has begun to evaluate this in the context of one low-cost management option: the integration of vegetative filter strips.

3.3 Fecal pathogen removal in VFS systems

Size and shape of *E. coli* influence their transport through VFS, infiltration and leaching into soil structure or texture, porosity or bulk density (Gannon et al. 1991a, b; Tan et al. 1991; Huysman and Verstraete 1993). Soil texture (saturated or unsaturated, water content) such as sand mixed with gravel and time influences these bacterial transport and fate (Bitton and Harvey 1992). In no-till soils, distribution and continuity of macropores notably, preferential flow pathways and initial water content play significant roles in the process (McMurry et al. 1998; Paterson et al. 1992). Leaching rates are higher in no-till than tilled soils (Van Elsa's et al. 1991). VFS enhances filtration of *E. coli*, adsorption on soil and plant surfaces and absorption by plants. Bermuda grass, for example, traps maximum percentages of *E. coli* at varying distances including sand (3 m), silt (15 m) and clay (122 m) from the manure application area, respectively (Douglass-Mankin 2011). Tall vegetation is an effective media to reduce *E. coli* yield by reducing surface overland flow, increasing infiltration, and protecting the soil surface from detachment or deterioration because of direct rainfall impact (Duchemin and Hogue 2009; Martinez et al. 2014). *E. coli* and other fecal microorganism from point source pollutants (e.g., septic effluents) or non-point source pollution are transported, leached and infiltrated through soils and subsurface flow from a few centimeters on the surface to 830 cm into the soil matrix. Bacteria move faster in soils than protozoan parasites such as *Cryptosporidium parvum* (Mawdsley et al. 1996). VFS enables overland flow and microorganisms to infiltrate into the soil profile (Fajardo et al. 2001). Filter media drag resistance is the dominant force in retarding the surface overland flow evidenced when using artificial filter strip to develop an equation of flow by employing the momentum balance principle (Kao and Barfield 1978). Sedimentation is insignificant for *E. coli* (Gannon et al. 1991a). Since the density of *E. coli* is usually in the range of 1.0–1.1 g/cm⁻³, nearly that of density

Fig. 2 Transport and fate of overland flow relative to VFS

of water, sedimentation may not happen for *E. coli* (Characklis and Marshall 1990). This statement is supported by previous studies on the surface and vertical transport of fecal coliforms (Walker et al. 1990; Edwards et al. 2000). There is a knowledge gap existing on quantitative rates and extent of *E. coli* and other fecal microorganisms' leaching at the field or watershed scale. *E. coli* and other fecal microorganisms sedimentation occurs when the organisms move vertically through the soil profile or by retention as described by Correll and Weller (1989) and Muñoz-Carpena and Parsons (2011) (Fig. 2).

4 Improving modeling of fate and transport of fecal organisms in overland flow and VFS

4.1 Release of fecal pathogens into overland flow

The plethora of diverse models developed and applied to simulate the release of manure-borne *E. coli* and other fecal microorganisms is largely based on the exponential release at the plot, pedon, hill slopes and watershed scales. Two prominently used model by government and regional monitoring agencies include Hydrological Simulation Program-FORTRAN (HSPF, Bicknell et al. 1997) and Soil and Water Assessment Tool (SWAT, Sadeghi and Arnold 2002; Vadas et al. 2004; Bradford and Schijven 2002); they were developed and validated using rainfall-induced storm events and natural tracers (organic carbon and chloride ions) for modeling of fate and transport of coliforms and other manure constituents applied to topsoil, (Guber et al. 2006), but have not focused on the transport of specific

pathogens present in overland flow from agro-pastoral land-use systems (Tyrrel and Quinton 2003; Jamieson et al. 2004; Paul et al. 2004; Cardoso et al. 2012; Allaire et al. 2015).

