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Review

Perspectives on Using a Competitive Exclusion Approach to Control *Listeria monocytogenes* in Biological Soil Amendments of Animal Origin (BSAAO): A Review

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Abstract: Biological soil amendments of animal origin (BSAAO), such as animal waste or animal-waste-based composts, may contain foodborne pathogens such as *Listeria monocytogenes*. Due to the ubiquitous nature of *Listeria*, it is essential to understand the behavior of *L. monocytogenes* in BSAAO in order to develop preharvest prevention strategies to reduce pathogen contamination. As biological control agents, competitive exclusion (CE) microorganisms have been widely utilized in agriculture to control plant- or foodborne pathogens. Due to the diverse microbial community, animal wastes and composts are the potential sources for isolating CE strains for pathogen control. To explore the potential of using CE to control *L. monocytogenes* in BSAAO, we thoroughly reviewed the studies on the fate of *L. monocytogenes* in the agriculture field, and in the isolation and identification of CE from different matrices, and the applications of CE as a biological control method. Future studies using a next-generation sequencing approach to identify and characterize CE strains in complex microbial communities can provide a comprehensive picture of the microbial interactions between invading pathogens and the indigenous microbiota in BSAAO. This comprehensive review will provide insight into the development of effective biological control measures for preventing *L. monocytogenes* contamination in the agricultural field and enhancing food safety.

Keywords: BSAAO; compost microbiome; competitive exclusion; foodborne pathogen; survival

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1. Introduction

Listeria monocytogenes is a significant foodborne pathogen that poses a serious threat to human health. This bacterium is responsible for listeriosis, which can result in a high fatality rate of up to 30% among high-risk individuals [1]. It is commonly associated with and can survive in various foods or food-associated systems, particularly fresh produce [2–5]. Due to the vulnerability of fresh produce to physical decontamination, physical approaches such as pasteurization are typically not applied in preventing pathogen contamination in fresh produce [6,7]. Additionally, *L. monocytogenes* can survive and grow in cold temperatures, increasing the risk of contamination of even properly stored produce [8]. Therefore, postharvest control methods are limited for fresh produce and effective preharvest control measures to prevent *L. monocytogenes* contamination are critical for ensuring fresh produce safety.

Biological soil amendments of animal origin (BSAAO) including raw animal manures and composts are commonly used to enhance the yield of fresh produce and other agricultural crops [9]. However, inadequately treated BSAAO can also be a potential source of *L. monocytogenes* contamination in fresh produce [10]. While studies have been focused on the fate of *L. monocytogenes* in BSAAO, the essential factors that can impact the persistence of *L. monocytogenes* in BSAAO have not been comprehensively reviewed [11]. Therefore, it is important to understand the behavior of *L. monocytogenes* in BSAAO and the potential preharvest prevention measures which can be used for fresh produce.

Raw animal manure contains feces, urine, bedding materials, and other secretions from the animal. As the rich sources of plant nutrients, animal wastes are commonly used as fertilizers or biological soil amendments [12,13]. However, the application of untreated animal wastes may introduce potential microbial hazards to crop fields; thereby, it is required that the raw animal manure be incorporated into the soil more than 90 days prior to harvest for crops that have no direct contact with soil, and 120 days if the produce has direct contact with soil [14]. The application of raw manure must not contact produce during application, and the potential for contact with produce after application should be minimized [14]. Sheng et al. [15] conducted a 2-year field study to evaluate the impacts of dairy manure fertilizer application on the microbial safety of red raspberries. Although no Shiga-toxin-producing *E. coli* (STEC) or *L. monocytogenes* was detected in fertilizer, soil, foliar, or raspberry fruit samples throughout the sampling period of 2 years, *Salmonella* in soil amended with contaminated fertilizer was reduced to an undetectable level after 2 or 4 months of application.

The harmful or pathogenic microorganisms in BSAAO can be reduced or eliminated through composting. Composting is a controlled biological process that broadly consists of four typical phases based on the temperature generated and active microbial community: mesophilic, thermophilic, cooling, and maturation phases. Normally, composting process proceeds with solid or liquid materials within a moisture level range of 40 to 50% or 90 to 98%, respectively [16]. During a satisfactory composting process, mesophilic, thermophilic, and thermotolerant bacteria, fungi, and actinomycetes are actively involved [17]. Pathogens are killed primarily by the accumulation of heat (45 to 75 °C) generated by indigenous microorganisms during the early phases of aerobic composting of animal manures [18–20]. However, due to the complex composting process or the recontamination during storage, the pathogenic bacteria can be reintroduced to the finished compost. As specified by the Food Safety Modernization Act (FSMA) Produce Safety Rule, microbial standards for biological soil amendments of animal origin include less than 0.3 most probable number (MPN) per gram or milliliter of analytical portion for *E. coli* O157:H7, less than 3 MPN per 4 g or mL of total solids for *Salmonella* spp., and less than 1 CFU per 5 g or mL of analytical portion for *L. monocytogenes* [14]. To achieve these standards, the FSMA's Produce Safety Rule mandates the incorporation of alternative treatments for reducing or eliminating human pathogens in raw animal wastes before land application [21].

Physical and chemical methods for controlling pathogens in BSAAO often have adverse environmental impacts, such as greenhouse gas emissions and odor pollution, and may be costly [11,22]. To address these challenges, researchers have explored biological methods for reducing or inhibiting pathogen populations in BSAAO [22]. One promising approach is the use of competitive exclusion (CE) microorganisms, in which multiple beneficial microorganisms are allowed to grow and establish a community that can inhibit the growth of pathogens like *L. monocytogenes* [23,24]. CE offers a cost-effective and environmentally sustainable means of reducing pathogen populations in BSAAO by leveraging the natural properties of microbiological communities [25]. Moreover, the metabolic activities of microbiological communities in BSAAO can provide essential nutrients for plant growth, making this approach both effective and sustainable [11]. Lactic acid bacteria have been well studied to competitively exclude pathogens like *Escherichia coli* O157:H7, *Salmonella*, and *L. monocytogenes* in foods [26,27], but their effectiveness against *L. monocytogenes* in BSAAO is not conclusive. Furthermore, microbial communities, including other species that effectively control *L. monocytogenes* are unclear.

