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REVIEW ARTICLE

Effects of climate change on the persistence and dispersal of foodborne bacterial pathogens in the outdoor environment: A review

Rosalee S. Hellberg and Eric Chu

Food Science and Nutrition Program, Schmid College of Science and Technology, Chapman University, Orange, CA, USA

Abstract

According to the Intergovernmental Panel on Climate Change (IPCC), warming of the climate system is unequivocal. Over the coming century, warming trends such as increased duration and frequency of heat waves and hot extremes are expected in some areas, as well as increased intensity of some storm systems. Climate-induced trends will impact the persistence and dispersal of foodborne pathogens in myriad ways, especially for environmentally ubiquitous and/or zoonotic microorganisms. Animal hosts of foodborne pathogens are also expected to be impacted by climate change through the introduction of increased physiological stress and, in some cases, altered geographic ranges and seasonality. This review article examines the effects of climatic factors, such as temperature, rainfall, drought and wind, on the environmental dispersal and persistence of bacterial foodborne pathogens, namely, *Bacillus cereus*, *Brucella*, *Campylobacter*, *Clostridium*, *Escherichia coli*, *Listeria monocytogenes*, *Salmonella*, *Staphylococcus aureus*, *Vibrio* and *Yersinia enterocolitica*. These relationships are then used to predict how future climatic changes will impact the activity of these microorganisms in the outdoor environment and associated food safety issues. The development of predictive models that quantify these complex relationships will also be discussed, as well as the potential impacts of climate change on transmission of foodborne disease from animal hosts.

Keywords

Climate change, food safety, foodborne pathogens, predictive models, zoonotic pathogens

History

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Introduction

Warming of the climate system has been determined to be undeniable and has been associated with trends such as increasing atmospheric and oceanic temperatures (Figure 1), diminishing amounts of snow and ice and rising average sea level (IPCC, 2013). Future predictions based on several emissions scenarios suggest a continuation of these trends over the twenty-first century, including increased intensity of extreme weather events along with rising temperatures. These climatic changes are expected to result in a global increase in the risk of food and waterborne diseases, through both direct and indirect routes (Ebi et al., 2006; Rose et al., 2001). Growth and survival of foodborne bacterial pathogens is dependent on certain environmental conditions, such as temperature, pH and water availability (Montville et al., 2012), and changing climate patterns and meteorological events may significantly affect the persistence and dispersal of these pathogens. Microorganisms can also be dispersed in the environment through a variety of means, including wind, water, animals and humans (Figure 2), all of which are impacted directly or indirectly by climatic factors (Boxall et al., 2009; Lake et al., 2012). For example, expected

increases in rainfall in certain areas may directly affect pathogen dispersal through flooding or may indirectly affect pathogen dispersal by altering the geographic range or biological activity of a particular animal reservoir.

Pathogens that are ubiquitous in the environment and/or zoonotic have increased potential to be influenced by climate change. These include several foodborne bacterial pathogens, such as *Bacillus cereus*, *Brucella*, *Campylobacter*, *Clostridium*, *Escherichia coli*, *Listeria monocytogenes*, *Salmonella*, *Staphylococcus aureus*, *Vibrio* and *Yersinia enterocolitica*, which, when combined, have been estimated to cause approximately 3.5 million cases of foodborne illness each year in the USA alone (Scallan et al., 2011). The majority of these pathogens cause gastrointestinal illness in humans and, in some cases, more serious medical conditions like hemolytic-uremic syndrome (HUS), Guillain-Barré syndrome, septicemia, paralysis and meningitis (FDA, 2012). The animal reservoirs of these pathogens, such as livestock and wildlife, are also expected to be impacted by the changing climate. Their physiological responses to extreme weather and environmental stress may subject them to certain diseases and bacterial infections (Tirado et al., 2010). Furthermore, changes in livestock management practices due to altered climate conditions, such as indoor housing, will impact the exposure of livestock to certain pathogens.

Climatic variability and change may also result in altered seasonal patterns for wildlife, changes in population

Address for correspondence: Dr Rosalee S. Hellberg, PhD, 2. Food Science and Nutrition Program, Schmid College of Science and Technology, Chapman University, Orange, CA, USA 92866, USA. E-mail: hellberg@chapman.edu

Figure 1. Observed global mean combined land and ocean surface temperature anomalies, from 1850 to 2012 from three data sets. *Top panel:* annual mean values. *Bottom panel:* decadal mean values including the estimate of uncertainty for one dataset (black). Anomalies are relative to the mean of 1961–1990. Credit: IPCC (2013).

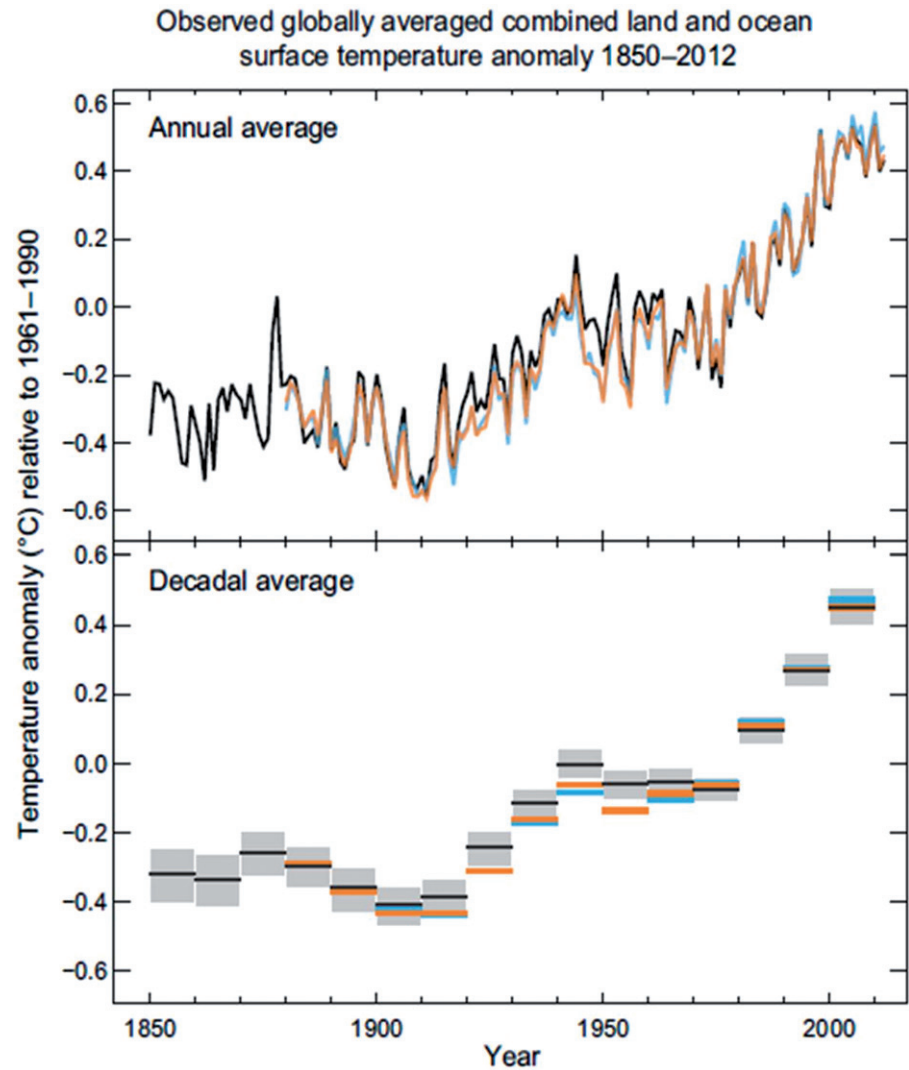
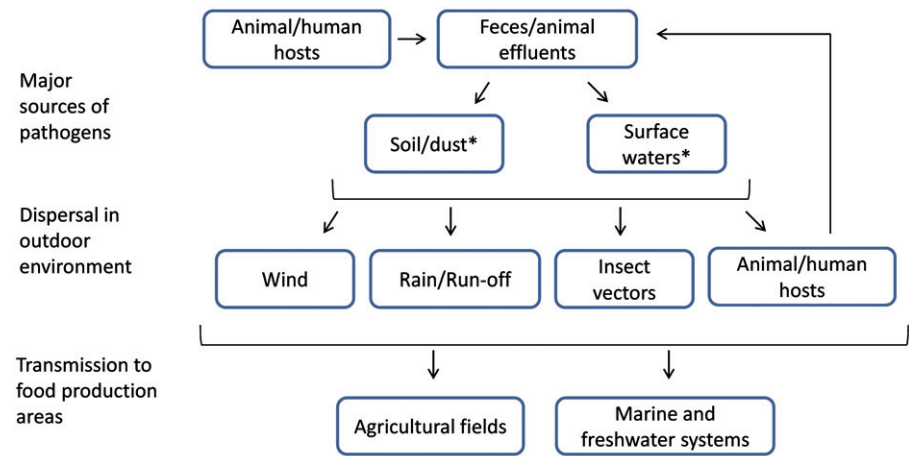


Figure 2. Overview of major sources of foodborne pathogens discussed in this review, common dispersal routes for these pathogens in the outdoor environment and transmission to food production areas.



*Some pathogens are naturally occurring in soil/dust and surface waters, while others enter these environments from animal/human sources.

abundance, and expansion into previously inhibitory geographic areas (Parmesan, 2006; Parmesan & Yohe, 2003; Tirado et al., 2010; Walther et al., 2002). The interactions of wildlife with humans and domestic animals are expected to increase in the USA as a result of ecosystem changes (Portier

et al., 2010), increasing the potential for transmission of zoonotic diseases. However, the effects of climate change on these relationships are poorly understood and challenging to predict (Mills et al., 2010). This is, in part, due to the complex interactions between a pathogen and its animal and human

hosts, as well as the varying impacts that climate change has on each component of this relationship.

The potential effects of climate change on the persistence and dispersal of foodborne pathogens in the outdoor environment are multifaceted, as other factors such as epidemiology, geography, infrastructure and human behavior play important roles. While it is difficult to predict the whole spectrum of effects that climate change will have, general trends may be deduced from our current knowledge of pathogens and their movement in the environment via abiotic and biotic means. The purpose of this literature review is to: (1) examine the potential effects of climate change on the persistence and dispersal of foodborne bacterial pathogens in the outdoor environment and (2) identify the food safety implications of current knowledge as well as needs for future research. This article begins with an overview of the major foodborne bacterial pathogens of concern, followed by a discussion of the relationship between climatic factors and the persistence and dispersal of these pathogens in the environment.

Foodborne bacterial pathogens of concern

Bacillus cereus

Bacillus cereus is a Gram-positive, spore-forming bacterium that is widespread in the outdoor environment (Stenfors Arnesen et al., 2008). It is commonly associated with decaying organic matter, soil, sediment, dust and plants and it can also colonize the intestinal tract of animals. *B. cereus* spores are highly resistant to adverse conditions and are typically spread to foods as a result of environmental contamination. These spores are exceptionally adhesive and hydrophobic, allowing them to become persistent in food production areas (Montville et al., 2012; Stenfors Arnesen et al., 2008). For example, *B. cereus* spores can attach to cow udders during grazing, enter the milk production area and attach to dairy pipelines to result in persistent contamination of the final product. *Bacillus cereus* causes two types of foodborne illness depending on the strain involved and the toxin produced – a diarrheal type and an emetic type. The diarrheal type is associated with a variety of foods, including dairy products, meats and vegetables, while the emetic type is associated primarily with starchy foods, such as rice and pasta. *B. cereus* is a facultative anaerobe that is able to tolerate salt levels as high as 7.5% and most strains are motile (FDA, 2012). Many strains of *B. cereus* exhibit mesophilic growth, with an optimal temperature of 35–40 °C and a range of 10–50 °C (Stenfors Arnesen et al., 2008). However, psychrotrophic strains of *B. cereus* have also been discovered that are able to grow at 7 °C, but not at 43 °C. These strains have been given their own species name of *B. weihenstephansensis*. The variable tolerance to temperatures exhibited by strains of *B. cereus* and closely related species has been identified as a potential mechanism by which this organism may be able to adapt to climate change (Carlin et al., 2010).

Brucella

Brucella spp. are Gram-negative, non-motile aerobic bacteria that can be transmitted to humans from animal hosts such as

cattle, sheep, goats and pigs (Guerra, 2007). While several species of *Brucella* are known to be infectious to humans, illness is primarily caused by either *B. melitensis* or *B. abortus*, and is most commonly due to contact with infected animals or ingestion of unpasteurized dairy products (Atluri et al., 2011). Infection can also occur through the cutaneous route or through the respiratory route due to inhalation of contaminated aerosols or dust (FDA, 2012; Gorvel, 2008). Brucellosis has varying forms of severity, with patients often experiencing symptoms such as intermittent fever, sweating, weakness and joint and muscle pain. The infection can sometimes become chronic and complications can arise such as endocarditis, meningoencephalitis or spondylitis. Although brucellosis has been eradicated in most developed countries, it remains endemic in other areas of the world, such as the Mediterranean basin, the Middle East, Africa and Latin America (Mwebe et al., 2011). *Brucella* spp. are facultative intracellular pathogens, but the extent to which they can proliferate outside of their host is not well understood (FDA, 2012). *Brucella* spp. are shed by animals during parturition and human brucellosis cases have been linked seasonally to parturition periods for livestock, especially for occupational infections (Minas et al., 2007).