This gap in modeling reflects the limited information available on the factors affecting manure dissolution rates, release of the microorganisms in overland and transport state along a vegetated buffer filter strips (Guber et al. 2006, 2007; Keewok et al. 2014). As vegetated filter strips management and implementation evolves, it will be critical to integrate this information to adequately protect public health. *Cryptosporidium parvum* and *Giardia duodenalis* oocysts from dairy calf manure were analyzed in the overland flow water, and transport is influenced by both organism-specific factors and environmental factors (Bradford and Schijven 2002). Release magnitude and subsequent transport of microorganisms in overland flow is affected by duration of rainfall and age of fecal deposits (Thelin and Gifford 1983). Microbial fate is determined by attenuation by environmental factors such as sunlight radiation, soil pH and soil moisture and die-off following first-order decay (Tian et al. 2002). The surface characteristics and size of microbes will impact the partitioning between settling, release into the water column, and aggregation with particles for transport. Point source contamination, such as sewer discharge, further complicates determination of the quantity of microorganisms from nonpoint source agro-pastoral land-use system. Even in non-managed lands, surface overland flow passes through indigenous grassed vegetation that holds back some microbes through in-rill mobilization and infiltration losses (Fig. 1). Even with respect to *E. coli*, there are

discrepancies within the literature with respect to longevity of microorganisms within Cowpat and nature of release and transport into overland flow, suggesting management decisions must be site specific. While Muirhead et al. (2005, 2006a, b) showed retention of significant amounts of *E. coli* within cowpat for more than 30 days and noted that eventual release was as single, transportable cells (Muirhead et al. 2005, 2006b), whereas other work has indicated substantial decay in stored manure as a means to reduce fecal loading to overland flow (Meals and Braun 2006) and the association of *E. coli* and enterococcus with particles in release and overland transport (Soupir et al. 2010).

Very few studies have evaluated this release or transport (including settling velocities, association with particulates) in the context of the presence of native grasses, but the work that has been done has emphasized the importance of hydrologic soil surface conditions (Cardoso et al. 2012; Fox et al. 2011). Further studies integrating microorganism release from cowpat and transport characteristics within the context of native grasses and VFS will not only lend insight into this avenue for management but also assist with understanding influencing factors on nature of release (Olilo et al. 2016).

4.2 The soil matrix

There is more information available as to how various microbial contaminants interact once they enter the soil matrix. In addition, as VFS models were originally designed and tested with impact on sediment, organic matter and nutrients in mind, the impact on these can have a resulting impact on microorganism retention, release and transport, though the interaction varies considerably. Soil structure or texture, porosity or bulk density and bacterial or pathogen size influence transport, infiltration and leaching in soils (Gannon et al. 1991a; Huysman and Verstraete 1993; Jamieson et al. 2004). Soil structure and texture influence the soil macropores and movement of microorganisms in the soil column, thus influencing infiltration and leaching of water. In the water, microorganisms are moving together attached or unattached to soil particles vertically.

In particular, no till soils management (soils that are not ploughed and are left undisturbed) influences distribution and continuity of macropores, and preferential flow pathways in the soil matrix and initial water content (Allaire et al. 2015). Leaching rates are higher in no-till than in tilled soil (Goss and Richards 2008), suggesting a possible another management to critically evaluate in the context of VFSs. It is well established that protozoal pathogens undergo a substantially slower and different route of transport than microbes (Dumetre et al. 2012; Mawdsley et al. 1995), while there are less available data for virus

transport and characterization of interactions with the soil matrix (Oliver et al. 2005); however, it is clear traditional indicator organisms in this context will not sufficiently enable transport characterizations of diverse organism types (Oliver et al. 2005) and much further characterization needs to be done, particularly in the context of VFS. From nutrient and microbiology data, it is evident that VFS helps to facilitate in filtration from overland flow into the soil profile (Fajardo et al. 2001).

VFS enhances vegetated filtration of suspended sediment, adsorption on soil and plant surfaces and absorption of soluble pollutants by plants. Pioneering work with Bermuda grass has demonstrated the importance of critical evaluation of sediment trapping in various soils, with the greatest amount of sediment settling within 3 m for sand, 15 for silt and much further for clay (122 m) from the manure application site (Douglass-Mankin 2011). In addition, tall vegetation enhances retention by slowing overland flow rates, facilitating infiltration, and protecting the soil surface from detachment or deterioration from direct rainfall impact (Duchemin and Hogue 2009; Martinez et al. 2014).