To fill the current knowledge gaps, we therefore conducted a comprehensive review on understanding the potential of using a CE approach to control *L. monocytogenes* in BSAAO used for agriculture production. We thoroughly reviewed the studies on the fate of *L. monocytogenes* in the agriculture field, the isolation and identification of CE from different matrices, and the applications of CE as a biological control method. This information can provide insight into the development of effective biological control measures for preventing *L. monocytogenes* contamination in the agriculture field and enhancing food safety.

2. Factors That Impact the Fate of *L. monocytogenes* in BSAAO

The presence of *L. monocytogenes* has been reported in both pre- and post-harvest environments, including fresh vegetables, processing environments, soil, animal feces, and irrigation water [3,28,29]. Studies from the last 20 years have reported that animal wastes or associated produce fields can become contaminated with *L. monocytogenes*, and the prevalence level ranged from 0 to 50% [3,29–37]. Livestock manure and manure-contaminated water have been identified as potential sources of high levels of *L. monocytogenes* [36]. *L. monocytogenes* was often isolated from both farm and processing environments because it can mediate a saprophyte-to-cytosolic-parasite transition by modulating the activity of a virulence regulatory protein called PrfA, using available carbon sources [38–40]. *L. monocytogenes* can form biofilms, allowing it to establish and persist for extended periods in various environments [41]. A comprehensive understanding of the survival characteristics of *L. monocytogenes* is therefore crucial reducing food contamination with this pathogen.

The growth and survival of *L. monocytogenes* on fresh produce have been extensively reviewed [40,42]. Worldwide, the prevalence of *L. monocytogenes* in fresh produce was 0.9 to 25%, and the highest level was identified in parsley in Malaysia [40,43]. The growth and survival of *L. monocytogenes* on intact fresh produce varied depending on the type of commodity, and the highest growth rates were observed at temperatures of 20 °C or higher. Importantly, both of these studies suggested that *L. monocytogenes* contamination on fresh produce can occur directly or indirectly via fecal and compost contamination. Therefore, it is essential to identify the factors that can significantly affect the survival of *L. monocytogenes* in animal wastes and composts derived from animal waste to better understand the fate of this pathogen in such materials.

According to the challenge studies published from 2000 to 2023 on the fate of *L. monocytogenes* in BSAAO, the initial level of spiked pathogens ranged from 2 to 8 log CFU/g or mL, depending on the research purpose (Table 1). The factors that influenced the fates of *L. monocytogenes* in BSAAO can be grouped as follows: (i) Types and physical-chemical characteristics of BSAAO; (ii) storage temperature of BSAAO; and (iii) background microbial community in BSAAO. Depending on these factors and experimental design, pathogens in animal wastes or composts derived from animal waste can survive better in dairy manure, at a lower temperature, and with a reduced background microbial load. Notably, most of the studies were carried out for the evaluation of several confounding factors together.

Microbial growth and metabolic processes depend on moisture content and nutrients. Factors including moisture content (ranging from 20 to 80%), water activity (ranging from 0.89 to 0.75), and extra organic matter (ranging from 2 to 7%) [44–50] have shown the impacts on the survival of *L. monocytogenes* in different types of animal waste. Dairy slurries can support *L. monocytogenes* survival for up to 28 days at 25 °C, compared to other animal wastes like those from pigs, poultry, or sheep [44,47]. *L. monocytogenes* were unchanged in the sawdust manure mix and untreated liquid swine manure for up to 28 days at 25 °C [44]. Adding 2% dry matter (e.g., hay, straw, or bedding materials) enhanced pathogen survival [50]. Most importantly, it is not surprising that the microbiota in BSAAO can also be impacted by the aforementioned factors and therefore impact the pathogen survival.

BSAAO, in the form of animal manure or animal-waste-based compost, can be considered a rich source for microbiomes. Microbial species, such as *Aeromonas hydrophila*, *Arobacter butzleria*, *Bacillus anthracis*, *Brucella abortus*, *Campylobacter jejuni*, *Chlamydia psittaci*, *Clostridium perfringens*, *Clostridium botulinium*, *Coxiella burneti*, *E. coli*, and *Yersinia* spp., were found in animal manure or animal waste [12]. During the composting process, mesophilic bacteria (i.e., *Pseudomonaceae*, *Erythrobacteraceae*, *Comamonadaceae*, *Enterobacteriaceae*, *Streptomycetaceae*, and *Caulobacteraceae* families) could break down the organic matter in the initial stage [51]. In the finished compost, the typical microorganisms presented include *Alcaligenes faecalis*, *Arthrobacter*, *Brevibacillus*, *Enterobactericae*, *Bacillus* species, *Thermus* spp.,

Streptomyces, *Aspergillus fumigatus*, and *Basidiomyces* spp., which belong to groups of bacteria, actinomycetes, or fungi [52]. The type of raw manure can significantly impact the microbial members in the finished compost product; for example, Proteobacteria and Chloroflexi were the major phyla in sheep and cattle manure composts, and Firmicutes dominated in pig and chicken manure composts [53]. Some of these active microbial members in BSAAO, such as *Bacillus* or actinomycetes, can surely impact the behaviors of invasion pathogens present in the BSAAO by competition or other mechanisms.

Many studies have shown that the fate of *L. monocytogenes* in animal manure and the BSAAO-amended soil ecosystem was affected by the composition of background microbial communities [54–58]. In most cases, the reduced indigenous microbial load favored the persistence of pathogens in animal manure or BSAAO-amended soil. For example, the quick die-off of pathogens in nonsterile soil was mostly due to the antagonistic effects against *L. monocytogenes* by the indigenous microflora. In contrast, Desneux et al. [54] found that the behavior of *L. monocytogenes* was not influenced by the taxonomic composition of pig manure. The authors suspected that *L. monocytogenes* entered a viable but non-culturable stage in the pig manure during storage. However, modifications in the indigenous microbial community, such as autoclaving or diluting, omitted effects on the natural microbiota. As such, the complex interactions between the invasion pathogens and indigenous microflora still require further research.