Campylobacter

Campylobacter spp. are motile, Gram-negative bacteria within the family Campylobacteraceae (Montville et al., 2012). *Campylobacter jejuni* and *C. coli* are the two species of *Campylobacter* most commonly associated with foodborne disease, with *C. jejuni* responsible for about 90% of *Campylobacter*-associated illnesses (Altekruse & Tollefson, 2003). *Campylobacter* is estimated to be the third-leading cause of bacterial foodborne infection in the US, with over 800 000 cases annually, and typically causes a form of self-limiting gastroenteritis called campylobacteriosis. However, it has been associated with severe complications in a small percentage of cases, including the autoimmune disorder Guillain-Barré syndrome. *Campylobacter* spp. typically reside in the gastrointestinal tract of warm-blooded animal hosts, with the major reservoir being poultry. Other reservoirs include cattle, sheep, pigs and domestic pets. Most outbreaks of *Campylobacter* have been associated with animal products, such as improperly handled or undercooked poultry, raw milk and cheeses made from raw milk, as well as contaminated water (FDA, 2012). Although incidence of *Campylobacter* in farm animals is comparable to that of *E. coli* O157:H7 and *Salmonella*, this organism cannot survive for long periods in the open environment and few outbreaks have been linked to fresh produce (Mandrell, 2009). The reduced ability of *Campylobacter* to survive outside its host is due factors such as its sensitivity to oxygen, drying and acidic conditions (Montville et al., 2012). Unlike other foodborne pathogens discussed here, *C. jejuni* is thermophilic and microaerophilic, making it unable to grow at temperatures below 30 °C or at atmospheric oxygen levels. However, this organism can remain dormant in water in a viable but non-culturable (VBNC) state and some outbreaks have been linked to contaminated water or water supplies (Rosef et al., 2001). Human cases of campylobacteriosis have been linked to

seasonality, with many study populations experiencing a peak in cases of illness during the spring or summer months, depending on the country and the vehicle (Kovats et al., 2005; Montville et al., 2012).

Clostridium

Foodborne illness due to *Clostridium* spp. is most commonly associated with *C. botulinum* and *C. perfringens*. These organisms are Gram-positive spore-formers that are ubiquitous in nature and commonly associated with soil, sediments and intestinal tracts of animals (FDA, 2012). Spores of *C. botulinum* and *C. perfringens* are able to survive under adverse environmental conditions and exhibit high heat resistance. Both species exhibit anaerobic metabolism, but *C. perfringens* is aerotolerant whereas *C. botulinum* is unable to grow in the presence of oxygen. *C. botulinum* is motile and produces the neurotoxin that causes botulism, a severe form of food poisoning that can lead to paralysis and death. Botulism is commonly associated with improperly canned foods that are low in acid (pH > 4.6). Some types of *C. botulinum* are capable of psychrotrophic growth and are problematic in items such as vacuum-packed fish products (Montville et al., 2012). Most forms of botulism are due to production of the toxin prior to ingestion of a food, as the organism cannot compete well with the human gut microbiota in healthy individuals. However, individuals with compromised immune systems or infants may suffer from what is known as “intestinal botulism” or “infant botulism”, which is caused by colonization of the intestinal tract by *C. botulinum*. This form of botulism is primarily associated with honey, a known reservoir of *C. botulinum* spores. Many strains of *C. perfringens* are non-pathogenic; however, some are able to produce an enterotoxin in the small intestine that is associated with a usually mild and self-limiting form of gastroenteritis (FDA, 2012). Other toxin-producing strains of *C. perfringens* can cause a rare, but severe form of illness called enteritis necroticans, which is associated with pain and bloating of the abdomen as well as diarrhea and vomiting, and is often fatal. *Campylobacter perfringens* is non-motile and exhibits rapid growth under optimal conditions, with the ability to double in number in less than 10 min at temperatures of 43–45 °C (Montville et al., 2012). *C. perfringens* requires several amino acids for growth and foodborne illness from *C. perfringens* is most commonly caused by high-protein foods that have been subjected to temperature abuse, such as meats, gravies and stews (Montville et al., 2012). *C. perfringens* is one of the leading causes of foodborne illness in the US, while illness from *C. botulinum* is rare, with only a few cases reported annually. Due to its resistance to adverse conditions and its presence in human and animal feces, *C. perfringens* is commonly used as an indicator of fecal contamination in surface waters (Brynestad & Granum, 2002).

Escherichia coli

Escherichia coli are a group of motile, Gram-negative facultative anaerobes that are part of the natural microflora in the intestinal tracts of humans and other warm-blooded animals (Montville et al., 2012). While most strains are harmless, some are pathogenic and cause a diarrheal infection

ranging from mild to severe, with complications arising in some individuals. These pathogenic strains are largely transmitted via the fecal-oral route and have been categorized into groups based on their virulence, pathogenic mechanisms, clinical syndromes and serotypes. The diarrheagenic *E. coli* include: enteropathogenic *E. coli* (EPEC), enterotoxigenic *E. coli* (ETEC), enteroinvasive *E. coli* (EIEC), diffusely adhering *E. coli* (DAEC), enteroaggregative *E. coli* (EAEC) and enterohemorrhagic *E. coli* (EHEC). Combined, strains of diarrheagenic *E. coli* have been estimated to cause over 200 000 cases of foodborne disease each year in the US, resulting in close to 2500 hospitalizations (Scallan et al., 2011). EHEC strains are able to produce cytotoxic factors named verotoxins or Shiga toxins (Stx), and infection with these strains can lead to serious complications, such as hemorrhagic colitis, kidney failure, HUS, thrombotic thrombocytopenia purpura (TTP) and death (FDA, 2012). *Escherichia coli* O157:H7 is the predominant serotype of EHEC implicated in human illness, accounting for about 75% of infections globally, and it has a very low estimated infectious dose of 10–100 cells (FDA, 2012). *E. coli* O157:H7 generally grows best around 37 °C (Doyle & Schoeni, 1984); however, the optimal growth temperature varies depending on the strain (Gonthier et al., 2001). Although *E. coli* O157:H7 is not able to maintain growth at reduced temperatures (e.g. ≤ 10 °C), it is able to survive freezing for long periods of time (Doyle & Schoeni, 1984). *Escherichia coli* O157:H7 is also exceptionally tolerant of acidic conditions as compared to most other foodborne pathogens, with growth occurring as low as pH 4.0–4.5 (Montville et al., 2012). Interestingly, sublethal exposure to one type of environmental stress has been shown to increase the overall resistance of this organism to other types of stressors, thereby enhancing its survival in these circumstances (Franz & van Bruggen, 2008).

Early outbreaks of foodborne illness from *E. coli* O157:H7 were predominantly associated with the consumption of undercooked beef products. While beef products continue to be implicated in many *E. coli* O157:H7 infections, there has been an increasing trend for contamination of fruits and vegetables as well, such as unpasteurized juices, fresh lettuce, sprouts and bagged spinach (FDA, 2012). Fresh produce may become contaminated with this pathogen in the pre-harvest environment through contact with fecal material from sources such as domestic livestock and wildlife (Mandrell, 2009). For example, during a 2006 outbreak investigation of *E. coli* O157:H7 in spinach, matches to the outbreak strain were detected in feral swine feces, cattle feces and soil/sediment samples collected near the spinach field (Jay et al., 2007). Some potential means of dispersal for *E. coli* O157:H7 into production fields include watersheds, aerosols, animal effluents or animal intrusion (Fremaux et al., 2008b; Mandrell, 2009). Once in the soil, *E. coli* can survive for extended periods of time, potentially contaminating fruits and vegetables (Fremaux et al., 2008b) and migrating to other areas, such as groundwater (van Elsas et al., 2011).

Listeria monocytogenes

Listeria monocytogenes is a Gram-positive, non-spore-forming bacterium that is ubiquitous in nature and can withstand

adverse environmental conditions (Montville et al., 2012). This organism is motile, facultatively anaerobic and psychrotrophic, with a growth temperature range of 0–45 °C. *Listeria monocytogenes* demonstrates tolerance to salt, dehydration and acidic conditions, and can survive for extended periods in or on food, soil, plants and hard surfaces. *Listeria monocytogenes* has several known animal reservoirs, such as cattle, deer and goats, and can also proliferate in water environments, including surface waters of canals and lakes, ditches and sewage. Thirteen serotypes of *L. monocytogenes* have been recorded, but the majority of human cases (95%) have been associated with serotypes 1/2a, 1/2b or 4b (Montville et al., 2012). While human infections with *L. monocytogenes* are less numerous than those with other foodborne pathogens, the effects can be severe and it is one of the leading causes of death from foodborne illness in the US (FDA, 2012). Cases of listeriosis range from mild, self-limiting gastroenteritis to serious, invasive infections with complications such as meningitis, septicemia and abortion or stillbirth in pregnant women. Listeriosis is primarily associated with ready-to-eat foods, milk products, cheeses, meat and poultry products and seafood. As it does not survive most heat treatments, *L. monocytogenes* usually contaminates these foods in the post-processing environment, such as through food-contact surfaces or cross-contamination with raw materials (Montville et al., 2012). It can also be found in foods that are not heat-treated prior to consumption, such as unpasteurized milk and cheeses made from unpasteurized milk (Silk et al., 2013). There is an emerging link between *L. monocytogenes* and fresh produce outbreaks. For example, a 2011 outbreak of *L. monocytogenes* in fresh whole cantaloupe represented the deadliest outbreak of foodborne listeriosis in the USA (Laksanalamai et al., 2012) and the first outbreak of this pathogen in a whole fruit raw agricultural commodity (FDA, 2011). Contamination was found to be most likely due to factors associated with the growing environment, the packing facility and the process for cold storage. Additional outbreaks linking *L. monocytogenes* to fresh produce include an outbreak of raw sprouts in 2008–2009 and pre-cut celery in 2010 (Gould et al., 2011; Silk et al., 2013).

Salmonella

Non-typhoidal *Salmonella* spp. are the leading cause of foodborne illness, hospitalization and death among bacterial pathogens in the US, with over 1 million cases annually (Scallan et al., 2011). Like *E. coli*, *Salmonella* are motile, Gram-negative facultative anaerobic bacteria that belong to the family *Enterobacteriaceae* and exhibit optimal growth around 37 °C (Montville et al., 2012). These organisms are classified into over 2500 serovars of two species – *S. enterica* and *S. bongori*. While both species are known pathogens, *S. enterica* is responsible for the majority of *Salmonella*-associated foodborne illness, with 99% of reported human isolates in the USA belonging to *S. enterica* subsp. *enterica* (CDC, 2011). Non-typhoidal *Salmonella* strains are widespread in nature, including pond-water sediment, and can colonize the intestinal tracts of vertebrate animals, including livestock, wildlife, domestic pets and humans (FDA, 2012). These strains exhibit a great deal of diversity, with variations

in factors such as metabolic properties, survivability and virulence factors (Montville et al., 2012). For example, some strains of *Salmonella* are capable of growth at psychrotrophic temperatures (≥ 2 °C) while others have been found to grow at elevated temperatures (up to 54 °C). In general, *Salmonella* are resilient to environmental conditions and are able to persist in the environment outside of an animal host, with extended survival times as compared to *E. coli* in terrestrial habitats (Franz & van Bruggen, 2008; van Elsland et al., 2011). Similar to *E. coli* O157:H7, *Salmonella* has demonstrated an ability to grow in acidic environments and increased survival under adverse conditions following exposure to acid stress (Montville et al., 2012). Increased temperatures can further enhance the ability of *Salmonella* to demonstrate resistance to environmental stresses (Montville et al., 2012). These bacteria are spread to humans through the fecal-oral route and cause a gastrointestinal illness called salmonellosis which is usually self-limiting in healthy individuals. Salmonellosis has traditionally been associated with animal products, such as undercooked poultry and eggs; however, more recently other food items have also been implicated, including fresh produce, nuts and spices. The presence of *Salmonella* in the outdoor environment and its transmission among animals make it a problem in the food supply. Incidence of salmonellosis has been correlated to increased ambient temperatures in studies carried out in regions of Australia, Canada and Europe (Tirado et al., 2010). For example, a time-series analysis carried out among 10 European countries found that, for most of the countries analyzed, each 1 °C increase in temperature above a 6 °C threshold corresponded to a 5–10% increase in cases of salmonellosis (Kovats et al., 2004). However, these associations may be related to seasonal effects on human behaviors rather than direct effects of climate on the dispersal and persistence of the pathogen in the environment.