Figure 2 illustrates the possible fate of *E. coli* and other fecal microorganisms released into overland flow, and sedimentation occurs when the organisms move vertically through the soil profile or by retention; while sedimentation is likely insignificant for individual organisms given their size and density (Gannon et al. 1991a), those associated with colloidal particles moving through overland flow and subsequently being retained need to be further investigated in the context of VFS, particularly with regard as to how to best manage VFS to facilitate sedimentation and deposition.

4.3 Role of biofilms

Most pathogens adsorb to particulates more than 16 µm in size that help them move at faster rates in developed overland flow models; (Haydon and Deletic 2006) in contrast, the interactions within agro-pastoral systems have not been well described. In addition to the role of native grasses on release of pathogenic organisms from manure and dispersion into overland flow, more physical-chemical interactions at the microscopic level can be profoundly changed by biofilm formation and other survival strategies of microorganisms. It is imperative to incorporate the growing body of knowledge in the biology of these organisms into predictive models since life strategies can impact survival, fate and even pathogenicity. Future research to enhance existing VFS models must focus on partitioning coefficients between attached and unattached phases of bacteria and other microorganisms to particulates

and elucidate factors that influence this partitioning (Jamieson et al. 2002, 2004; Muirhead et al. 2006b).

The biofilm formation by *E. coli* strains in environmental studies have indicated adaptation to secondary habitats outside their primary hosts including vegetation such as macroalgae and vegetative filter strips (Byappanahalli et al. 2003; Moreira et al. 2006; Quero et al. 2015). Since pathogenic strains of *E. coli* utilize attaching and effacing histopathology induced through selective expression of virulence genes for Enteropathogenic *E. coli* (EPEC) and Enterohaemorrhagic *E. coli* (EHEC) that are expressed during biofilm formation (Kaper 2005; Kaper et al. 2004) and could play a role in biofilm development in removal from overland flow (Kaper et al. 2004; Moreira et al. 2006). Biofilm forming (auto aggregation) pili are responsible for bacterial aggregation during biofilm development. Since virulence traits of EPEC pathotype including biofilm forming pili (BFP) and encoding secreted proteins (EspA, EspB and EspD) are entangled in biofilm development, it will be important to understand how this impacts retention or removal of pathogenic versus non-pathogenic strains of *E. coli* and the resulting impact partitioning relationship.

Partitioning of *E. coli* between overland flow and sediment, then between soil micropore solution and solid phases, then between stream bottom and bank sediments has been described in groundwater models to affect the transport and adsorption of microorganism (Pachepsky et al. 2006). Partitioning of fecal bacteria into the attached and unattached phases occurs during initial release from manure, overland flow and subsurface transport, and stream and bed transport is assumed to be linear, but certain kinetic assumptions such as instantaneous equilibrium may not adequately predict discrepancies between the solid-liquid distribution of *E. coli* or the presence of biofilm formation, which could be enhanced in the presence of VFS, since time of contact, mixing intensity, and access to different parts of micropore space influence kinetics of equilibrium (Kaper et al. 2004; Pachepsky et al. 2006). It will be important to incorporate more nuanced approaches to modeling if we are accurately to predict human health risk.

It will also be important to determine soil characteristics and how those will be altered by the presence of native grasses. Established factors that encourage *E. coli* attachment to soil particles include soil hydrophobicity, presence of other bacteria, ions and electrostatic interactions (Pachepsky et al. 2006); less data are available for other bacteria, protozoa or viruses. Furthermore, the distribution of *Giardia* oocysts could be explained by their attachment or straining in disturbed soil columns (Kuczynska et al. 2005). Extensive work has been done in recent years to describe and define surface characteristics of protozoa,

such as *Giardia* and *Cryptosporidium*, in addition to the development of non-pathogenic surrogates for the purposes of transport studies (Dumetre et al. 2012). These have yet to be applied within agro-pastoral models managed with VFS and can lend insight into pathogen retention and breakthrough, particularly with respect to movement through macropores of undisturbed, no-till soil. Macropores have been identified as critical environment for potential re-release of pathogenic bacteria in overland flow, particularly under heavy rainfall events resulting in re-suspension and movement of sediments (Guber et al. 2006; Pachepsky et al. 2006). The decreased attachment of bacteria to particulate matter in the presence of manure is possibly mediated by competition between bacteria and dissolved organic matter for attachment sites on soil, modification of soil mineral surfaces by soluble manure constituents, or modification of bacterial surfaces by dissolved organic matter (Guber et al. 2005a, 2006), while the interaction of biofilms with bacterial mobility through soil has been documented, with the resulting impact of reduced soil porosity, in turn resulting in more bacterial retention or less transport (Gerba and Smith 2004).