Because amending agriculture soil with treated animal manure instead of fresh manure released less potential *Listeria* in the environment [59], biological treatment options, including composting (aerobic) and biogas (anaerobic) processes, can be used as pathogen control treatments in addition to recycling raw animal wastes back into the soil for crop use. The finished compost should be thoroughly decomposed and thereby pathogen-free. However, sporadic cases have been reported of the presence of foodborne pathogens in finished compost, indicating that the inadequately treated composts made from animal waste are potential sources for pathogens [58,59]. These pathogens either survived the composting process or were cross-contaminated with raw manure, and had growth potential during the storage of the compost. To meet the microbial standards for BSAAO, the incorporation of alternative treatments, such as competitive exclusion strategies, for reducing or eliminating human pathogens in raw animal wastes before land application is required [21].

Table 1. Summary of reported studies on the factors affecting survival of *L. monocytogenes* in animal wastes and animal-wastes-based compost (2000 to 2023) [1].

Matrix Used	Initial Levels	Treatment	Significant Findings	Reference
Bovine-manure-amended soil	5 to 6 log CFU/g	Temp: 5, 15 or 21 °C; BMC: manure-amended autoclaved soil	*L. monocytogenes* survived longer at lower temperatures in the manure-amended autoclaved soil.	[55]
Pig manure	N.A.	Temp: 8 and 20 °C; AWT: raw and biological treated manures; BMC: 81.5–94.8% and 67.8–79.2% VBNC cells	*L. monocytogenes* increased more at 20 °C. *L. monocytogenes* can enter VBNC state in the pig manure during storage and the behavior of *L. monocytogenes* was not influenced by the taxonomic composition of pig manure.	[54]
Dairy manure compost	7.4 log CFU/g	ST: Solid or liquid manure with different compost pile size	*L. monocytogenes* can survive in solid manure pile for at least 29 weeks; compost pile size and temperature affect the pathogen survival.	[60]
Composted livestock manure or sewage sludge	5–6 log CFU/g	Temp: 50 °C; TD: 3 months; AWT: dairy cattle, beef cattle, pig, poultry layer, and sheep	Pathogen survival time order (shorter to longer): dairy cattle = pig < poultry layer = sheep < beef cattle.	[49,61]

Table 1. *Cont.*

Matrix Used	Initial Levels	Treatment	Significant Findings	Reference
Farmyard manure (FYD)	2.1–4.9 log CFU/mL	AWT: dairy FYD, pig FYD, broiler liter, dairy slurry, and dirty water	Maximum pathogens survival period during storage: dairy FYD = pig FYD (regardless turned or unturned) < broiler litter < dairy slurry with 7% dry matter < dairy slurry with 2% dry matter.	[50]
Liquid swine manure and sawdust manure mix and dairy manure compost	6 log CFU/g	ST: sawdust manure mix or untreated swine manure or pack storage; Temp: 25 to 55 °C	*L. monocytogenes* were unchanged in the sawdust manure mix and untreated liquid swine manure for up to 28 days at 25 °C. *L. monocytogenes* was destroyed most rapidly under thermophilic composting and persisted the longest in pack storage or low-temperature composting.	[44,47]
Dairy compost extract	3 log CFU/mL	Temp: 22 to 35 °C; AWT: water extract of dairy compost of different ratios (1:2,1:5, and 1:10, *w*/*v*)	Indigenous microflora suppressed the pathogen regrowth in compost extract, especially at 35 °C.	[62]
Animal-manure-based compost	7 log CFU/g	Temp: 20 to 40 °C; MC: 30 to 60%; AWT: dairy, chicken, and swine compost mixed with supplements	Volatile acids promoted pathogen inactivation when temperatures were too low or quick heat was lost at the surface of compost piles. Suboptimal MC (30–40%) were less effective for pathogen inactivation.	[63,64]
Dairy manure	7 log CFU/mL	Temp: 30, 35, 42, and 50 °C; ST: anaerobic (AN) and limited aerobic (LA)	Temp: Reduction in PA increased with higher temperature. ST: Effects of both LA and AN condition in pathogen reductions were similar. Pathogen survival time order (shorter to longer) was: *L. monocytogenes* < *Salmonella* < *E. coli*.	[48]
Anaerobic Biogas Digestates	7 log CFU/g	Temp: 1.1 to 19.1 °C AWC: pig, cattle, poultry, and horse slurry mixed with maize silage	Temp: Reduction in PA increased with higher temperature. Pathogen survival time order (shorter to longer) was: *Salmonella* < *E. coli* < *L. monocytogenes*.	[65]

[1] Temp, Temperature; MC, Moisture content level; ST, Storage condition; BMC, Background microbial community; SE, Season; TD, Testing duration; AWT, Animal waste types.

3. Competitive Exclusion (CE) Strategies to Control Pathogens

Over the decades, biological control strategies have also been developed to kill pathogens and ensure microbiological safety. Among these strategies, competitive exclusion (CE) has emerged as an effective method to mitigate the impact of pathogens. CE involves the use of non-pathogenic microorganisms to boost microbial competition, ultimately reducing the number of pathogens in a certain environment [66,67]. Traditionally, CE cultures isolated from animals have been added to animal feed to promote interactions between gut microbiota and non-pathogenic microorganisms, resulting in an effective barrier in animal guts. In addition to animal feed, CE cultures can also be used in the agriculture and food industries to control the growth and spread of foodborne or plant pathogens. This strategy is ecofriendly and does not involve the use of chemical agents or other harmful substances.