Staphylococcus aureus

Staphylococcus aureus is a Gram-positive, non-spore-forming facultative anaerobe that is ubiquitous in the outdoor environment, including soil, dust, water and air (FDA, 2012). This organism is also part of the natural microbiota associated with humans and animals and is predominately found on the skin, hair or in the nasal passages (Le Loir et al., 2003; Madigan et al., 2012). *Staphylococcus aureus* typically enters foods through contamination from humans, animals, or the environment (FDA, 2012). *Staphylococcus aureus* causes a number of human illnesses, including foodborne intoxication due to the ingestion of highly heat-stable enterotoxins produced in foods. Staphylococcal foodborne illness is associated with acutely intense gastroenteritis, including vomiting and diarrhea, which is normally of short duration and self-limiting in healthy individuals. Foods commonly associated with *S. aureus* intoxication are those that require substantial handling for preparation and those that are held at ambient temperatures for extended periods, such as dairy products, meat and poultry products, ready-to-eat salads, such as egg, tuna and potato and bakery products. *Staphylococcus aureus* is non-motile and mesophilic, with optimal growth occurring around 35 °C. It is among the most highly resistant

non-spore-forming human pathogens and is exceptionally osmotolerant. For example, it can survive in a dry state for extended periods of time and is able to grow in foods with water activity as low as 0.83–0.86 (FDA, 2012; Montville et al., 2012).

Vibrio

Vibrio species are a group of Gram-negative, facultatively anaerobic bacteria that are naturally found in marine and coastal estuarine environments (Montville et al., 2012). These organisms are motile and are also capable of taking on a VBNC state. Several *Vibrio* species have been associated with human illness, especially *V. parahaemolyticus*, *V. vulnificus* and *V. cholerae*, although the majority of isolates recovered from these species are non-pathogenic. *Vibrio cholerae* is able to grow in either freshwater or salt water, whereas *V. vulnificus* and *V. parahaemolyticus* both require salt for growth (Horseman & Surani, 2011; Reidl & Klose, 2002; Su & Liu, 2007). These organisms grow optimally around 37°C and are more commonly isolated during the warmer months of the year. *Vibrio* infections in the US have been linked to seasonality, with an increase in the late spring/early summer months, a peak in August and then a gradual decline during September–October (CDC, 2012). Infection with pathogenic forms of *Vibrio* is primarily manifested as gastroenteritis, wound infection and, in some cases, septicemia (Montville et al., 2012). *Vibrio parahaemolyticus* is the leading cause of shellfish-associated gastroenteritis in the US, and the incidence of infection with this species has increased 76% when comparing 2011 levels to 1996–1998 levels (CDC, 2012). While *V. vulnificus* infection is rare, it has the highest case-fatality rates among foodborne pathogens, with an estimated 96 cases of foodborne illness and 36 deaths per year in the US (Scallan et al., 2011). Cholera, caused by *V. cholerae* O1/O139, occurs only sporadically in developed countries and is largely associated with waterborne illnesses in developing countries that lack a safe drinking water supply (WHO/WMO, 2012).

Yersinia enterocolitica

Yersinia enterocolitica is a Gram-negative, facultative anaerobe that is not part of the normal human microflora (FDA, 2012). Similar to *L. monocytogenes*, *Y. enterocolitica* is a psychrotrophic organism, with an optimal growth temperature around 28–30°C and an ability to survive freezing for extended periods of time (Montville et al., 2012). *Y. enterocolitica* is also motile, salt-tolerant and can grow over a wide pH range (4–10), with notable tolerance to alkaline conditions. It is prevalent in the environment, including soils and surface waters, and has been isolated from animals such as pigs, birds, frogs, flies and fleas (FDA, 2012). There is a great deal of diversity among strains within this species and most isolates are not pathogenic (Montville et al., 2012). Subtyping is performed based on biochemical and antigenic properties of each isolate, with most pathogenic isolates belonging to biovars 1B, 2, 3, 4 and 5. *Yersinia enterocolitica* is commonly transmitted to humans through the fecal-oral route as well as through consumption of contaminated animal products, including pork, unpasteurized

milk and oysters. Infection with pathogenic strains of *Y. enterocolitica* is most common in young children and is associated with high fever and stomach pain. Fatalities from yersiniosis are rare, but complications can arise, such as reactive arthritis, endocarditis and unnecessary appendectomies. *Yersinia enterocolitica* has been estimated to cause approximately 100 000 cases of foodborne illness annually in the USA (Scallan et al., 2011). Interestingly, yersiniosis is far more common in Northern Europe, Scandinavia and Japan as compared to the USA (FDA, 2012).

Influence of climatic factors on foodborne bacterial pathogens

Given the dependence of foodborne bacterial pathogens on their environment, there is a strong likelihood that climate change will impact the persistence and dispersal of these microorganisms. This section will incorporate climate change predictions with known effects of temperature, seasonality, precipitation, soil characteristics, drought and wind on foodborne bacterial pathogens. The potential for these climatic factors to affect the animal reservoirs of foodborne pathogens will also be discussed, where applicable. Trends discussed in the text are summarized in Tables 1–4 and the strength of the evidence for these trends is rated within each table according to levels described in Box 1.

Temperature and seasonality

Mean global temperatures are expected to increase over the next century, along with warming trends such as warmer days and nights over most land areas (IPCC, 2013). In comparison to 1986–2005 levels, predictions for the future state of the climate include an increase in global average surface temperature of about 0.3–0.7°C over the years 2016–2035, with an average global temperature increase of 0.3–4.8°C by the end of the twenty-first century, under different scenarios for future emissions (IPCC, 2013). Along with this warming trend, it is expected that there will be increases in the frequency of hot extremes over most land areas on a daily and seasonal scale, with short-term increases in seasonal and annual mean temperatures expected to be greatest in the tropics and subtropics as compared to the mid-latitudes. The frequency and duration of warm spells and heat waves is also expected to increase over most land areas. As the optimal temperature for growth of most foodborne bacterial pathogens is close to that of the human body (i.e. 37°C), rising temperatures would be expected to increase the growth rate of these organisms. However, growth is also dependent factors such as osmotic pressure, competitive microorganisms, water availability and nutrient availability. In fact, as shown in Table 1, several studies have reported low temperatures (above freezing) to have a protective effect on the survival of foodborne pathogens in soils (García et al., 2010; Girardin et al., 2005; Strawn et al., 2013). These findings are likely related to a decrease in the metabolic activity of competitive and antagonistic microflora combined with retention of moisture content at lower temperatures (Fremaux et al., 2008b). For instance, one study conducted in France over 2 years found that *L. innocua*, a surrogate for *L. monocytogenes*, showed increased survival in soil during

Table 1. Effects of temperature and seasonality on the persistence and dispersal of foodborne pathogens in the environment.

Pathogen	Environment or animal host	Effects of temperature and seasonality on pathogen	Strength of evidence*	Selected references
<i>Campylobacter</i> , <i>L. monocytogenes</i> , <i>Salmonella</i> , <i>Y. enterocolitica</i>	Animal effluents, soils, and surface waters	Decreased survival at higher temperatures	A	Asadishad et al., 2013; García et al., 2010; Korhonen & Martikainen, 1991; Mannion et al., 2007; Strawn et al., 2013
STEC, <i>L. monocytogenes</i> , <i>Salmonella</i> , <i>Y. enterocolitica</i>	Animal effluents, manure-amended soils, soils, surface waters	Decreased survival due to fluctuating ambient temperature or freeze-thaw events	A	Asadishad et al., 2013; Ivanek et al., 2009; Natvig et al., 2002; Semenov et al., 2007
STEC	Manure-amended soils, animal feces, water	Varying associations with temperature	B	Fremaux et al., 2008b; Fukushima et al., 1999; Jiang et al., 2002; Mukherjee et al., 2006; Wang & Doyle, 1998
<i>Salmonella</i>	Farm environment	Most studies report increased detection in summer; one study reported increased detection in cooler months	B	Branham et al., 2005; Pangloli et al., 2008; Rodriguez et al., 2006
<i>L. monocytogenes</i>	Livestock, soil, and farm environment	Increased detection in winter	A	Guerini et al., 2007; Nightingale et al., 2005; Strawn et al., 2013
<i>Y. enterocolitica</i>	Swine	Most studies report increased detection in cooler months; one study reported increased detection in spring and summer	B	Bhaduri et al., 2005; Fondrevez et al., 2014; Milnes et al., 2008; Ortiz Martinez et al., 2010
<i>Salmonella</i> , STEC	Cattle	Most studies show increased shedding and carcass contamination during summer months; some studies report no seasonal effect	B	Barkocy-Gallagher et al., 2003; Brichta-Harhay et al., 2008; Liu et al., 2013; Rhoades et al., 2009
<i>Bacillus</i>	Cattle	Increased detection in milk during late spring and summer	C	Bartoszewicz et al., 2008
<i>Campylobacter</i> , <i>Salmonella</i>	Poultry	Increased detection in summer and/or with increasing temperature	A	Jonsson et al., 2012; McCrea et al., 2006; Zdragas et al., 2012
<i>Campylobacter</i>	Flies	Possibility for increased transmission to poultry during the summer	D	Hald et al., 2004; Shane et al., 1985
<i>Y. enterocolitica</i>	Small mammals	Increased detection at cooler temperatures	C	Servan et al., 1979
<i>Salmonella</i>	Oysters	Increased detection frequency at higher temperatures	C	Brands et al., 2005
<i>V. parahaemolyticus</i> and <i>V. vulnificus</i>	Shellfish	Increased levels at higher temperatures	A	DePaola et al., 1990; Lhafi & Kühne, 2007; Parveen et al., 2008
<i>Campylobacter</i> , <i>Salmonella</i>	Surface waters	Varying associations with temperature	B	Haley et al., 2009; Martinez-Urtaza, 2008; Simental & Vereen Jr et al., 2013; Vereen et al., 2007
<i>Vibrio</i> spp.	Coastal waters	Increased levels at higher temperatures	A	Johnson et al., 2012; Louis et al., 2003; Vezzulli, 2012

*Refer to Box 1 for a description of the levels used to rate the strength of the scientific evidence

the winter as compared to the spring (Girardin et al., 2005). While cooler temperatures favor the psychrotrophic pathogens, like *L. monocytogenes*, as compared to other foodborne pathogens, freezing and freeze-thaw cycles can have an inhibitory effect (Asadishad et al., 2013; El-Kest et al., 1991; Ivanek et al., 2009). In a study that investigated the influence of meteorological factors on the prevalence of foodborne pathogens, Strawn et al. (2013) found that during the winter season *L. monocytogenes* was more frequently detected in areas where the temperatures had been above freezing prior to sampling. The warming trends expected with climate change can mean fewer freezing events and consequently may lead to increased prevalence of certain pathogens, such as *L. monocytogenes*, in geographic areas that were previously inhibitory.

A number of studies have been carried out on the survival of foodborne pathogens in animal effluents (manure and slurries) and effluent-amended soils at various temperatures (reviewed in Fremaux et al., 2008b; Jacobsen & Bech, 2012; Ongeng et al., 2013). Effluents are used to fertilize agricultural fields and can lead to bacterial contamination of fruits and vegetables if good management practices are not followed (Fremaux et al., 2008b; Liu et al., 2013). The majority of studies on this topic have reported decreased survival of foodborne pathogens, including *Salmonella*, Shiga toxin-producing *E. coli* (STEC), *Campylobacter* and *L. monocytogenes*, in animal feces, effluents and amended soils at higher temperatures (Arrus et al., 2006; Fremaux et al., 2008b; Fukushima et al., 1999; Himathongkham et al., 1999; Mannion et al., 2007; Moriarty et al., 2011, 2012;

Table 2. Effects of rainfall on the persistence and dispersal of foodborne pathogens in the environment.