4.4 Microbe survival and die-off

Soil geochemical conditions and availability of substrates predominantly influence the decay or die-off and growth of microorganisms (Kei et al. 2002). Microbial decay in soil has long been recognized to follow three distinct patterns, namely first-order decay, growth followed by first-order decay; and first-order decay with variable die-off rates (Bradford and Segal 2009; Doran and Linn 1979; Oliver et al. 2006; Wang et al. 2004; Zhai et al. 1995) (Table 2). First-order decay equation has largely described decay in stored manure, soil, land-applied manure, streams and groundwater, but some studies have shown that a first-order decay model with a two-stage function better represents the longevity of *E. coli* inoculated in soils (Mubiru et al. 2000; Zhai et al. 1995).

Environmental factors such as solar radiation, soil moisture content, temperature and pH have been incorporated into decays model over time, along with the possibility for re-growth in the field (Oliver et al. 2006; Pachepsky et al. 2006; Wang et al. 2004). Recent work has put these models into practice to critically evaluate management techniques for reducing public health risks in all three decay situations. For example, recent work evaluated first-order decay of generic *E. coli*, *E. coli* 0157:H7 surrogates, *Salmonella senftenberg*, *S. typhimurium*, and *Listeria monocytogenes* surrogates, in static manure piles maintained in four different configurations; composting facilitated by use of straw for increased aeration, self-

Table 2 *E. coli* die-off and first-order decay rates in freshly excreted dairy cow manure

Description of study	Organism	Environmental variables	Length of study (days)	Die-off rate, k (days ⁻¹)	References
Die-off in freshly excreted dairy cow manure					
Laboratory based	<i>E. coli</i>	Three moisture contents (30, 55 and 83 %) and three temperatures (4, 27 and 41 °C)	Ranged from 35 to 103	0.11 day ⁻¹ at 4 °C 0.20 day ⁻¹ at 27 °C 0.32 day ⁻¹ at 41 °C	Wang et al. (2004)
Dairy manure, inoculated with <i>E. coli</i> O157:H7					
Laboratory based	<i>E. coli</i> O157:H7	Variable moisture and temperatures	Ranged from 27 to 60	Top layer 0.111 day ⁻¹ at 4 °C (75 % RH), 0.046 day ⁻¹ at 20 °C (50 % RH) and 0.112 day ⁻¹ at 37 °C (30 % RH) Middle and bottom layer 0.054 day ⁻¹ at 4 °C, 0.074 day ⁻¹ at 20 °C, and 0.279 day ⁻¹ at 37 °C	Himathongkham et al. (1999)
Freshly deposited cattle feces (steers)					
Laboratory based	<i>E. coli</i>	Incubated at 15 °C, 25 % and 50 % moisture	111	0.054 day ⁻¹ (25 % moisture) and 0.058 day ⁻¹ (50 % moisture)	Oliver et al. (2006)
Milk, heifer and beef cowpats on grazed pastureland					
Field based	<i>E. coli</i> and fecal coliform	Two seasonal studies, deposition in late April and mid-July	60–120	April deposition: 0.01593 day ⁻¹ July deposition: 0.02332 day ⁻¹	Mostaghimi et al. (1997)
In-field monitoring of bacterial, cowpats applied to pasturelands					
Laboratory and field based	<i>E. coli</i> and enterococci	Four seasonal studies, the spring, summer, fall and winter	120	Enterococci ($k = 0.0978$ day ⁻¹), <i>E. coli</i> ($k = 0.0995$ day ⁻¹), ($k = 0.0581$ day ⁻¹ for <i>E. coli</i> and $k = 0.0557$ day ⁻¹ for enterococci)	Soupir (2007)

heating capacity and heat retention was found to enhance decay across organisms, thus reducing public health risk when applied to managed lands (Millner et al. 2014). Other work has emphasized nutrient management plans to match the evapotranspiration rate so that little advective transport of fecal indicators (enterococcus, fecal coliforms and total *E. coli*), occurred below the root zone and that rapid die-off (<1 month) occurred for remaining microorganisms (Bradford and Segal 2009). The batch experiments suggested biotic factors played a larger role in decay in the soil environment. Work now needs to continue to evaluate discrepancies of decay across organisms and in different management scenario, including the utilization of VFS under various configurations and with native grasses with variable root zone penetration and cover.