CE microorganisms can be isolated from different sources, as documented in previous publications. The utilization of culture-based methods is crucial for isolating microorganisms, including candidate CE strains, from various environments. The environments to which these strains have adapted are the sources of CE microorganisms [67,68]. Nutrient media can be used to directly isolate bacterial culture from processing facilities or fecal samples without a history of pathogen contamination (Table 2). The antagonistic activ-

ities of CE isolates against pathogens are confirmed using spot-on-lawn, patch plate, or agar cylinder techniques, while cell-free supernatant fluids can be evaluated using disc diffusion or agar well diffusion techniques. It should be noted that if the CE microorganism is suspected of producing bacteriocin-like antibacterial compounds, spot-on-lawn is preferable for the confirmation test. In natural environments, such as soil or animal waste samples, CE species may be non-culturable or difficult to cultivate. Specific growth nutrients or growth-promoting factors, as well as changes in the isolation agar preparation and incubation conditions, may thus be required for isolating or resuscitating VBNC or difficult-to-culture microorganisms from environmental samples [69–71]. The recovery and identification of CE microorganisms are significantly influenced by culture-based methods and growth conditions. Direct culturing is still a viable method for isolating CE from various environments, but VBNC cultures require additional steps and more optimal conditions. Confirming antagonistic activities against pathogens is the first step to identify the potential of CE strains to control pathogenic bacteria in various matrices.

CE microorganisms inhibit human pathogens in the natural environment through the production of antibacterial substances, a fast growth rate, competition for limited nutrient sources, and attachment to favorable surfaces. These desired features can collaborate to increase the efficacy of CE strains. The production of antibiotics by CE microorganisms must be regulated to an adequate level to suppress the growth of pathogens effectively, and the quorum-sensing mechanism is involved in this process [72]. Additionally, the higher growth rate and the capacity to uptake the scarce supply of essential nutrients from the growth environment are crucial elements in establishing the dominance of the CE strains when different species of bacteria coexist in one environment [73]. For example, the siderophore production for acquiring iron and the competitive uptake of glucose have been proven to be mechanisms of inhibiting the growth of a fish pathogen (*Aeromonas hydrophila*) by *Bacillus cereus* [74]. Competition for attached sites between CE microorganisms and pathogens can occur through co-attachment on the same surface or the displacement of pathogen colonization by CE. The capability of the selected *Lactobacillus* strain to displace pathogen colonization on the mucosal surface was confirmed in a study by Gueimonde et al. [75]. The use of highly motile microorganisms as CE candidates is an important consideration because highly motile cells can access more nutrients; motility can contribute to dispersal and affect bacterial competitive activity [73].

Table 2. Methods for isolating CE microorganisms to control major foodborne pathogens since 2000.

Isolation Matrix	Isolation or Screening Methods	Comments	Reference
Biofilm samples collected from floor drains at food processing plants	Spot-on-lawn: Samples were plated onto nutrient agar, followed by spot-on-lawn inoculation using double-layer assay.	Bacterial isolates were identified as lactic acid bacteria.	[23]
Dry sausages processing facility	Agar well diffusion and overlay agar assay: The bacterial culture or cell-free culture supernatant was inoculated into agar well.	The production of bacteriocins only on agar plated in overlay assays, not in cell-free culture supernatant.	[76]
Fresh peeled baby carrots	Spot-on-lawn and growth on paper disk.	*Pseudomonas fluorescens* 2–79 or *Bacillus* YD1 at 5 to 6 log CFU/g as used in this study can provide 3.8–4.0 log reduction in foodborne pathogens.	[77]
Raw milk sample and feces sample	Spot-on-lawn using double-layer assay.	Lactic acid bacteria isolated from raw milk had a low antagonistic activity against *E. coli*. A total of 25 CE strains were isolated from feces samples.	[67,78]

Table 2. *Cont.*

Isolation Matrix	Isolation or Screening Methods	Comments	Reference
Fern plant	Patch plate method: Bacterial isolates were patched inoculated onto plates.	Endophytic bacteria [1] can produce antibiotic substances that could control *L. monocytogenes*, *B. cereus*, *S. aureus*, *E. coli*, and *S.* Typhimurium.	[67,78,79]
Soil samples	Agar cylinder diffusion assay: Agar cylinder was cut and removed from the agar plates inoculated with diluted soil sample after 2 days of growth.	The purified isolates of actinomycetes belonged to *Streptomyces* spp, but some inhibition was not clearly observed due to the cell morphology.	[80]
Dairy products	Involved enrichment step: Samples were enriched first in MRS broth, then spread plated onto MRS agar, followed by confirmation using spot-on-lawn method.	The enrichment step can promote the isolation of *Lactobacillus* from dairy products.	[81]
Kefir and kefir grains	Triple-agar-layer.	The second layer of agar supplemented with Natamycin can prevent the fungal growth.	[82]
Dairy and poultry compost	Double- and triple-agar-layers.	Double-agar-layer method used for initial screening and triple-agar-layer used for hard-to-culture bacteria.	[71]

[1] Endophytic bacteria: *Bacillus* sp. *cryopeg*, *Paenibacillus*, *Staphylococcus warneri*, and *Bacillus psychrodurans*.

4. Application of CE Strategies to Biologically Control Plant- or Foodborne Pathogens in the Agricultural Field

CE microorganisms as biological control agents can be applied to suppress plant-/soilborne pathogens [83]. In fact, plant disease caused by plant pathogens is a major contributor to crop yield loss (ca. USD 60 billion worldwide) [84], suggesting an economic benefit of using biological control to defeat plant disease. Clearly, there are growing interests and opportunities in using microbial biological control agents against plant diseases.

Plant pathogens can induce plant diseases, such as damping-off and loss of crop yield by *Rhizoctonia solani* [85,86], vascular wilts by *Fusarium oxysporum* [87,88], and fire blight disease in pear by *Erwinia amylovora* [89]. Beneficial microorganisms, such as *Bacillus subtilis* or *Bacillus* spp., *Lactobacillus plantarum*, *Pseudomonas* spp., *Pantoea agglomerans*, *Rahnella aquatilis*, *Trichoderma asperellum*, or other yeasts, have been used as biocontrol agents against various plant pathogens [90–92]. Some of them became commercially available for treating plant diseases caused by soil-borne pathogens [93,94]. It should be noted that biological control agents should be introduced in accordance with pathogen development, such as in the early stages, in order to achieve a stable beneficial microbial community prior to pathogen invasion [95].