Pathogen	Environment or animal host	Effects of rainfall on pathogen	Strength of evidence*	Selected references
<i>Campylobacter</i> , <i>Salmonella</i>	Watersheds and/or coastal waters	Increased detection frequency in some studies; decreased detection frequency in others	B	Jokinen et al., 2010; Simental & Martinez-Urtaza, 2008; Vereen Jr et al., 2013; Wilkes et al., 2009
STEC	Watershed	Increased detection; possible long-distance dispersal	C	Cooley et al., 2007
<i>V. alginolyticus</i>	Mussels	Decreased levels	C	Miller et al., 2006
<i>V. vulnificus</i>	Coastal waters	Decreased levels in one study; no significant association in another study	B	Lipp et al., 2001b; Yamazaki & Esiobu, 2012
<i>V. alginolyticus</i> , <i>V. carchariae</i> , <i>V. parahaemolyticus</i>	Coastal waters	Increased levels	C	Yamazaki & Esiobu, 2012
<i>Campylobacter</i>	Run-off water from combined sewer overflow and non-point sources	Increased levels	C	Rechenburg & Kistemann, 2009
<i>L. monocytogenes</i>	Fish farm	Increased levels, likely due to run-off from nearby rivers and streams	C	Miettinen & Wirtanen, 2006
<i>Campylobacter</i> , STEC, <i>Y. enterocolitica</i>	Agricultural run-off and drainage	Dispersal into soil or water bodies	A	Donnison & Ross, 2009; Walker & Grimes, 1985
<i>L. monocytogenes</i> , <i>Salmonella</i>	Soil	Increased survival in moist conditions	A	Chandler & Craven, 1980; Holley et al., 2006; Welshimer, 1960
<i>Salmonella</i>	Soil	Increased lettuce internalization rate	C	Ge et al., 2012
<i>Listeria</i> , <i>Salmonella</i>	Soil or mulch	Splash dispersal onto plant surfaces	A	Cevallos-Cevallos et al., 2012a; Girardin et al., 2005
<i>Salmonella</i>	Rodents and amphibians	Increased possibility for pathogen transmission due to increased populations of animal hosts	D	Srikantiah et al., 2004; Mills et al., 2010; Mills & Childs, 1998
<i>Campylobacter</i>	Chickens	Increased detection frequency associated with increases in rainfall and temperature	A	Jonsson et al., 2012; Jorgensen et al., 2011; Rushton et al., 2009

*Refer to Box 1 for a description of the levels used to rate the strength of the scientific evidence

Nicholson et al., 2005; Oliveira et al., 2012; Semenov et al., 2007). Interestingly, different serotypes of *E. coli* and *Salmonella* have shown varied levels of survival in animal effluents. For instance, *E. coli* O157:H7 exhibited enhanced survival during storage at 5 °C after 4 weeks as compared to the serotypes *E. coli* O11:H- and O26:H11 (Fukushima et al., 1999), and *Salmonella* Derby had significantly longer survival times than *Salmonella* Typhimurium during storage in a pig slurry over both the summer and the winter months in Ireland (Mannion et al., 2007). STECs and commensal *E. coli* have demonstrated persistence in manure-amended soils at a range of temperatures (Fremaux et al., 2008b). For example, Fremaux et al. (2008a) reported survival of STEC O26:H11 for at least 1 year in manure-amended soil held at temperatures of both 4 and 20 °C in a laboratory setting. In contrast to the above studies reporting a protective effect at lower temperatures, some studies have reported decreased survival of STECs in manure-amended soil or animal feces at lower temperatures (4–5 °C) as compared to 21 °C (Jiang et al., 2002) or ambient temperatures of about 12–15 °C (Fukushima et al., 1999; Mukherjee et al., 2006). These differences may be due to variations in experimental designs and in the settings/environments in which the studies were carried out. As noted earlier, complex interactions exist

between pathogens and their environment. Decreased temperatures in some settings may facilitate bacterial survival by decreasing the metabolic reactions of competitive bacteria, while temperature fluctuations can have harmful effects on bacterial survival. For example, *Salmonella* and *E. coli* have both exhibited decreased survival in manure-fertilized soil during periods of frequent fluctuations in ambient temperature as well as during freeze–thaw events (Natvig et al., 2002; Semenov et al., 2007). Based on pathogen survival studies such as those discussed above, recommendations are made for agricultural practices, such as effluent storage times prior to land application and time intervals between land application and planting/harvesting of crops (Nicholson et al., 2005). As warming trends continue over the coming century, it will be important to continually monitor these practices for instances of increased survival (e.g. if fewer freeze–thaw events take place) or decreased survival due to rising temperatures.

Temperature is likely to have varied effects on the animal reservoirs of foodborne pathogens, in some cases extending their geographic ranges or seasonality (Parmesan, 2006; Parmesan & Yohe, 2003; Tirado et al., 2010; Walther et al., 2002). Numerous studies have reported seasonal effects on the prevalence of foodborne pathogens

Table 3. Effects of drought on the persistence and dispersal of foodborne pathogens in the environment.

Pathogen	Environment or animal host	Effects of drought on pathogen	Strength of evidence*	Selected references
STEC	Soil	Decreased survival with increasing soil salinity or reduced water content	A	Gutierrez-Rodriguez et al., 2012; Ma et al., 2012
<i>Salmonella</i>	Soil	Increased internalization by lettuce	C	Ge et al., 2014
<i>V. cholerae</i> , <i>V. parahaemolyticus</i> , <i>V. vulnificus</i> , total <i>Vibrio</i> spp.	Oysters and coastal waters	Increased abundance within optimal salinity range; inhibitory effects outside of range	A	Hsieh et al., 2008; Lipp et al., 2001; Louis et al., 2003; Martinez-Urtaza et al., 2008; Zimmerman et al., 2007

*Refer Box 1 for a description of the levels used to rate the strength of the scientific evidence.

Table 4. Effects of wind and/or dust events on persistence and dispersal of foodborne pathogens in the environment.

Pathogen	Environment or animal host	Effects of wind and/or dust events on pathogen	Strength of evidence*	Selected references
Total <i>Vibrio</i> spp.	Estuary	Increased levels in water and sediments following cyclones	A	Fries et al., 2008; Lara et al., 2009
<i>Vibrio cholerae</i>	Non-biting midges in air	Possible dispersal by wind	D	Broza et al., 2005; Paz, 2009
Total <i>Vibrio</i> spp., <i>V. alginolyticus</i> , <i>V. cholerae</i>	Coastal waters	Increased proliferation with addition of Saharan dust	C	Westrich et al., 2013
<i>E. coli</i> (incl. pathogenic serotypes)	Airborne and settled dust in a residential area	Possible dispersal by wind	D	Rosas et al., 1997
<i>Campylobacter</i> †, <i>E. coli</i> O157, <i>S. aureus</i> , and/or <i>Salmonella</i>	Air and airborne dust on the farm environment	Possible airborne dispersal over short distances	D	Chinivasagam et al., 2009; Iwabuchi et al., 2010; Miller et al., 2008; Sargeant et al., 2004; Schulz et al., 2012
<i>K. pneumoniae</i> , <i>Salmonella</i> , <i>Y. enterocolitica</i>	Air above landfills	Possible dispersal by wind into nearby agricultural lands	D	Flores-Tena et al., 2007; Rosas et al., 1996
<i>Bacillus</i> , <i>Clostridia</i> , <i>Staphylococcus</i>	Dust storms	Dispersal in air during dust storms	A	Griffin, 2007; Polymenakou et al., 2008
<i>Brucella</i> , <i>C. perfringens</i> , <i>B. cereus</i>	Airborne dust	Possible dispersal by wind	D	Leski et al., 2011

*Refer Box 1 for a description of the levels used to rate the strength of the scientific evidence.

†*Campylobacter* appears to be a poor survivor during airborne transport.

Box 1. Levels used to rate the strength of the scientific evidence for trends presented in Tables 1–4.

Level	Description
A	Multiple peer-reviewed studies showing a quantifiable, consistent trend.
B	Multiple peer-reviewed studies showing a quantifiable, inconsistent trend.
C	One peer-reviewed study showing a quantifiable trend.
D	Peer-reviewed research indicates a possible trend that has not been quantified.

in livestock and the surrounding farm environment (Table 1). As cattle are a major reservoir for STEC, extensive research has been carried out to investigate seasonal effects on this pathogen–host relationship. Most of these studies have reported increased prevalence and shedding of STEC in the warmer months (reviewed in Liu et al., 2013; Rhoades et al., 2009); however, it has been demonstrated that factors besides temperature, including day length, may be affecting this correlation (Edrington et al., 2006; Liu et al., 2013). Studies on the contamination of cattle hides and carcasses with

foodborne pathogens, including STEC, *Salmonella* and *L. monocytogenes*, have shown inconsistent results related to seasonality, with some papers reporting seasonal effects (Barkocy-Gallagher et al., 2003; Guerini et al., 2007; Rivera-Betancourt et al., 2004) and other research reporting no seasonal effects (Brichta-Harhay et al., 2008). Similarly, *Salmonella* prevalence in the farm environment or in grazing lands has shown conflicting seasonal effects, with one study reporting the highest isolation rates in the cooler months (October–March) as compared to the warmer months (April–September; Rodriguez et al., 2006), and other studies reporting the highest isolation rates to be during the summer months (Branham et al., 2005; Pangloli et al., 2008). All three studies were carried out in the USA, but the former study examined farm environments for a variety of animals (e.g. beef and dairy cattle, swine and poultry) located across five states, while the latter two were each conducted on one farm environment in one geographic location. Some of the variation reported among seasonal trends may also be due to seasonal differences in the housing of livestock. For example, one study conducted in Poland found significant seasonal differences for *B. cereus*/*B. weihenstephanensis* in

raw and processed milk, with the highest levels in the late spring and summer and the lowest levels in the fall and winter (Bartoszewicz et al., 2008). However, this may have been due to reduced exposure of cows to the bacteria in the cooler seasons, during which time they are housed in sheds and fed hay instead of grazing outdoors. Indeed, raw milk from cows that were pastured has previously been reported to exhibit significantly higher levels of *B. cereus* spores as compared to milk from cows that were housed during the same time period (Slaghuis et al., 1997). In a study on pathogen prevalence on swine farms in Canada, Farzan et al. (2010) reported increased likelihood for detection of *Salmonella* and *Campylobacter* in the summer, while *E. coli* O157:H7 was most likely to be recovered in the fall; however, none of the associations was statistically significant. Similarly, no significant seasonal effects were found for prevalence of *Salmonella*, *Campylobacter* and *E. coli* O157 in swine at slaughter in Great Britain (Milnes et al., 2008). The study also examined the prevalence of these three microorganisms in cattle and sheep and found a significant seasonal effect of *E. coli* O157 prevalence in cattle, with the highest detection in the summer, and a significant seasonal effect of *Campylobacter* prevalence in sheep, with the highest detection rates in the winter. Overall, the above studies indicate the complex interactions between pathogen, host and environment, and show that trends observed in one geographic location or farm environment cannot be generally applied to other regions.

The psychrotrophic foodborne pathogens *L. monocytogenes* and *Y. enterocolitica* have both shown increased prevalence on the farm environment during cooler months, in agreement with research described above for their survival in soil. Nightingale et al. (2005) reported the prevalence of *L. monocytogenes* on cattle, goat and sheep farms to be seasonal, with a peak prevalence in the winter. Prevalence rates for *Y. enterocolitica* in swine have been reported to increase in the winter in studies carried out in the USA (Bhaduri et al., 2005), Germany (Weber & Knapp, 1981), Japan (Fukushima et al., 1983) and in the UK (Milnes et al., 2008; Ortiz Martínez et al., 2010). For example, in a study examining fecal shedding of *Y. enterocolitica* by swine in the USA, Bhaduri et al. (2005) reported a significant higher rate of detection from January to March 2001 as compared to September to December of the previous year. One study reported the highest likelihood of detecting *Y. enterocolitica* in swine fecal samples to be during the spring in Canada, but the finding was not statistically significant (Farzan et al., 2010). On the other hand, detection of *Y. enterocolitica* in tonsil swabs from swine was reported to be significantly higher in France during the warmer months of the year (i.e. March through October) (Fondrevez et al., 2014). However, a direct correlation with temperature was not observed in this study, suggesting that additional factors were influencing carriage rates. Interestingly, France, Finland and Sweden have all observed increased human yersiniosis cases during the warmer months, while other countries tend to experience a higher number of cases in the cooler months (Fondrevez et al., 2014).

Seasonal effects of foodborne pathogens in poultry have also been reported, with most studies finding increased

prevalence of *Salmonella* and *Campylobacter* in the summer months (Table 1; EFSA, 2011; Jorgensen et al., 2011; McCrea et al., 2006; Zdragas et al., 2012). In some cases, increased temperature specifically has been reported to be associated with the prevalence of *Campylobacter* in poultry (Guerin et al., 2008; Hartnack et al., 2009; Jonsson et al., 2012; Jorgensen et al., 2011; Patrick et al., 2004). For example, one study carried out in Great Britain over the course of 2004–2006 found the average temperature during rearing to have the greatest individual influence on the prevalence of *Campylobacter* in broiler flocks at slaughter, but the strongest effect was found using a multivariable approach combining the ambient temperature at slaughter, number of sunshine hours in the placement month and total rainfall in the placement month (Jorgensen et al., 2011). *Campylobacter* prevalence in flocks was significantly higher during July, August and September than during the rest of the year. In another broiler flock study, Jonsson et al. (2012) examined data from over 600 farms in Norway tested over the period 2002–2007 and found that daily mean temperatures above 6°C during rearing were significantly associated with *Campylobacter* prevalence, while daily mean temperatures below 0°C showed an inverse association. Heavy rainfall 11–30 days prior to slaughter was also significantly associated with *Campylobacter* prevalence in the broiler flocks. Possible explanations for the climatic associations found in these studies include changes in flock management, the thermophilic nature of this microorganism, its sensitivity to drying and/or contact with vectors (esp. flies) or wildlife carrying *Campylobacter* (Jonsson et al., 2012; Jorgensen et al., 2011). Flies thrive during the summer months and have been shown to be capable of transmitting *Campylobacter* to broiler chickens in a laboratory setting (Shane et al., 1985). Furthermore, *Campylobacter* was cultured from 8.2% of flies captured outside a broiler house in Denmark during the summer, suggesting them to be an important source of infection (Hald et al., 2004).