4.5 *E. coli* and other fecal microorganisms' pathogens transport models

The majority of fate and transport models have been developed and tested with indicator organisms rather than pathogenic organisms (Pachepsky et al. 2006). While necessary in development of models due to limitations imposed by cost, need to compare to existing standards, and protection of public health (by unwanted release of pathogenic organisms into the environment), the advent of avirulent pathogens or innocuous surrogates has allowed for the integration of expanding understanding of discrepancies in both the physicochemical properties of the organisms and biology (Sinclair et al. 2012). As our understanding of biological die-off/regrowth, partitioning,

Table 3 Summary of methods, their description, application and reference for application of method

Test/type of technology	Description	Application (indicator, source tracking, strain identification)	Type (presence/absence, quantification)	Turn around time for results (h)	References for application of method
I. Partitioning and separation of microorganisms					
i. Filtration					
	The membrane filtration method gives a straightforward count of bacteria in the water medium based on the growth of colonies on the upper part of the membrane filters. When water is passed through membrane filters, it retains the bacteria. After filtration, the membrane is placed on a selective and differential medium, mTEC, incubated at 35 ± 0.5 °C for 2 ± 0.5 h to resuscitate injured or stressed bacteria, and then incubated at 44.5 ± 0.2 °C for 22 ± 2 h. Following incubation, the filter is transferred to a filter pad saturated with urea substrate. After 15 min, yellow, yellow-green or yellow-brown colonies are counted with the aid of a fluorescent lamp and a magnifying lens	Indicator	Presence/absence	22 ± 2	Francy and Darner (2000), Dawson et al. (1981), Ling et al. (2002)
ii. Centrifugation					
	The method frequently used to determine partitioning between unattached and particulate attached bacteria is centrifugation. Using centrifugation to separate microbial fractions assumes that microbial sorption was not affected during the process. Centrifugation was also used to determine attachment of <i>E. coli</i> to montmorillonite and kaolinite. Bacteria have been separated between phases by injecting a Nycodenz solution below the suspension and then centrifuging the samples. Differential centrifugation separates <i>E. coli</i> from soil particles while estimating adsorption process	Indicator	Presence/absence	48	Characklis et al. (2005), Huysman and Verstraete (1993), Muirhead et al. (2005)
iii. Homogenization					
	This process is for settling microorganism after sampling and separation from other particles	Indicator	Presence/absence	48	Davies et al. (1995), McDaniel and Capone (1985)
iv. Sonication					
	Sonication is a dispersion technique or chemical surfactant, which disrupts the attachment of bacteria to surfaces, for example, sonification was used to disperse bacteria present in bottom soil. Those methods are good for dislodging and enumerating bacteria attached to sediments	Indicator	Presence/Absence	48	Epstein and Rossel (1995), Davies et al. (1995), Yoon and Rosson (1990)