In addition to plant pathogens, research on CE has traditionally focused on controlling the colonization of *Salmonella* in the gastrointestinal tract of chickens. When CE cultures are used in animal feed, they can promote a healthy host immune system. These kinds of microorganisms can work as probiotics for farm animals [96]. Promising results have been reported for LAB culture in the control of *E. coli*, *Yersinia pseudotuberculosis*, and *S. enterica* in chickens, cattle, and pigs [97,98]. The most common microbial genera used as probiotics are *Enterococcus*, *Bifidobacterium*, nonpathogenic *E. coli*, *Lactobacillus*, and *Saccharomyces* [25]. Probiotics have replaced antimicrobials in animal feed and benefited the host gut. CE cultures in animal feed compete with pathogens and boost host animal vitamin and antioxidant production [99].

The published literature reviews have focused primarily on using CE as probiotics for farm animals, but the potential use of CE cultures in the food industry in recent years has not been reviewed in detail. There is a need to identify competitive exclusion strategies used to control major foodborne pathogens from the farm to food processing plants. By searching the literature for the application of biological control strategies on controlling foodborne

pathogens in the food-related system from 2000 to 2023, we found that there was a strong research trend in isolating bacteria (i.e., lactic acid bacteria) that have antagonistic activity against pathogenic bacteria in the food system (Figure 1). The capability for bacteriocin production has been the major selection criteria for CE strains in reducing pathogen by CE bacteria, including *Salmonella*, in the poultry industry (Figure 1). From 2015 to 2020, the research interest on studying antimicrobial activities combined with biological control with essential oil increased. However, the use of the CE approach to control foodborne pathogens has not been well summarized.

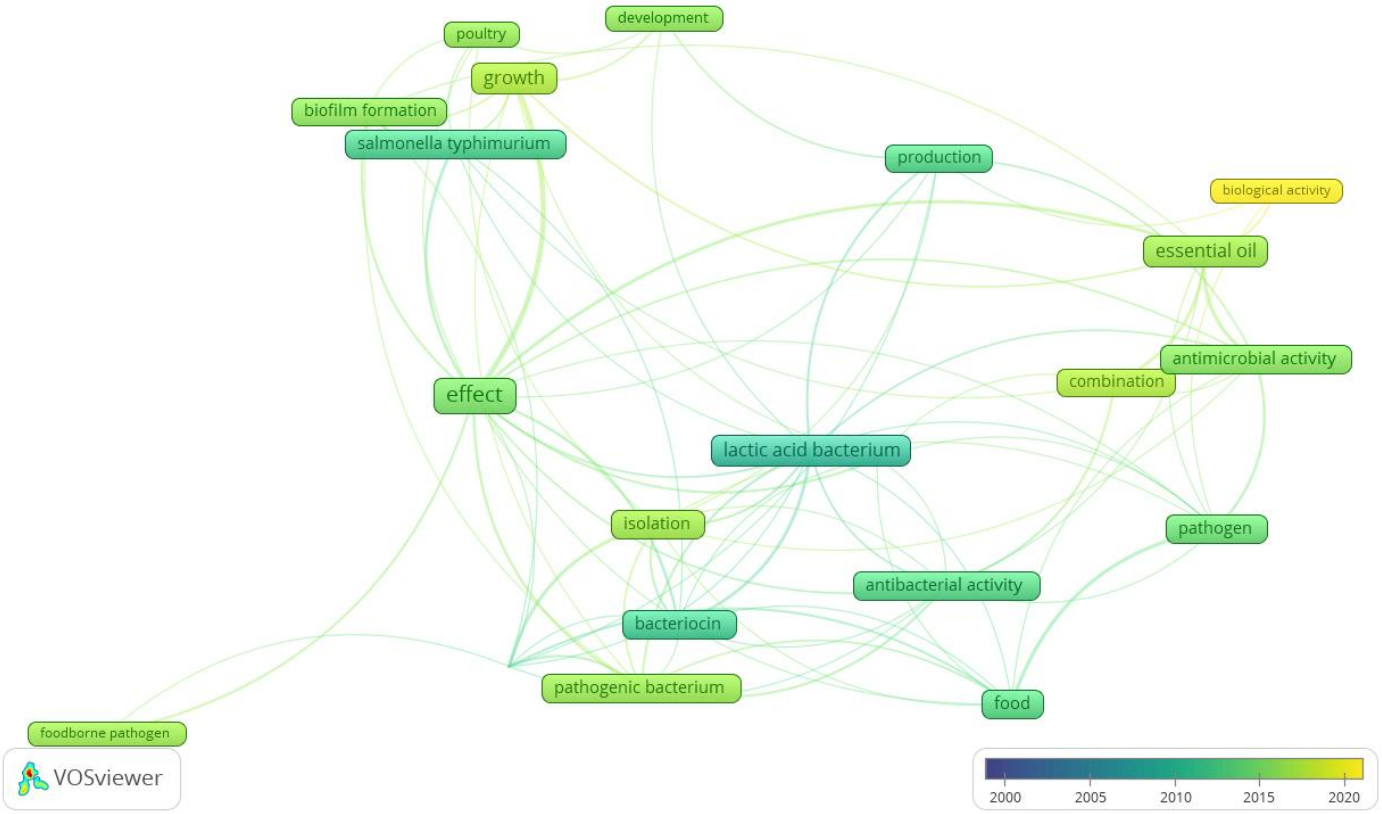

Figure 1. Literature search network overview on biological control of foodborne pathogens in food system from 2000 to 2023. Figure was created using VOSviewer Version 1.6.19.

In controlling foodborne pathogens, CE cultures such as lactic acid bacteria, *Enterococcus*, *Pseudomonas*, *Paenibacillus*, *Streptomyces*, *Bacillus*, and some commercially produced bacterial cultures have been widely used (Table 3). Targeted pathogens include *L. monocytogenes*, Shiga-toxin-producing *E. coli* (STEC), *Salmonella*, *B. cereus*, and *S. aureus*. Defined or undefined CE cultures at concentrations ranging from 3 to 9 log CFU/g or mL have been used to reduce pathogen populations and prevent cross-contamination in a variety of study matrices, including co-culture, biofilm, fresh produce, packaged food, dairy products, and food processing facilities. Various testing procedures for antagonistic activities have been employed. The inhibition effects of CE on foodborne pathogens, as evaluated by pathogen reductions (no reduction to >7 log reduction) or inhibition zones (2 mm to 3 cm). differed among studies (Table 3). In general, pathogen reduction increased with increasing CE concentration due to the production of more antimicrobial compounds or the effect of population competition [77,100].