Wildlife, such as rodents, deer and birds, are also known sources of some foodborne pathogens and can transport these pathogens into the agricultural environment. Research into the links between seasonality or temperature and the prevalence of foodborne pathogens in wildlife has been limited. One study conducted in France on this topic from December 1974 to April 1976 found an inverse relationship between temperature and isolation frequency of *Y. enterocolitica* in small mammals, including several species of mice and voles (Servan et al., 1979). The two species most frequently captured for testing, the common vole (*Microtus arvalis*) and the wood mouse (*Apodemus sylvaticus*), had *Y. enterocolitica* infection rates of 80% and 30%, respectively, in January 1976. This is consistent with trends mentioned earlier for *Y. enterocolitica*, which show increased prevalence in the outdoor environment during cooler months. Another study found an inverse relationship between temperature and survival of *Campylobacter* in the inoculated feces of Canada goose (*Branta Canadensis*), a known carrier of foodborne pathogens (Moriarty et al., 2012). *Campylobacter* was found to be capable of surviving up to 7 days in goose feces placed on a pasture in New Zealand in the winter but less than 2 days in the summer. On the other hand, the

indicator bacteria *E. coli* and enterococci showed rapid initial growth rates in goose feces during the summer, but little to no growth in the winter. These trends were similar to those found in a previous study by the same group examining *Campylobacter* and indicator bacteria survival in cattle feces (Sinton et al., 2007). These may be reflective of an increased sensitivity of *Campylobacter* to drying in the outdoor environment during the summer months.

In general, warming trends and changes in seasonality are impacting wildlife in various ways, including range shifts towards the poles and higher elevations (Mills et al., 2010). For example, the hispid cotton rat (*Sigmodon hispidus*) and the white-footed deer mouse (*Peromyscus leucopus*) have shown northward and/or altitudinal expansions in their population distributions over the last few decades. These species are both known hosts of several bacterial and/or viral pathogens, including the hantavirus, which causes hantavirus pulmonary syndrome (HPS). Furthermore, a study into small mammals in Yosemite National Park, California, USA, found large upward shifts in elevation (average = 500 m) for half of the 28 species examined, including several species of mice, when compared to records from about 100 years earlier (Moritz et al., 2008). In some cases, the range was expanded [e.g. the pocket mouse (*Chaetodippus californicus*), the harvest mouse (*Reithrodontomys megalotis*) and the California vole (*Mirotus californicus*)], while in others both the minimum and maximum range limits were shifted towards a higher altitude [e.g. the pinyon mouse (*Peromyscus truei*)]. Although there is a lack of information on the relationship between climate change and carriage of foodborne pathogens by wildlife, shifts in geographic ranges could result in the presence of host–pathogen systems in previously uninhabitable agricultural areas and increase the likelihood of foodborne disease transmission. On the other hand, climate change could also have the opposite effect, pushing wildlife out of previously inhabitable areas near agricultural fields. For instance, in their Yosemite study, Moritz et al. (2008) reported a range contraction for the long-tailed vole (*Microtus longicaudus*), a known carrier of the waterborne parasite *Giardia* (Pacha et al., 1987).

Along with increasing warming trends over land areas, surface water temperatures are also expected to rise for both freshwater and marine systems (Hofstra, 2011; IPCC, 2013). Increasing water temperatures can be expected to have a variable effect on foodborne bacterial pathogens. Slight increases in water temperature will likely promote bacterial growth in nutrient-rich waters, but higher water temperatures can ultimately become inhibitory to some pathogens (Guan & Holley, 2003; Hofstra, 2011). For example, some studies have found positive correlations between water temperature and *Salmonella* (Haley et al., 2009) and *Campylobacter* (Vereen Jr et al., 2007) while others have found non-linear (Setti et al., 2009) or negative associations (Simental & Martinez-Urtaza, 2008; Vereen Jr et al., 2013). Vereen et al. (2013) reported a significant inverse correlation between water temperature and detection frequency of *Campylobacter* in a rural mixed-use watershed in the USA studied over 2 years (2007–2009), but no significant associations for water temperature and detection frequency of *Salmonella*, while Simental & Martinez-Urtaza (2008) found a significant inverse correlation between

temperature and *Salmonella* in coastal areas of Baja California, Mexico. Another study on a mixed-use agricultural river basin in Canada over the years 2004–2006 found the greatest prevalence of *Salmonella* and *Campylobacter* in the fall and the greatest prevalence of *L. monocytogenes* in the spring (Wilkes et al., 2009). However, very few samples were collected during the winter months. Studies conducted in Norway and Finland found the highest frequency of *Campylobacter* detection in the autumn (Brennhovd et al., 1992) or spring (Hörman et al., 2004), respectively. *Campylobacter*, STEC and generic *E. coli* have been shown to exhibit greater survival at low water temperatures (4–8 °C) compared to high water temperatures (21–25 °C; Korhonen & Martikainen, 1991; Rice et al., 1992; Wang & Doyle, 1998), however the presence of birds in the water system can be a confounding factor for the detection of *Campylobacter*, as birds are a major reservoir for this microorganism. For example, Hörman et al. (2004) reported a significantly higher detection frequency for *Campylobacter* in August 2001 (23 detections) compared to February to March of the same year (0 detections), which was thought to be due to the presence of birds in the watershed in August. Interestingly, Cheyne et al. (2010) found an inverse relationship between surface water temperature in a mixed-use watershed in Canada and the detection of two *Y. enterocolitica* virulence genes, possibly due to the ability of this organism to outcompete other bacteria at cooler temperatures.

Climate change has also been associated with an increase in sea surface temperatures, showing an average increase of 0.13 °C in sea surface temperature per decade over the last century (EPA, 2013). Increases in ocean temperature are expected to continue during the twenty-first century, with estimates of surface water (top 100 m) warming by 0.6–2.0 °C (IPCC, 2013). This trend is concerning, in part because *Vibrio* spp., which inhabit marine and coastal estuarine waters, have been associated with warmer temperatures. For example, a number of studies have reported a relationship between temperature and *V. cholerae* (Chavez et al., 2005; Colwell & Huq, 1998; Gil et al., 2004; Hashizume et al., 2011; Jiang & Fu, 2001; Lipp et al., 2002; Louis et al., 2003; Mishra et al., 2012; Moreno, 2006; Paz, 2009), and illness from *V. cholerae* has been linked to El Niño-related ocean warming events in South America (Moreno, 2006) as well as to higher sea surface temperatures in Southeastern Africa (Paz, 2009). Increasing sea surface temperature has been found to positively correlate to concentrations of other *Vibrio* species as well, such as *V. parahaemolyticus*, *V. vulnificus* and *V. alginolyticus*, throughout the world (Alam et al., 2003; Böer et al., 2013; Cantet et al., 2013; Johnson et al., 2012; Lipp et al., 2001b; Motes et al., 1998; Oberbeckmann et al., 2011; Pfeffer et al., 2003; Vezzulli, 2012; Vezzulli et al., 2010; Wetz et al., 2013). For example, Alam et al. (2003) found a positive association between climate-induced ocean warming and the *Vibrio* population in the North Sea, and Vezzulli (2012) found that occurrence of *V. parahaemolyticus* increased during the warm weather season along the coast of Japan. Oberbeckmann et al. (2011) also found higher densities of *V. parahaemolyticus* and *V. alginolyticus* in German waters when temperatures were >18 °C in the summer months. In a study conducted along the East, West and Gulf Coasts of the

US, abundance of both *V. parahaemolyticus* and *V. vulnificus* was found to be positively associated with sea surface temperature (Johnson et al., 2012). Interestingly, the study found that temperature was a strong predictor for detection of certain virulence genes associated with *V. vulnificus* and *V. parahaemolyticus*, with three genes having a direct correlation with temperature and one having an inverse correlation. These results, along with those of previous studies (DePaola et al., 2003; Rodriguez-Castro et al., 2010), indicate that temperature can influence the virulence properties of *Vibrio* spp. Furthermore, phytoplankton blooms, which occur primarily in the spring and summer and can be detected remotely by measuring chlorophyll, have also been correlated to increased levels of *Vibrio* spp., including *V. cholerae* and *V. parahaemolyticus* (Lipp et al., 2002; Phillips et al., 2007). For example, Phillips et al. (2007) found a positive correlation between remotely-sensed chlorophyll levels and *V. parahaemolyticus* densities in the Gulf Coast, although the analysis was based on a limited number of samples.

Prevalence of *Salmonella*, *V. parahaemolyticus* and *V. vulnificus* in shellfish has also been associated with seasonality and temperature, with numerous studies finding increased prevalence during warmer periods (Brands et al., 2005; Cook et al., 2002; DePaola et al., 1990, 2003; Duan & Su, 2005; Johnson et al., 2012; Lhafi & Kühne, 2007; Miller et al., 2006; O'Neill et al., 1992; Parveen et al., 2008). For example, Parveen et al. (2008), reported density of *V. parahaemolyticus* in oysters in the Chesapeake Bay, USA, to be correlated with water temperature. Most oyster samples with detectable levels of *V. parahaemolyticus* were collected between the months of April and October, when water temperature was above 14 °C. Likewise, in research conducted along the West, East and Gulf Coasts of the US, *Salmonella* was more frequently isolated from oysters in the warmer months (May–September) as compared to the cooler months (November–March; Brands et al., 2005). This may be related to the ability of *Salmonella* to tolerate elevated salt levels as temperatures increase in the range of 10–30 °C (Montville et al., 2012), although salinity in coastal waters generally increases in the summer months (Motes et al., 1998). Warming sea-surface temperatures are likely to expand the geographic regions in which *Salmonella* and *Vibrio* populations are found. Indeed, geographic expansion has already been observed for outbreaks of *V. parahaemolyticus* in areas such as Peru and Alaska, and seasonal expansion has been observed for *V. vulnificus* illnesses in the Gulf of Mexico (Martinez-Urtaza et al., 2010). In the case of Alaska, rising ocean temperatures (>15 °C) were linked to one of the largest outbreaks of *V. parahaemolyticus* in the USA and extended the geographic range of oyster-associated illness from this pathogen by 1000 km (McLaughlin et al., 2005).

In summary, climate-induced changes in temperature and seasonality will be expected to impact persistence and dispersal of foodborne pathogens in several ways. Increasing temperatures in the mid-latitude regions will likely decrease the overall survival of foodborne pathogens in soils, manure-amended soils and surface waters. However, exceptions may be observed in certain geographic areas and/or on certain farm environments due to factors that confound the effects of temperature, such as nutrient and moisture levels. On the

other hand, increased temperatures will likely lead to increases in the geographic ranges and seasonality of some pathogens, such as *Vibrio* spp. or *Salmonella*, either through increased temperatures in coastal waters or by altering the behavior of their animal hosts.

Rainfall

According to climate modeling carried out by the Intergovernmental Panel on Climate Change (IPCC), an increase in the intensity and frequency of heavy precipitation events for the mid-latitude land masses (e.g. the USA and much of Europe) and wet tropical regions is very likely by the end of this century (IPCC, 2013). Furthermore, mean precipitation levels are expected to increase over the mid-latitude wet regions. Hydrological effects play an important role in the dispersal of foodborne pathogens such as *E. coli* O157:H7, *Salmonella* spp. and *Campylobacter* spp. (Buchan & Flury, 2004; Dorner et al., 2006; Ferguson et al., 2003). Some pathogens are able to persist in the environment for long periods of time and may be spread to foods through contaminated water sources (Miraglia et al., 2009; Montville et al., 2012). For example, heavy precipitation that results in flooding and runoff is a means of dispersal for microorganisms (Figure 2), potentially spreading them to new areas, such as agricultural croplands or bodies of water. These events can also overwhelm sewer systems and increase the possibility of sewage overflows, as well as increase water turbidity, resulting in re-suspension of pathogens from the sediment (Hofstra, 2011).

Many studies examining the effects of precipitation on bacterial dispersal have focused on indicator organisms, such as *C. perfringens*, fecal coliforms and generic *E. coli*, to reveal the possibility of fecal contamination. In general, a positive correlation has been found between rainfall and levels of these indicator organisms in rivers and estuaries (Cooley et al., 2007; Kim et al., 2013; Lipp et al., 2001a; Vermeulen & Hofstra, 2013; Wilkes et al., 2009; Wu et al., 2009). For example, a study conducted over the course of 1 year in Charlotte Harbor, Florida, reported rainfall to be significantly associated with the detection of enteroviruses and fecal indicators (i.e. fecal coliform bacteria, enterococci, *C. perfringens* and coliphage) in the estuary (Lipp et al., 2001a). Positive associations were reported for 7-day antecedent rainfall, mean daily discharge and stream flow. The greatest levels of enteroviruses, fecal coliform bacteria, enterococci and coliphages were detected during a period of especially wet weather coinciding with the El Niño-southern oscillation (ENSO) in the late fall and early winter of 1997–1998. ENSO occurs every few years and is associated with a warming of the waters in the eastern equatorial Pacific Ocean, which leads to global changes in weather patterns (Lipp et al., 2002). A study on the fate and transport of *E. coli* spp. in the Blackstone River watershed in Massachusetts, USA, determined that *E. coli* densities in the water generally increased >10-fold during wet weather events as compared to periods of dry weather (Wu et al., 2009). The upstream and downstream tracking of *E. coli* in the Blackstone River also revealed downstream travel of bacterial isolates and transportation of isolates from sediments into the water column during wet

weather events. Moreover, a study investigating the influence of flooding on pre-harvest *E. coli* contamination in the Salinas Valley watershed determined that months with the highest measured water flow corresponded to the highest concentrations of generic *E. coli* in the water (Cooley et al., 2007). Levels of generic *E. coli* in water samples increased five-fold during months of peak flooding while the incidence of *E. coli* O157:H7 increased from undetectable levels to more than 85% of the samples testing positive.