Table 3 continued

Test/type of technology	Description	Application (indicator, source tracking, strain identification)	Type (presence/absence, quantification)	Turn around time for results (h)	References for application of method
2. Microscopy					
i. Light					
a. Epifluorescent microscopy	Microscopic observations of cells in natural environments often exceed the cultured cells by orders of magnitude. Light microscopy has been leading in detection of <i>E. coli</i> and other fecal microorganism pathogens where samples could be fixed with methanol or iodine, stained with Giemsa stain and visualized and photographed in inverted or normal microscope for enumeration in epifluorescence microscopy	Strain identification	Quantification	1–2	Mukamolova et al. (2003)
b. Light microscopy without epifluorescence	Light microscopy has been leading in detection of <i>E. coli</i> and other fecal microorganism pathogens where samples could be fixed with methanol or iodine, stained with Giemsa stain and visualized and photographed in inverted or normal microscope for enumeration	Strain identification	Quantification	1–2	Moreira et al. (2006), Mukamolova et al. (2003)
ii. Electron	Electron microscopy has been leading in detection of <i>E. coli</i> and other fecal microorganism pathogens where samples could be fixed with methanol or iodine, stained with Giemsa stain and visualized and photographed in electron microscope for enumeration	Strain identification	Quantification	1–2	Mukamolova et al. (2003)
3. Radioisotope labeling	The state combined in situ radioisotope labeling of sediment bacteria, bacteria dislodging by ultrasonic treatments, and enumeration using fluorescent staining to determine bacteria enumeration in sandy soil, the protocol accounted for between 88 to 98 % of all bacteria present in soil	Source tracking	Quantification	24–48	Epstein et al. (1997)
4. Enzyme-based technology	Enzyme-based methodologies, which simultaneously detect both total coliforms and <i>E. coli</i> , are the standard for microbiological analysis of water. These tests base their detection power on enzymes β -D galactosidase and β -D glucuronidase. Enzyme-based coliform and <i>E. coli</i> methods must include enhancements in order to work effectively in a variety of water matrices, because buffers, salts and micronutrients enhance enzyme expression. These additives are particularly important in tests that permit enumeration, where the enzyme production from a single organism is detected. Another important ingredient in these tests is an antibiotic (i.e., Cefsulodin) added to suppress the activity of non-coliforms while leaving the coliforms unaffected	Indicator	Presence/absence	18–48	USEPA (2002)

Table 3 continued

Test/type of technology	Description	Application (indicator, source tracking, strain identification)	Type (presence/absence, quantification)	Turn around time for results (h)	References for application of method
5. Molecular cloning and biotechnology					
i. Recombinant DNA	Recombinant DNA techniques such as plasmid purification involves inserting pieces of a foreign DNA into a plasmid such as insulin generation	Strain identification	Quantification	18–48	Sambrook et al. (1989), Quero et al. (2015)
ii. Polymerase Chain Reaction (PCR)	<p>Polymerase chain reaction (PCR), involving cell digestion, ligation, transformation could be used for the amplification of the DNA particles. It is an existing molecular cloning technique required to separate bacterial cells to magnify the DNA fragments. PCR is an amplification process that requires a DNA template together with a free 3'-OH. The reaction occurs in three sequential steps involving a host start-denaturation at a specified time at a specified temperature, where the DNA is heated to 95 °C to make it single stranded. This is followed by annealing process where the two primers bind the appropriate complementary strand, during cooling to some specified temperature, followed by an addition of <i>Taq</i> DNA polymerase stock solution in a DNA thermal cycler. The third a final step is primer extension at 72 °C, where DNA polymerase extends the primer by its polymerase process. A base pair product is usually observed when amplified with a primer pair and a DNA template. The cycling process usually consists of 35 cycles of denaturation at a specified temperature for some seconds, annealing at some specified temperature for some seconds, and primer extension at a specified temperature for some seconds. A final extension at some temperature for some time followed by soaking at some temperature could conclude the process. The thermal cycle could continue until all the molecules are completely amplified</p>	Strain identification	Quantification	18–48	Olandi and Lampel (2000), Quero et al. (2015), Sambrook et al. (1989)
iii. DNA electrophoresis	DNA electrophoresis could be the existing molecular cloning techniques required to separate bacterial cells into different molecular weights, because each molecule travels at a different speed depending on its molecular weight	Strain identification	Quantification	18–48	Sambrook et al. (1989), Quero et al. (2015)

Table 3 continued

Test/type of technology	Description	Application (indicator, source tracking, strain identification)	Type (presence/absence, quantification)	Turn around time for results (h)	References for application of method
iv. Western blotting	A useful technique in both cell and molecular biology techniques. It is used to identify proteins located from complex protein mixture. These tasks are accomplished through size separation, transferring to a solid system and using primary and secondary antibody to visualize marking target protein	Strain identification	Semi-quantification	18–48	Sambrook et al. (1989), Quero et al. (2015)

infiltration, straining, and adsorption/detachment expands, studies need to be done to validate models across organism types. While convective phenomenon of pathogenic microorganisms has been described to some extent at the plot level, little data exist on differences in mobility of manure-derived pathogens transport at hill slope and watershed scales, particularly in the context of VFS (Collins and Rutherford 2004; Davis et al. 2009). In addition, within VFS removal of sediment, nutrients and indicator microorganisms from overland flow, there is now a need to incorporate newer tools, such as surrogates and source tracking to more accurately predict public health risk (Guber et al. 2006).