CE strains can prevent foodborne pathogens in many settings. CE cultures directly decompose pathogenic biofilms, inhibiting *L. monocytogenes*, *Salmonella*, *S. aureus*, and *Hafnia alvei* by 2–6 logs [23,68,76]. The biofilm produced by CE strains can act as a barrier against pathogen contamination. The populations of *E. coli* O157:H7, *S. aureus*, *L. monocytogenes*, and *Salmonella* were reduced after inoculation on a stainless-steel coupon-containing biofilm constructed by CE (i.e., *Paenibacillus polymyxa*, *Streptomyces spororaveus* strain Gaeunsan-18, *Bacillus safensis* strain Chamnamu-sup 5-25, *Pseudomonas azotoformans* strain Lettuce-9, *Pseudomonas extremorientalis* strain Lettuce-28, *Paenibacillus peoriae* strain Lettuce-7, and *Streptomyces cirratus* strain Geumsan-207) [101–105]. For example, biofilms formed by *Lactobacillus sakei* M129-1 and *Pediococcus pentosaceus* M132-2 inhibited > 6 log of pathogenic bacteria (*B. cereus*, *L. monocytogenes*, *Salmonella*, *S. aureus*, and *E. coli* O157:H7) artificially inoculated on stainless steel surfaces within 12–48 h in a dry environment [105]. When CE treatment was applied to fresh produce and packaged foods, the efficacy of CE treatment was impacted by the vegetable type and packaging materials. No noticeable antagonistic action against *E. coli* O157: H7 and *L. monocytogenes* induced by *Lactobacillus* was found in fresh-cut cabbages [106], but 1–2 logs of these two pathogens were found to be reduced on lettuce and spinach in a field study [107]. These observations were probably due to the catalase activity in the cut cabbages, which adversely affects the function of CE. In contrast, the use of *L. sakei* with the modified-atmosphere packaged sausage had a synergistic inhibitory effect on controlling the post-processing contamination in cooked meat produced by *L. monocytogenes* [108]. The findings from published studies have provided scientific evidence on the practical use of CE microorganisms to control foodborne pathogens in different environmental niches.

CE microorganisms isolated from compost can suppress pathogens. As a nutrient-rich ecosystem, the rhizosphere is known to contain highly competitive activities among microbiota. Studies also revealed that the application of organic compost as a fertilizer in soil can suppress soilborne pathogens by regulating microbial community in the rhizosphere [109]. Several beneficial microorganisms with antagonistic activities against soilborne pathogens were identified from compost [93,110,111]. For example, several bacterial strains isolated by Al-Ghafri et al. [92] from compost were screened for their inhibition ability against plant pathogens. As a result, the antagonistic activity of *Pseudomonas aeruginosa* ISO1 and ISO2 against *Pythium aphanidermatum* and *Fusarium solani* was confirmed by the observation of the pathogen's morphological change under an electron microscope. Beneficial microorganisms have been added to thermophilic composting stage to increase soilborne pathogen suppression in the compost [92,111]. Nonetheless, there are very limited studies documenting the isolation and use of CE as a biological control agent to eliminate human pathogens in animal wastes or other soil amendments. In a lab-scale study, Puri and Dudley et al. [112] investigated the survival of *E. coli* O157: H7 in compost slurry. Results from this study indicated that the presence of cycloheximide-sensitive eukaryotic species can limit the growth of *E. coli* O157: H7 by ca. 4 log in the compost. In another study performed by Wang and Jiang [71], 17 CE strains that can inhibit more than 10 fresh-produce outbreak strains of *L. monocytogenes* were isolated from compost. *L. monocytogenes* was reduced up to 2.2 logs when co-culturing with CE strains. In compost samples, the addition of CE strains reduced the *L. monocytogenes* population by ca. 1.3 log at 22 °C after 24–168 h of incubation compared to the no significant change in *L. monocytogenes* population in compost samples without CE strains. These CE strains include *Bacillus* spp., *Kocuria* spp., *Paenibacillus* spp., *Brevibacillus* spp., and *Planococcus* spp. Many studies have concluded that microbial diversity is a key barrier against pathogen contamination in various matrixes, such as the rhizosphere, mice gut, and soil [112–116]. It is important to expand the knowledge of the microbial community to animal wastes or animal-wastes-based compost, which can aid the isolation of CE cultures.

Table 3. Summary of application of CE strategies to control major foodborne pathogens since 2000 as indicated by major CE species, inoculation used, target pathogens, and study matrix.