Interestingly, a study conducted in a lagoon in the South of France found that *E. coli* concentrations in water were significantly higher during periods of rainfall as compared to dry weather, but an opposite effect was observed for concentrations of the bacteria in oysters (Derolez et al., 2013). Rainfall was associated with increased turbidity and decreased salinity, both of which are known to reduce the filtration rates and efficiency of bivalves and therefore may have decreased accumulation of *E. coli* in oysters. Similarly, another study reported no significant association between antecedent rainfall and levels of *V. cholerae* in mussels and an inverse association for antecedent rainfall and levels of *V. alginolyticus* in mussels (Miller et al., 2006). On the other hand, turbidity has been associated with increased density of *V. parahaemolyticus* in oysters, possibly due to the re-suspension of *Vibrio*-containing sediments into the water column (Johnson et al., 2010; Parveen et al., 2008). Turbidity and 2-day antecedent rainfall have also been positively associated with levels of pathogenic *Vibrio* spp. (i.e. *V. alginolyticus*, *V. carchariae*, *V. parahaemolyticus* and *V. vulnificus*) in coastal waters (Johnson et al., 2010; Yamazaki & Esiobu, 2012). However, an earlier study found no significant association between antecedent precipitation and levels of *V. vulnificus* in coastal waters (Lipp et al., 2001b). These findings indicate a complex relationship between rainfall and *Vibrio* spp. in shellfish and seawater, which is likely influenced by a combination of environmental factors, including temperature and salinity.

In Table 2, variable relationships have also been reported between rainfall and other foodborne pathogens. Several studies have reported a positive relationship between rainfall and *Campylobacter* presence in watersheds (Vereen Jr et al., 2007, 2013; Wilkes et al., 2009), as well as between rainfall and *Salmonella* presence in coastal waters or watersheds (Haley et al., 2009; Jokinen et al., 2010; Levantesi et al., 2012; Martinez-Urtaza et al., 2004; Setti et al., 2009; Simental & Martinez-Urtaza, 2008; Wilkes et al., 2009). For instance, one study conducted off the Northwest coast of Spain found that a combination of rainfall and southwesterly wind increased detection frequency of several *Salmonella* serotypes (Martinez-Urtaza et al., 2004), as these weather conditions led to the retention of storm-generated water flows and a lack of circulation in the estuarine environment. On the other hand, inverse relationships were reported between rainfall and the detection frequency of *Salmonella* (Vereen Jr et al., 2013) and *Campylobacter* (Jokinen et al., 2010) in watersheds, possibly due to a dilution effect following heavy rains. Interestingly, higher median accumulative rainfall was associated with absence of *L. monocytogenes* but presence of *Salmonella* and *Campylobacter* in a study conducted on the Pacific coast of Baja California, Mexico (Wilkes et al., 2009).

Temperature variations associated with rainfall may explain some of the differences in these relationships, as *L. monocytogenes* is a psychrotrophic organism whereas *Salmonella* and *Campylobacter* are not; however, this parameter was not included in the analysis. Another study found that *Salmonella* detection frequency in a produce region decreased in the months with peak rainfall events, but then increased in the month(s) following these events (Gorski et al., 2011), indicating a transitory dilution effect.

Positive relationships between rainfall and bacterial detection in water are likely due in part to contaminated runoff or drainage during periods of heavy rainfall (Fremaux et al., 2008b; Levantesi et al., 2012; Simental & Martinez-Urtaza, 2008; Vermeulen & Hofstra, 2013). For example, Rechenburg & Kistemann (2009) found that during and after heavy rainfall events, run-off from combined sewer overflow and non-point sources was associated with high levels of *Campylobacter* and indicator organisms in a watershed in Germany. Further, a study conducted among fish farms in Finland found increased levels of *Listeria* spp., including *L. monocytogenes*, following periods of rainfall, which were likely due to contaminated runoff from nearby brooks and rivers (Miettinen & Wirtanen, 2006). Pandey et al. (2012) reported the association between in-stream *E. coli* concentrations and 15-day cumulative rainfall to be influenced by nearby areas of manure application and cropped land cover, likely due to rainfall-induced drainage or runoff. Indeed, several studies have described dispersal of foodborne pathogens, including *Y. enterocolitica*, *Campylobacter* and *E. coli* O157:H7, as well as fecal indicator bacteria, in agricultural runoff (Brooks et al., 2009; Ferguson et al., 2007; Muirhead et al., 2006; Thurston-Enriquez et al., 2005; Walker & Grimes, 1985) or drainage (Donnison & Ross, 2009; Esseili et al., 2012). Donnison & Ross (2009) observed increased levels of bacteria (i.e. *Campylobacter* and *E. coli* O157:H7) transferred from soil to drainage at higher rainfall rates. These pathogens were found to drain from soil held at 10 °C for 3–4 weeks following application of an inoculated dairy effluent. Contaminated runoff can move into the soil and into sources for drinking water for animals and humans (Fremaux et al., 2008b; Levantesi et al., 2012; Signor et al., 2007). For example, Kistemann et al. (2002) found increased levels of *C. perfringens* and *E. coli* in tributaries of multiple drinking water reservoirs in Germany following extreme rainfall and runoff from surrounding agricultural and forest lands. The increase in intensity and frequency of extreme weather events, such as rainstorms and hurricanes, expected with climate change may result in increased risks for bacterial contamination when current water infrastructures become overwhelmed (Miraglia et al., 2009).

Available water and its drainage class in soil also greatly influence the likelihood of detecting bacterial pathogens and indicator organisms. Specifically, soil with high levels of moisture and poor drainage have been associated with greater survival of *L. monocytogenes*, *Salmonella* and *E. coli* (Chandler & Craven, 1980; Holley et al., 2006; Ohtomo et al., 2004; Solo-Gabriele et al., 2000; Welshimer, 1960), as may be expected based on the moisture needs of these organisms. However, resistance to dry conditions has also been demonstrated, with one study reporting that *E. coli* and *Salmonella*

left in dry soil up to 14 days were able to grow again with the addition of sterile water (Chandler & Craven, 1980). A study conducted on farms in New York found that proximity to pastures increased the likelihood of detecting *L. monocytogenes* in a soil sample (Strawn et al., 2013). Sampling locations with high proximity to impervious surfaces (i.e. within 9.5 m of urban development or roads) had a predicted *L. monocytogenes* prevalence of 20% compared to 5% for samples from other locations. The authors suggested that this observation may have been due to the fact that drainage ditches are often located next to impervious surfaces to channel excess water off the surfaces. These drainage ditches are used as nesting habitats for some wildlife and thus become a source of fecal contamination. Microorganisms in these ditches may then be spread to nearby locations due to events such as heavy precipitation, human activities or foraging wildlife.

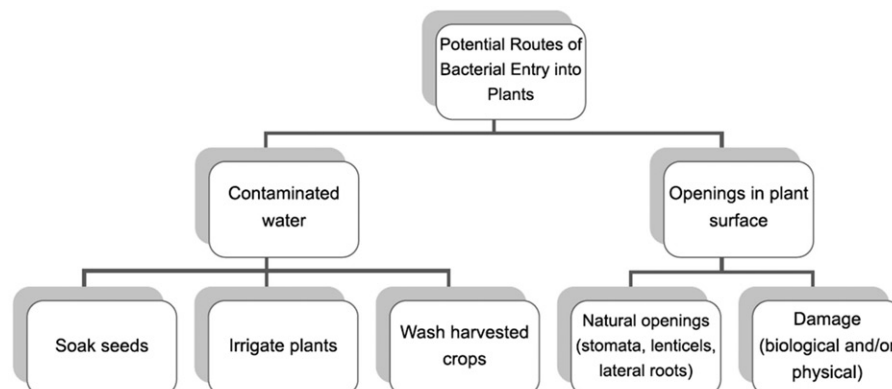
Rainfall can also influence contamination of plants by foodborne pathogens, either through internalization by the root system or from dispersal onto plant surfaces and subsequent internalization (Figure 3). Specifically, heavy rainfall was found to increase the rate of *Salmonella* internalization by lettuce from soil with high levels of the pathogen (Ge et al., 2012). Interestingly, drought-induced conditions also led to increased internalization rates when the soil was highly contaminated with *Salmonella*, indicating that uptake is facilitated during extreme weather events. This study is concerning given that extreme precipitation events in some regions are likely to increase over the next century and that these events can transfer pathogens from contaminated areas into croplands, resulting in the possibility of plant internalization. Direct dispersal of *Salmonella*, *Listeria* and *E. coli* from the ground onto plants or other surfaces during rainfall has also been reported (Cevallos-Cevallos et al., 2012a,b; Girardin et al., 2005; Monaghan & Hutchison, 2012). Cevallos-Cevallos et al. (2012a) determined that adhesion and splash dispersal of *Salmonella enterica* Typhimurium on tomato leaflets was dependent on rain intensity and duration, and the type of planting material. The authors found that high rain intensity (110 mm/h) resulted in a significantly higher population of *Salmonella* being dispersed from the soil onto tomato plants 1 cm above ground when compared with low rain intensity (60 mm/h). Duration of rainfall also affected the levels of *Salmonella* on surfaces: rainfall for 5 and 10 min durations resulted in a progressive increase in the levels of

dispersed *Salmonella* on all surfaces, but rainfall for 20 and 30 min periods led to decreases in the levels of *Salmonella* on surfaces, likely due to a washout effect. The use of mulch in the planting material was found to increase both the dispersal distance and the population of dispersed *Salmonella* as compared to use of soil alone, with plastic mulch having the greatest effect, followed by organic mulch. Furthermore, *Salmonella* dispersed by rain was found to survive on tomato leaflets at 3 cm above the soil for 3 days when held at temperatures of 22–26 °C. Overall, the study found that many factors, including rain intensity and duration, plant foliage and planting material, will affect the concentration and duration *Salmonella* may persist in a crop environment.

In a follow-up study, Cevallos-Cevallos et al. (2012b) discovered that *Salmonella* may become aerosolized during periods of rainfall. The authors simulated rain intensities of 60 and 110 mm/h for periods ranging from 5 to 30 min. Both intensities resulted in *Salmonella* detection in Petri plates containing media at heights of at least 85.5 cm, and increasing the duration resulted in increased frequency of detection for the 60 mm/h intensity. For the 110 mm/h intensity, increasing the duration of rainfall resulted in increased frequency of detection up to a time point of 10 min, after which the frequency of detection decreased. The greatest recovery level of *Salmonella* from air was obtained following simulated rainfall at 60 mm/h for 10 min. The bacteria were recovered from tomato surfaces at heights of 10–80 cm when tested 15 h following the rain simulation, with the greatest frequency of detection occurring after the 10 min rainfall events. However, no *Salmonella* was recovered from the leaflets and it is suspected that polyphenolic compounds on the leaves adversely affected the bacteria. The study results suggested that light rainfall of short duration or application of water-based sprays may promote aerosols of bacteria that can then be dispersed to fruit surfaces. However, heavy rainfall or rainfall for a long duration would likely reduce the level of aerosolized bacteria due to a washout effect of the cells in the air.

Changes in precipitation can also influence the range, abundance and seasonality of animal reservoirs or vectors of disease (CDC, 2008). For instance, rodent populations have been reported to increase following mild and wet winters in temperate regions (Mills & Childs, 1998). Increased abundance of rodents can enhance the spread and persistence of the pathogens they are carrying (Davis et al., 2004; Mills et al., 2010). As mentioned earlier, rodents are known carriers

Figure 3. Major potential routes of entry for bacteria into plant structures. Used with permission from Deering et al. (2012).



of foodborne pathogens such as *Salmonella* and *Campylobacter*. While increased rainfall has not been directly linked to increased transmission of foodborne pathogens from rodents, positive associations have been found between rainfall and transmission of other diseases, such as hantavirus, from rodents (Zell, 2004). Studies examining human cases of plague in the states of Arizona and New Mexico, US, found a positive correlation between precipitation and cases of illness (Ensore et al., 2002; Parmenter et al., 1999). The authors suggested that rainfall in this semi-arid region increases the availability of food sources for rodents, which can carry fleas containing the bacterium *Yersinia pestis*, the causative agent of plague. Rainfall can also lead to increases in the numbers of some amphibian species, which are known to carry *Salmonella* (Srikantiah et al., 2004). In fact, during a period of exceptionally high rainfall in the summer of Mississippi, USA, there was a marked increase in the number of amphibians in the area as well as a seven-fold increase in *Salmonella* infections (Srikantiah et al., 2004). Touching, owning or seeing an amphibian on one's property was found to be a significant risk factor for infection. In the case of foodborne transmission, increased abundance of animal reservoirs in the wild could result in an increased likelihood of transferring pathogens to domestic livestock and/or agricultural crops. Several studies have reported a correlation between rainfall and *Campylobacter* detection in broiler flocks, although this was often observed in combination with a temperature effect (Jonsson et al., 2012; Jorgensen et al., 2011; Rushton et al., 2009). These conditions may have increased the abundance of *Campylobacter* reservoirs and provided a means for dispersal of the pathogen through farmyard runoff. Increased prevalence of brucellosis in livestock has also been associated with peak rainfall seasons in Uganda, although this trend was thought to be due to the fact that these seasons correspond with peak periods of parturition and lactation for livestock, during which time *Brucella* is shed at greater levels (Mwebe et al., 2011).