As the impacts of global climate change become more apparent to the modeling of agro-pastoral impacts on surface waters (Mango et al. 2011), it is imperative to develop dynamic models that can simulate a wide range of hydrologic conditions. Munoz-Carpena and Parsons (2004, Muñoz-Carpena et al. (1999) first proposed and developed the VFSMOD-W model system. VFSMOD is an event-based model directing incoming hydrograph and sediment graph simulating outflow, sediment trapping and infiltration under field conditions (Sabbagh et al. 2009) and VFS using vegetated filter strip model-windows (VFSMOD_W), a software model for predicting the hydrograph and hydrograph (Fox et al. 2010). The model has largely been piloted with respect to pesticide applications, outside more traditional inputs such as sediment and nutrients loading, but holds much promise to advance knowledge about differences in transport of various pathogenic organisms in overland flow and through VFS.

4.6 Limitations of using *E. coli* as an indicator organism in overland flows

Enumeration of pathogenic microorganisms including bacteria or protozoa oocysts in natural water is a difficult and expensive exercise compared to other food and waterborne contaminants (Pachepsky et al. 2006). While there are no comprehensive methods (Table 3) or means to detect the broad array of organisms contaminating surface waters in order to protect public health, great strides have been made in recent years in both the development of low-cost, rapid, user-friendly and sensitive technologies and the integration of these technologies for a more robust risk assessment framework (Pandey et al. 2014; Ramirez-Castillo et al. 2015). Enzyme-based methodologies, which simultaneously detect both total coliforms and *E. coli*, are the standard for microbiological analysis of water (USEPA 2002). These tests base their detection power on enzymatic reactions. While these tests provide a basis and means for comparison between field studies and management techniques, they are subject to several limitations, including lack of specificity in relationship to

source and potential environmental differences in efficiency of removal (Pandey et al. 2014; Ramirez-Castillo et al. 2015).

Increasing evidence suggests that *E. coli* populations can become persistent and ubiquitous resident in soil under optimal environmental conditions, although soils are typically suboptimal environments for enteric organisms (Brennan et al. 2000, 2010). This finding may suggest that tropical zones will face more challenges in using it as an indicator organism. In addition, leached population of *E. coli* genotypic isolates from soil leachates do not necessarily form a single genetic grouping and there is some direct evidence that *E. coli* communities can alter considerably in transition from the primary host to the environment (Gordon et al. 2002). These studies support the hypothesis that *E. coli* populations can become naturalized in soil where conditions are favorable, forming a reservoir of *E. coli* in the environment (Brennan et al. 2010). The resulting lack of fecal specificity has serious implications for the use of this organism as an indicator of fecal pollution in the environment (Brennan et al. 2010).

5 Conclusions

In summary, critical evaluation of the fate and transport of both low and high pathogenicity *E. coli* and its predictive power for other manure-borne pathogens in overland flow and VFS is largely absent in the literature. While some preliminary work has been done at the plot level of VFS, these findings need to be extrapolated at the hill slope and watershed scales and existing model assumptions tested for validity. Discrepancies in biofilm attachment to soil particles and plant roots between strains of *E. coli* and between types of fecal pathogens need to be further teased apart with attention to implementation of VFS to reduce loading from overland flow in agro-pastoral settings. Advances in microbial source tracking will no doubt help identify target areas for fecal loading abatement, and the development of nonpathogenic surrogates should help improve modeling at larger scales. In addition, with the increasing impact of climate change on rainfall, drought and flooding, particularly in tropical zones, will continue to test the limits in the applications of models to overland flow and VFS management strategies. With VFS as a growing field of interest as an economical conservation practice, it will no doubt continue to be vetted with FIB, including *E. coli*, as a means to compare with, improve upon and complement other management strategies; however, nuanced studies are needed to understand either biological or environmental differences in the fate and transport of the diverse types of fecal pathogens within these settings. As an avenue for conservation of resources for small-scale agro-pastoral

operations, these interventions should include management strategies to reduce initial fecal load from either applied manure constituents or shedding from free-range animals.

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