CE Species	CE Level	Pathogens/Level	Study Matrix/Test Methods	Reference
Bacillus	Cell-free supernatants	*B. cereus*, *E. coli* O157: H7, *L. monocytogenes*, *Salmonella*, *S. aureus*, *P. aeruginosa*	Disc diffusion assay	[117]
Bacillus spp., *Kocuria* spp., *Paenibacillus* spp., *Brevibacillus* spp., and *Planococcus* spp.	7 log CFU/g for coculture	*L. monocytogenes*/1.1–1.3 log CFU/g	Solid composts	[72]
Lactobacillus rhamnosus GG (LGG) (Culturelle®)	9 log CFU/g for coculture	*Salmonella*, and *L. monocytogenes*/3–4 log CFU/g for co-culture	Spot-on-lawn and co-culture in cook–chill cream of potato soup	[118]
Commercially protective bacterial cultures [1]	9 log CFU/mL	*L. monocytogenes*, *Salmonella*, and STEC/7 log CFU/mL	Spot-on-lawn	[119]
Endophytic bacteria: *Bacillus* sp. *Cryopeg*, *Paenibacillus*, *Staphylococcus warneri*, and *Bacillus psychrodurans*	N.A.	*B. cereus*, *E. coli* O157: H7, *L. monocytogenes*, *Salmonella*, *S. aureus*	Spot-on-lawn	[79]
Enterococcus mundtii	6 log CFU/mL	*L. monocytogenes*	Soil model systems	[120]
Erwinia persicina	5–8 log CFU/mL	*Salmonella*/3 log CFU/mL	Spot-on-lawn and co-culture in alfalfa seed soak water	[101]
Lactic acid bacteria including *Lactobacillus* spp., *Enterococcus durans*	7 log CFU/g	*E. coli* O157: H7 and *L. monocytogenes*/5.5 log CFU/g	Cut cabbages	[107]
	5 log CFU/mL	*L. monocytogenes*/3 log CFU/mL	Co-culture in TSB-YE and biofilms formation on stainless steel coupons	[24]
	9 log CFU/mL	*L. monocytogenes*/3.6–7.5 log CFU/100 cm^2	Floor drains of a poultry processing plant	[121]
	7 log CFU/mL	*L. innocua*, *S. aureus* or *Hafnia alvei*/5 log CFU/mL	Biofilm growth model	[77]
	3–4 log CFU/g	*L. monocytogenes*/3–4 log CFU/g	Co-culture in sliced sausage with different packaging types	[109]
	N.A.	*L. monocytogenes* and *E. coli*/8 log CFU/mL	Raw milk sample with spot-on-lawn	[80]
	8 log CFU/mL	*Salmonella*/8 log CFU/mL	Co-culture in mixed culture	[122]
	5 log CFU/mL	*L. monocytogenes*/5.5 log CFU/mL	Cheese and biofilm	[123]
	6 log CFU/mL	*L. monocytogenes*/3 log CFU/g	Co-culture in cheese	[124]
	Biofilm formed by CE with 9.46 and 9.66 log CFU/mL CE load	*L. monocytogenes*/8.01 log CFU/mL biofilm	Biofilm formed by CE	[125]
	N.A.	*S. aureus*, *B. subtilis*, and *P. aeruginosa*/overnight culture	Spot-on-lawn	[82]
	9 log CFU/mL	*L. monocytogenes*/at 4 °C: 7.1–7.7 log CFU/cm^2 at 8 °C: 7.5–8.3 log CFU/cm^2	Biofilms on coupons composed of different materials (stainless steel, plastic, rubber, glass, and silicone)	[69]
	2% LAB culture	*L. monocytogenes*/4–6 log CFU/mL	Co-culture in cheese	[126]
	8 log CFU/mL	*L. monocytogenes*/4–5 log CFU/mL	Biofilm on stainless steel	[127]

Table 3. *Cont.*

CE Species	CE Level	Pathogens/Level	Study Matrix/Test Methods	Reference
	7 log CFU/mL	*E. coli* O157: H7, *B. cereus*, and *S. aureus*/6 log CFU/mL	Agar well diffusion	[128]
	7 log CFU/mL	*Salmonella*/7 log CFU/mL	Co-culture in mixed culture	[129]
	Biofilm formed by CE with and 8 log CFU/mL CE load	*B. cereus*, *E. coli O157:H7*, *L. monocytogenes*, *S. aureus*, *and Salmonella enterica*/8 log CFU/4 cm^2	Biofilm formed by CE	[106]
	8 log CFU/mL	*L. monocytogenes*, *L. innocua* and *E. coli* O157:H7/1–2 log CFU	Lettuce and spinach plots	[108]
	Biofilm formed by CE with and 10 log CFU CE load	*E. coli*, *S. aureus*, and *L. monocytogenes*/2, 4, and 1 log CFU/mL, respectively	Biofilm formed by CE	[105]
Leuconostoc	5–9 log CFU/g	*L. monocytogenes*/3–4 log CFU/g	Co-culture on wounds of fruit and vegetable	[130]
Paenibacillus polymyxa	6 log CFU/mL	*E. coli* O157: H7/2, 3, 4, or 5 log CFU/mL	Biofilm formed by CE	[102]
Pediococcus pentosaceus	Biofilm formed by CE with and log CFU/mL CE load	*B. cereus*, *E. coli O157:H7*, *L. monocytogenes*, *S. aureus*, *and Salmonella enterica*/8 log CFU/4 cm^2	Biofilm formed by CE	[106]
Phyllosphere-associated lactic acid bacteria	4 log CFU/5 cm^2	*Salmonella*/3 log CFU/5 cm^2	Co-culture on the surfaces of cantaloupes	[131]
Pseudomonas extremorientalis, *Paenibacillus peoriae*, and *Streptomyces cirratus*	8.6, 8.8, and 6.4 log CFU/coupon	*Salmonella*/4.1 log CFU/coupon	Biofilm formation on stainless steel surface	[104]
Pseudomonas spp.	5 log CFU/mL	*Salmonella*/3 log CFU/mL	Co-culture in TSB and alfalfa seed soak water	[132]
	Ca. 7 log CFU/mL	*L. monocytogenes* and *Salmonella*/5 log CFU/mL	Fresh-cut pear	[133]
	7 log CFU/mL	*L. monocytogenes*/5 log CFU/mL	Spot-on-lawn, and co-culture in melon plugs, and melon juice	[134]
Pseudomonas fluorescens AG3A (Pf AG3A) and Pf 2-79, and *Bacillus* YD1	5–8 log CFU/mL	*E. coli* O157: H7, *L. monocytogenes*, *Salmonella*, and *Yersinia enterocolitica*/5 log CFU/mL	Co-culture in TSB	[78]
Streptomyces spororaveus, *Bacillus safensis*, *and Pseudomonas azotoformans*	Biofilm formed by CE with 7.9–8.5 log CFU/coupon CE load	*S. aureus*/4.2 log CFU/coupon	Biofilm formed by CE on stainless steel	[103]
Streptomyces	2-day old culture	*L. monocytogenes*/24 h–culture	Agar cylinder diffusion assay	[81]

[1] Commercially produced protective bacterial cultures used were *Lactococcus lactis* subsp. *lactis* BS-10 (LLN), *Pediococcus acidilactici* B-LC-20 (PA), *Lactobacillus curvatus* B-LC-48 (LC) (Chr. Hansen Inc., Milwaukee, WI), *Lactobacillus plantarum* (LPP) Holdbac Listeria (DuPont Danisco USA Inc., New Century, KS, USA), *Lactobacillus rhamnosus* Lyofast LRB (LR), *Lactobacillus plantarum* Lyofast LPAL (LP), *Carnobacterium* spp. Lyofast CNBAL (CS) (Sacco Srl, Amerilac, Miami, FL), LALCULT Protect *Hafnia alvei* B16 (HA), LALCULT Protect *Staphylococcus xylosus* XF01 (SX) (Lallemand Specialty Cultures, Blagnac, France), and *Enterococcus faecium* SF68 (EF) (NCIMB 10415, Cerbios-Pharma SA, Barbengo, Switzerland).