Overall, increased rainfall in some areas of the world over the coming century is likely to impact the dispersal and survival of foodborne bacterial pathogens in the environment. Increased urban or agricultural runoff during heavy rainfall is likely to increase the transport of pathogens into nearby lands and water bodies, resulting in transmission to food production areas (Figure 2). However, rainfall will likely have a dilution effect on pathogens that are already present in these areas. While more research is needed, the possibility of splash dispersal and plant internalization may also become increasingly problematic during periods of rainfall, especially when increased levels of pathogens are transported to growing areas. Furthermore, areas that experience increased rainfall are likely to have an increase in the abundance of certain animal reservoirs for disease, such as rodents and amphibians, which may transfer pathogens directly to humans or indirectly through food sources such as livestock.

Drought

Whereas precipitation is expected to increase over the next century among the mid-latitude wet regions, many of the mid-latitude and subtropical dry regions, such as North Africa and

the interior regions of North America and Eurasia, will likely experience decreases in mean precipitation levels (IPCC, 2013). Reductions in rainfall can lead to drought conditions, which can subsequently alter the chemical properties of ecosystems such as soil and water bodies. Changes to the chemical properties of these ecosystems may promote or hinder the persistence, growth and dispersal of some foodborne pathogens, which are dependent on factors such as pH and nutrient availability (Table 3).

Over the coming century, some geographic areas such as the Southwestern USA, are expected to have increases in temperature, receive less springtime precipitation and have more frequent and severe droughts (Karl et al., 2009). Physiological stress, such as drought, can lead to a decrease in microbial diversity, favoring those organisms that are best adapted to the stress (Kohler et al., 2010). Losses in biodiversity are expected to occur due to climate change and these changes may allow for proliferation of pathogenic species due to a lack of competitor organisms (Altizer et al., 2013). For example, a previous study found that soil with reduced microbial diversity allowed for increased survival of an introduced *E. coli* O157:H7 derivative (van Elsas et al., 2007, 2011). Along these lines, drought may inhibit some populations of native soil microflora while allowing for some of the more resistant groups of pathogenic bacteria, such as *Staphylococcus*, *Clostridium* and *Bacillus*, to survive. However, most foodborne pathogens are likely to be negatively affected by drought due to their dependence on water activity for survival and growth. For example, soil salinity, which can increase in times of drought, has been found to be negatively correlated to the survival rate of *E. coli* O157:H7 in soils from leafy-green producing areas of the Southwestern USA (Ma et al., 2012). Similarly, another study found that populations of *E. coli* decreased when soil water content was reduced in a study carried out in the Salinas Valley of California (Gutierrez-Rodriguez et al., 2012). Although both attenuated *E. coli* O157:H7 and generic *E. coli* were influenced by water availability, generic *E. coli* showed greater survival rates under field settings, with viable populations being detected in soil with water content as low as 5.4%, after 14 and 21 days following inoculation. In comparison, viable populations of attenuated *E. coli* O157:H7 were only detected at 7 days following inoculation, corresponding to a water content of 9.3%. These findings are consistent with studies discussed earlier in this review that have reported different strains or serotypes of the same species to show varying responses to climatic factors (Fukushima et al., 1999; Mannion et al., 2007). Along these lines, an *E. coli* strain isolated from soil showed significantly greater survival rates under greenhouse conditions following inoculation on spinach plantlets (at 7 days) or potting mix (at 15 days) as compared to *E. coli* strains isolated from lettuce and irrigation water (Gutierrez-Rodriguez et al., 2012). The authors suggested that strains isolated from soil may have developed greater resistance to stress due to exposure to agricultural practices such as crop cultivation and intensive pest management programs. As this study was focused on one geographic region and only considered one strain from each source (i.e. soil, water and lettuce), further studies are needed to explore the differences in environmental fitness from

strains isolated from various sources. Of note, increased carbon dioxide (CO₂) levels have been found to lessen the negative effects of drought on the structural microbial diversity of soil (Kohler et al., 2010), possibly due to increased levels of organic carbon being released into the soil from plant systems. Atmospheric levels of CO₂ have risen by 40% compared to pre-industrial times and future increases are expected to be exacerbated by climate change (IPCC, 2013).

Drought-like conditions, such as those brought on by longer and drier summers, can lead to increases in soil surface hydrophobicity and cause more material to be transported as runoff when rain finally does arrive (Boxall et al., 2009). For example, drought, infected cattle and heavy rains were thought to be important factors in a large outbreak of *E. coli* O157 in Southern Africa, when a 3-month-long drought was followed by heavy rains and contamination of surface waters (Effler et al., 2001). As discussed previously, surface waters and produce items grown in the soil or close to the soil, such as root crops and leafy greens, are at risk for contamination by runoff waters. In addition, soil cracks may lead to expanded macropore systems in which pathogenic material can travel. Drought-induced conditions have also been found to increase the rate of *Salmonella* internalization by lettuce from inoculated soil, especially when high levels of the organism are present, but no effect of drought was observed when the lettuce surface was inoculated (Ge et al., 2014). Pathogens internalized by fresh produce are concerning for human health, as they cannot be fully removed through washing or sanitizing (Ge et al., 2014). On the other hand, drought conditions did not facilitate the internalization of *E. coli* O157:H7 in lettuce when the potting soil was inoculated (Zhang et al., 2009). Drought and other forms of stress have also been found to affect gene expression of defense-related genes in certain plants, thereby leaving them more vulnerable to plant pathogens (Gregory et al., 2009; Rose et al., 2001). Plant pathogens can cause lesions on the plant surface, thereby increasing the potential for colonization and internalization of other microorganisms, including foodborne pathogens (Figure 3; Deering et al., 2012; Ryser et al., 2009).

Besides the many impacts that drought can have on soil and agricultural systems, it can also result in increased salinity of surface waters (Froelich et al., 2012) and increased concentrations of pathogens during waste water discharge due to reductions in water levels (Senhorst & Zwolsman, 2005). Studies on *Vibrio* spp. have revealed a varying relationship between bacterial abundance and salinity, as salt is required for growth of many of these organisms, but excess levels become inhibitory. For example, one study reported a positive association between salinity and density of total *Vibrio* spp. in estuarine waters off the East Coast of the US (Hsieh et al., 2008), but an inverse correlation was observed in studies conducted in the Adriatic Sea and the North Sea, where salinity levels reached unfavorable levels (Caburlotto et al., 2012; Oberbeckmann et al., 2012). Similarly, a study focused specifically on *V. parahaemolyticus* reported a positive association between salinity and total and pathogenic levels of the organism in the Gulf of Mexico for one location sampled (Mississippi) but not for a second location

(Alabama; Zimmerman et al., 2007). Salinity levels at the Mississippi site were generally <10 PSU, whereas salinity levels at the Alabama site reached levels up to 28 PSU. Another study conducted in waters off the Northwest Coast of Spain reported a negative association between abundance of *V. parahaemolyticus* and salinity levels, which ranged from 31 to 36 PSU (Martinez-Urtaza et al., 2008). *Vibrio vulnificus* has also shown a varying relationship with salinity, with one study reporting a positive association at salinity levels below 15 PSU and a negative association once salinity exceeded this level (Lipp et al., 2001b) and another study reporting decreased survival of *V. vulnificus* in seawater at salinity levels ≥30 PSU (Kaspar & Tamplin, 1993). In an extreme case, Froelich et al. (2012) reported an apparent loss of *V. vulnificus* populations in oysters in the US estuary following historic drought conditions and elevated water column salinity, during which time levels were consistently above 15 PSU and were often between 20 and 25 PSU. Remarkably, when salinity levels returned to normal after the drought, the authors were still unable to isolate *V. vulnificus* from the oysters and hypothesized that a more halotolerant bacterium had colonized the oysters, displacing the resident *V. vulnificus* populations. Although *V. cholerae* is capable of growth in freshwater, it shows a similar trend as other *Vibrio* spp., with optimal growth at salinity levels between those of freshwater and seawater (Jiang & Fu, 2001; Lipp et al., 2002; Louis et al., 2003; Singleton et al., 1982).

Overall, climate-induced drought conditions for the mid-latitude and subtropical dry regions have the potential to impact the survival and dispersal of foodborne pathogens in several ways. These conditions are expected to lead to increasing salinity of water and soil systems, which will likely decrease levels of foodborne pathogens, such as STEC and *Vibrio* spp., in most circumstances. However, in situations where water salinity increases to more favorable conditions, increases in *Vibrio* spp. may be observed. Heavy rainfall following periods of drought will be expected to increase surface water runoff, thereby promoting transport of foodborne pathogens to neighboring surface waters or agricultural lands. There is also the potential for increased rates of pathogen internalization by certain crops during periods of drought, although more research is needed in this area.

Wind and dust

Pathogens dispersed by wind may become an increasing concern related to climate change, as the intensity of tropical cyclones (hurricanes and typhoons) is expected to increase in certain regions, in particular the Western North Pacific and North Atlantic (IPCC, 2013). One report discussing North Pacific and North Atlantic cyclones suggested that for each 1 °C increase in tropical sea surface temperature, surface wind speed of the strongest cyclones would be expected to increase by 1–8% and core rainfall rates would increase 6–18% (CCSP, 2008). Based on predictions that the global average sea surface temperature will rise by approximately 0.6–1.5 °C over the next 50 years as compared to 1986–2005 levels (Kirtman et al., 2013), this would correspond to an increase of 0.6–12% in wind speed and 3.6–27% for core rainfall rates

associated with the strongest cyclones. Furthermore, strong storms outside of the tropics are expected to increase in frequency, with stronger winds and maximum wave heights (CCSP, 2008). In a study into the effects of hurricanes on microorganisms in the atmosphere, samples collected in the mid and upper troposphere before, during and after two tropical hurricanes in the Caribbean Sea revealed that ~20% of all aerosolized particles in the 0.25–1 µm size range consisted of viable bacterial cells, indicating the importance of bacteria in the atmosphere (DeLeon-Rodriguez et al., 2013). Interestingly, the composition of microbial communities after the hurricanes was drastically different from the composition prior to hurricanes, suggesting that hurricanes have a major influence on aerosolizing and dispersing microorganisms. Samples collected during and after hurricanes demonstrated higher levels of marine bacteria and were the only samples associated with substantial levels of fecal bacteria, such as *Escherichia* spp., as compared to samples collected prior to the hurricanes. However, the exact species of bacteria in these samples could not be determined in this study, so it is unknown whether any foodborne pathogens were aerosolized. The authors explained the presence of marine bacteria as being likely due to the geographic origin of the hurricanes, while the presence of fecal bacteria was likely related to the passage of the hurricanes over populated areas. Bacterial cells carried by wind could potentially contaminate water sources or land on agricultural crops, where they may colonize the plant surfaces or even internalize into tissue openings and wounds (Figure 3; Deering et al., 2012).

Tropical cyclones and subsequent flooding events have been associated with food or waterborne diseases in several instances, including illness from *V. cholerae* associated with Hurricanes Katrina and Rita (CDC, 2005a,b; Watson et al., 2007). Cyclones followed by heavy rainfall have been found to increase levels of total *Vibrio* spp. in estuarine environments due to sediment resuspension and changes in salinity gradients (Lara et al., 2009). These events can result in increased levels of total *Vibrio* spp. and *E. coli* in the sediment for months afterwards, as was observed in the US estuary following Hurricane Ophelia in 2005 (Fries et al., 2008). Tropical cyclones may also provide a mechanism for airborne dispersal of microorganisms associated with aeroplanktonic organisms, such as midges. In an experimental setting, it has been demonstrated that *V. cholerae* can be transported aerially by non-biting midges, small flying insects that are carried by the wind, suggesting that these insects can act as a vector for cholera (Broza et al., 2005). In a follow-up study, wind direction was found to influence intracontinental spread of cholera outbreaks in Africa and India, supporting the hypothesis that *V. cholerae* may be carried aerially from one body of water to another, possibly due to its association with aeroplanktonic flies (Paz, 2009). However, further studies are needed to verify this transmission route.

Climate change and desertification have contributed to increased dust activity in some regions of the world (Griffin, 2007). High-speed winds and storms cause dust events in which soil is lifted into the atmosphere and transported long distances (Griffin et al., 2001). Areas that experience more frequent and severe droughts followed by strong storm systems could experience increased levels of wind-blown

dust in the environment (CCSP, 2008). Dust and particulates can travel as high as 10 km, and reach continents across bodies of water (Griffin et al., 2001). Wind and dust events also carry bacteria, fungi and viruses that can contaminate food and water sources (Figure 2). Studies have reported the detection of airborne *E. coli*, *Brucella*, *B. cereus*, *C. perfringens*, *Salmonella*, *Campylobacter* or *S. aureus*, as well as the transport of some of these organisms over short distances (Allen et al., 2007; Alvarado et al., 2009; Chinivasagam et al., 2009; Davis & Morishita, 2005; Harbaugh et al., 2006; Iwabuchi et al., 2010; Leski et al., 2011; Masclaux et al., 2013; Miller et al., 2008; Oliveira et al., 2006; Rosas et al., 1997; Schulz et al., 2012; Whyte et al., 2001). For example, *E. coli* was found in airborne and settled dust sampled from both indoor and outdoor settings in Mexico City (Rosas et al., 1997). The authors sampled dust from 30 residential homes and found a range of *E. coli* serotypes ($n = 89$), including some that were associated with pathogenic *E. coli* and/or resistant to multiple antibiotics. The levels of *E. coli* in proportion to the total number of Gram-negative bacteria cultured was highest for the samples collected from settled dust indoors (22.9%), as compared to settled dust from outdoors (9.6%), airborne dust indoors (2.7%) and airborne dust outdoors (1.2%). *Escherichia coli* levels may have been lower in the airborne dust due to damage inflicted during the aerosolization process, as isolation of this organism from airborne dust was improved when glycine betaine was included as an osmoprotector.

Many of the studies demonstrating airborne presence of foodborne pathogens have been conducted on the farm environment or in animal processing plants. For example, Iwabuchi et al. (2010) analyzed airborne dust samples collected from 203 layer farms in Japan and found that 23.6% of farms had dust samples that were positive for *Salmonella*. The presence of *E. coli* O157:H7 in the feces of feedlot cattle has also been positively associated with wind velocity, suggesting the importance of wind in pathogen dispersal on the farm environment (Sargeant et al., 2004). Another study reported wind-driven transport of methicillin-resistant *S. aureus* (MRSA), with airborne detection of the pathogen at distances of 50 and 150 m downwind of a MRSA-positive pig barn and detection in soil samples up to 300 m downwind of the pig barns (Schulz et al., 2012). Interestingly, Chinivasagam et al. (2009) found levels of *E. coli* in poultry litter (~10⁸ CFU/g) to be linked to levels in aerosols both inside and outside of a broiler poultry shed (10²–10⁴ CFU/m³). However, this relationship was not observed for *Salmonella* or *Campylobacter*. *Salmonella* was only present intermittently and at low levels in air samples (0.65–4.4 MPN/m³) and *Campylobacter* was only detected once in air samples and was at low levels (2.2 MPN/g), despite its presence in litter at levels of 10⁷ MPN/g late in the production cycle. *Campylobacter* is likely a poor survivor in the air environment due to its sensitivity to atmospheric levels of oxygen and to drying (Montville et al., 2012). Along these lines, multiple studies have reported an inability to culture *Campylobacter* from air samples in poultry houses, despite detection by PCR (Ahmed et al., 2013; Olsen et al., 2009), and another study determined that airborne *Campylobacter* was not a significant source of broiler carcass contamination

during defeathering, even though it was cultured from the surrounding air (Berrang et al., 2004).

Landfills have also been found to contain low levels of airborne enteric bacteria, including *Salmonella*, *Y. enterocolitica*, *E. coli* and *Klebsiella pneumoniae* (Flores-Tena et al., 2007; Rosas et al., 1996). Depending on proximity, high-speed winds may be capable of transporting microorganisms from these locations into food production areas. For example, a study which detected both *Salmonella* and *Y. enterocolitica* in air samples collected 2 m above a landfill reported the presence of farms less than 1 km from the landfill, as well as the presence of cattle grazing and drinking from water within a few meters of the landfill (Flores-Tena et al., 2007). These findings are concerning, as they suggest the possibility of airborne transmission of pathogens from the landfill to food and water sources for livestock. However, the levels of the pathogens were low (10^1 CFU/m³) and were not detected in soil or leachate samples collected at the landfill.

Interestingly, bacterial counts in atmospheric samples have been found to be higher during dust storms as compared to background levels (Griffin, 2007). A study conducted in Southwestern Japan revealed that that airborne dust carried 1.7–27 times more bacteria than non-dusty air, with total bacterial cell concentrations in airborne dust varying between 10^6 and 10^7 cells/m³ (Hara & Zhang, 2012). The levels of viable bacteria in dusty air (10^5 – 10^6 cells/m³) were similar to or higher than levels in non-dusty air (10^5 cells/m³). Survival of bacteria in dust samples would be expected to be greater for organisms that are resistant to multiple environmental stresses. While many pathogenic foodborne bacteria are non-spore formers and likely do not survive well in long distance travel by wind, spore-forming foodborne pathogens such as *C. botulinum*, *C. perfringens* and *B. cereus* may be a concern, as well as *S. aureus*, which is resistant to low water activity and drying. For example, a spore-forming bacterium native to desert soils (*Bacillus megaterium*) was reported to survive stresses associated with dust transport, such as UV exposure, low humidity and high temperatures, better than some non-spore-forming organisms (e.g. *E. coli*, *Salmonella*, *Pseudomonas* and *Staphylococcus aureus*; Toepfer et al., 2012). Among the non-spore formers, *E. coli* and *S. aureus* were found to have the best survival rates over a 1 month period in dry sand at ~25 °C and ~40–55% relative humidity. Non-spore-forming bacteria were greatly affected by UV radiation (wavelength = 254 µm) after a 2-min exposure period, whereas spore formers began showing sensitivity to the radiation after 4 min. Interestingly, organisms from the genera *Bacillus*, *Clostridia* and *Staphylococcus* have also been detected in studies analyzing the bacterial composition of dust storm samples originating from regions such as the Middle East and the Sahara and Sahel regions of North Africa (reviewed in Griffin, 2007; Polymenakou et al., 2008). The potential foodborne pathogens *C. perfringens*, *Brucella* and *B. cereus* have also been detected in airborne dust and fine topsoil particles collected in Iraq and Kuwait; however, the viability and virulence of these organisms was not tested (Leski et al., 2011). Moreover, dust is thought to be a major route for the contamination of honey with *C. botulinum* spores, resulting in cases of infant botulism (Nevás et al.,

2006). In addition to transporting microorganisms, dust events can also deliver nutrients that promote microbial growth. For instance, in field tests conducted in the Florida Keys, Westrich et al. (2013) demonstrated that addition of Saharan dust to seawater resulted in increased growth of total *Vibrio* spp. Furthermore, tests conducted in the laboratory revealed that addition of this dust to iron-depleted artificial seawater containing *V. alginolyticus* and *V. cholerae* resulted in increased growth of these organisms. Wind-blown Saharan dust is known to contribute to iron deposition in the Atlantic Basin, including the Southeastern US, and this study suggests the importance of this dust in the proliferation of *Vibrio* populations.

Overall, climate change is likely to contribute to increased levels of global dust activity due to desertification as well as increased wind speeds associated with storm systems. These events may promote the dispersal and persistence of some foodborne microorganisms in the environment, especially those that demonstrate higher levels of resistance to environmental conditions, such as spore-formers (Table 4). Although viable foodborne microorganisms have been detected in air and dust samples, more research is needed into the possibility for short- and long-distance airborne transport. Besides transport of pathogens directly, wind and dust events are likely to influence pathogen persistence by changing the composition of the immediate environment, such as through iron deposition.

Future areas of research and use of predictive models

The potential effects of climate change on the persistence and dispersal of foodborne pathogens in the environment remain to be fully understood. How pathogens will respond to climate change will depend on the various physiological parameters of each microorganism, as well as complex ecological interactions with their animal hosts and the outside environment. While change in some climatic factors will result in the inhibition of some pathogens, others will likely emerge or evolve to thrive in these altered ecosystems. Research will be needed to further our understanding of the potential for pathogens to develop resistance to external stresses and ways to limit or overcome this. Long-term studies on crop systems, climate and pathogens need to be initiated and utilized to understand the variables and their effects. Current agricultural practices and livestock cultivation will benefit from a proactive approach to avoid the potentially detrimental effects of climate change on food safety. Furthermore, improved methodologies for the rapid detection of foodborne pathogens and prevention of foodborne disease will be increasingly important, especially for use in the field following extreme weather events.

One way of anticipating the potential effects of climate change on food pathogens and foodborne illness has been the development of predictive models. These models correlate climatic factors to pathogen prevalence or foodborne illness in a specific geographic area and allow for the prediction of periods of increased risk. Identification of these risk periods allows food producers to take a proactive approach in promoting the safety of their product by taking actions such

as delaying harvest until the risk is reduced or diverting a product to undergo further processing. Tools such as these could also be used in the development of risk management systems to prevent and/or control microbiological contamination of foods such as fresh produce, as described in Jacxsens et al. (2010). Although the relationships between climate change and environmental levels of pathogens and/or disease incidence involve many complex variables, development of predictive models may be accomplished with some success by focusing on known and measurable correlations with factors such as temperature or precipitation (Hofstra, 2011). For example, predictive models have been developed for abundance of total *Vibrio* spp. in estuarine waters based on known relationships with temperature, salinity and extreme weather events (Froelich et al., 2013) as well as for levels of *Vibrio parahaemolyticus* in Gulf Coast Oysters in relation to sea surface temperature (Phillips et al., 2007). However, McEgan et al. (2013) reported an inability to predict *Salmonella* concentrations in surface waters of Florida, USA, using physicochemical parameters, such as temperature, pH and turbidity, reflecting the complex relationships involved. The effectiveness of predictive models appears to be increased for some geographic locations over others. For instance, models developed to predict levels of fecal contamination (i.e. *E. coli*) at inland beaches in Ohio, USA, in relation to climatic factors were only reported to be successful for a portion of the sites examined (Francy et al., 2013). Similarly, models developed to predict *E. coli* at Great Lakes beaches were successful for some beaches, but not all (Nevers & Whitman, 2005). Overall, few models have been developed to examine the relationship between climate change and foodborne pathogens in the environment and much work remains to be done in this area.

Another future area of research will be to examine the impact of climate change on the transmission of pathogens into the food supply from animal hosts. While it is well-recognized that climate change alters ecosystems (Parmesan, 2006; Walther et al., 2002), there is limited information concerning the association between climate change and disease transmission from animal reservoirs. This is due, in part, to the complexity of interactions between climate, host and pathogen, and to a lack of research in this area (Mills et al., 2010; Portier et al., 2010). This line of research is multidisciplinary, requiring a thorough understanding of the many factors influencing these complex relationships (e.g. climate science, epidemiology, biology and ecology) and will require movements such as the OneHealth Initiative (<http://www.onehealthinitiative.com/>) to unite scientists from multiple backgrounds. Improving our understanding of these links would facilitate the ability to predict potential spikes in disease transmission, thereby allowing for proactive adaptation to climate change and prevention of climate-related outbreaks of foodborne disease. Along these lines, a series of specific goals for future research in this area to better our understanding of these relationships are detailed in Mills et al. (2010), including the further identification and characterization of zoonotic and vectorborne pathogens; the establishment of baseline data on geographic and habitat distribution of these pathogens and their hosts; as well as conducting experimental and field studies on the effects of climate

change on hosts and their abilities to carry and transmit pathogens.

Conclusions

As demonstrated in this review, the effects of climate change on the persistence and dispersal of foodborne pathogens are complex and dependent on multiple factors. The effects of temperature and rainfall have been examined in numerous studies and have demonstrated variable effects depending on geographic locations and other climatic factors simultaneously involved. On the other hand, the effects of other climatic factors, such as wind and dust events, on foodborne pathogens are less well-studied but may become increasingly important as they increase in frequency and/or intensity over the coming century. How climate change will impact transmission of foodborne pathogens from animal hosts is one of the most complex areas of research discussed in this paper and, being a challenge to study, it is also poorly understood. Due to the numerous environmental routes by which livestock and agricultural crops can become contaminated by foodborne pathogens, proper management of water sources, soil, wildlife intrusion and manure application, combined with an awareness of the effects of climate change on these elements, will be paramount to food safety over the coming century. Seafood safety and waterborne disease is also a major concern in the face of predictions such as increased intensity of storm systems, which may bring more foodborne pathogens into the water column and elevate the risk of disease transmission. Overall, there remains much to be understood in this field of study and additional research is needed to quantify the effects of climatic factors on foodborne pathogens. As these relationships become better understood, they may be used to develop or improve upon predictive models that allow for a proactive approach to overcoming food safety risks presented by climate change. Importantly, advancement in this field will also require that scientists from multiple disciplines work together to address the complex interactions of climate, ecosystems and food safety.

Declaration of interest

The authors report no conflicts of interest. The authors alone are responsible for the content and writing of this article.

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