5. Using NGS Approach to Understand Microbial Interactions in BSAAO

BSAAO is abundant in numbers and varieties of microorganisms, particularly those beneficial microorganisms that may suppress foodborne pathogens in the finished compost. Microbial communities in animal waste or compost ecosystems play important roles, including carrying out nutrient degradation, composting processes, providing fertility to crops, and serving as a source of those beneficial bacteria. Like in the most environments, such as soil or animal waste, more than 90% of microorganisms cannot be cultured [135]. The emphasis needs to be shifted from the traditional culturing method to culture-independent techniques [136].

A number of techniques have been involved in studying the microbiota, which can be divided into the following groups: (1) community-level physiological profiling or metabolic potential analysis (e.g., Ecoplates, MicroPlates from Biolog) [137,138] and (2) DNA-based fingerprinting methods including cloning and sequencing, restriction fragment length polymorphism, and automated ribosomal intergenic spacer analysis, terminal restriction fragment length polymorphism, denaturing/temperature gradient gel electrophoresis, and so on [139–142]. Among them, polymerase chain reaction denaturing gradient gel electrophoresis (PCR-DGGE) fingerprinting was widely used to analyze the microbial community in compost. However, the potential bias includes PCR product purification and the final resolution of the gel image. In recent decades, in-depth screening of the microbial community in environmental samples has been possible achieved via next-generation sequencing (NGS).

As alluded to above, the involvement of technologies such as high-throughput sequencing allows us to understand microbial interactions at the community level in greater depth. In food processing facilities, the microbiome of *Listeria*-colonized and *Listeria*-free drains and apple washing conveyor belts was characterized as different, indicating that the occurrence of *Listeria* was closely associated with the background microbiota in these built environments [143,144]. In the animal intestinal ecosystem, host-pathogen interactions have been extensively reported [135,145]. There are few published studies focused on how the indigenous microflora respond to the invasive pathogenic bacteria in soil or BSAAO [103,116,117]. By building up the constructed microcosms using serially diluted soil samples (10^8–10^2 CFU/mL), Vivant et al. [115] found that there was a negative correlation between the level of diversity and the survival rate of spiked *L. monocytogenes*. Similarly, Schierstaedt et al. [146] demonstrated that the abundance of inoculated *Salmonella* decreased in soil with higher diverse indigenous microbial communities. In different compost samples, *Bacillus*, *Geobacillus*, *Lentibacillus*, and *Brevibacterium* can be the biomarkers that classify the compost samples into *Listeria*-inoculated and uninoculated samples [147]. Based on the metatranscriptomic sequencing result, the negative regulator of genetic competence was associated with *Geobacillus* spp., which suggests a potential competitive activity from *Geobacillus* spp. against *L. monocytogenes* [147].

NGS provided the approach on sequencing DNA or RNA from a mixed microbial environment, such as in BSAAO, and it can generate massive amounts of data for downstream analysis to identify the microorganisms present in the complex environment. In the context of discovering CE strains, NGS can be used to identify the microorganisms that are capable of outcompeting or inhibiting the growth of pathogenic bacteria and provide an in-depth explanation of the microbial interactions between invading pathogens and the indigenous microbiota.

Limitations and Challenges of using CE strains: There are challenges regarding the utilization of CE strains for controlling *L. monocytogenes* in food industry or BSAAO. Such obstacles include the difference in detection limits between traditional culture methods and NGS approaches, the recovery efficacy of hard-to-culture or VBNC strains, and the limitations of using CE strains for specific environmental conditions. In addition, in most studies on CE isolation, special conditions or experiment set-up, including anaerobic or facultative anaerobic conditions, were not used. Therefore, further development in these research areas is being pursued.

Importantly, the safety assessment of CE as a biological control agent needs to be performed and regulated in a valid manner. The CE strains must be devoid of risk factors such as antimicrobial resistance spread and virulence. For example, the Scientific Panel on Additives and Products or Substances Used in Animal Feed suggested using strains with intrinsic resistance or carrying acquired antimicrobial resistance genes (ARG) due to chromosomal mutation as feed additives in order to avoid the ARG exchange among bacteria via horizontal dissemination [148]. In consideration of the safety of using CE strains for pathogen control in the food industry or preharvest environment, additional research using WGS to fully characterize the CE strains for virulence and antibiotic resistance genes is needed prior to their real-world applications.

6. Conclusions

L. monocytogenes has been identified as one of the leading human pathogens causing foodborne illness, and fresh produce is highly susceptible to contamination even before harvest via raw animal manures or inadequately treated BSAAO. The types and physical–chemical characteristics of animal wastes, their storage conditions, and the background microbial community can all affect *L. monocytogenes*'s fate in BSAAO. As biological control agents, CE strategies have been widely utilized in agriculture to control plant- or foodborne pathogens. Due to its diverse microbial community, BSAAO is a potential source for isolating CE strains for pathogen control. High species diversity in animal wastes or animal-wastes-based compost can be an effective biological barrier that eliminates the invading pathogens, and the interactions between *L. monocytogenes* and compost microflora may result from the competition for limited nutrients and the presence of antimicrobials released from compost microbiota. NGS can be a valuable tool for identifying and characterizing CE strains in complex microbial communities by providing a comprehensive picture of the microbial interactions present in a given environment. Given that CE is a biological control strategy developed to reduce the impact of pathogens, it is worthwhile to attempt the isolation of effective CE strains from various sources. Future research is needed to optimize the use of CE isolates in different settings and fully understand their mechanisms of action. Additionally, utilizing NGS is desired to complement the culturing methods in CE identification and elucidate the genetic mechanisms underlying the function of CE strains against pathogens.

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